AUSTRALIA

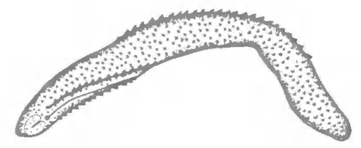
MOLLUSCA

The Southern Synthesis

Fauna of Australia

PHYLUM MOLLUSCA IN AUSTRALIA

The major molluscan groups recorded from the Australian region. Families not recorded from Australia are indicated with an asterisk (*). Families represented partially or entirely in Australia by introduced species are marked with an (I).



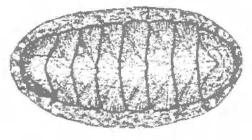
CLASS APLACOPHORA

Subclass CHAETODERMOMORPHA

- Family Chaetodermatidae
- Family Prochaetodermatidae

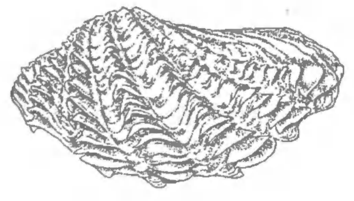
Subclass NEOMENIOMORPHA

- Family Dondersiidae
- Family Lepidomeniidae
- Family Neomeniidae
- Family Phyllomeniidae
- Family Pruvotinidae
- Family Proneomeniidae
- Family Epimeniidae



CLASS POLYPLACOPHORA

- Order NEOLORICATA
  - Suborder LEPIDOPLEURINA
    - Family Lepidopleuridae
    - Family Hanleyidae
    - Family Xylochitonidae*
    - Family Abyssochitonidae*
  - Suborder CHORIPLACINA
    - Family Choriplacidae
  - Suborder ISCHNOCHITONINA
    - Family Ischnochitonidae
    - Family Schizochitonidae
    - Family Mopaliidae
    - Family Chitonidae
  - Suborder ACANTHOCHITONINA
    - Family Acanthochitonidae
    - Family Cryptoplacidae



CLASS BIVALVIA

Subclass PROTOBRANCHIA

- Order NUCULOIDA
  - Superfamily NUCULOIDEA
    - Family Nuculidae
    - Family Pristiglomidae*
  - Superfamily NUCULANOIDEA
    - Family Malletiidae*
    - Family Neilonellidae
    - Family Nuculanidae
    - Family Sareptidae
    - Family Siliculidae*
    - Family Lametilidae*
- Order SOLEMYOIDA
    - Family Solemyidae
    - Family Nucinellidae

Subclass PTERIOMORPHIA

- Order MYTILOIDA
    - Family Mytilidae (I)
- Order ARCOIDA
  - Superfamily ARCOIDEA
    - Family Arcidae
    - Family Cucullaeidae
    - Family Noetiidae
  - Superfamily LIMOPSOIDEA
    - Family Limopsidae
    - Family Glycymerididae
    - Family Philobryidae
- Order PTERIOIDA
  - Superfamily PTERIOIDEA
    - Family Pteriidae
    - Family Malleidae
    - Family Isognomonidae
    - Family Pulvinitidae
  - Superfamily PINNOIDEA
    - Family Pinnidae
- Order LIMOIDA
  - Superfamily LIMOIDEA
    - Family Limidae
- Order OSTREOIDA
- Suborder OSTREINA
  - Superfamily OSTREOIDEA
    - Family Gryphaeidae
    - Family Ostreidae (I)
  - Superfamily PLICATULOIDEA
    - Family Plicatulidae
  - Superfamily DIMYOIDEA
    - Family Dimyidae
- Suborder PECTININA
  - Superfamily PECTINOIDEA
    - Family Pectinidae
    - Family Propeamussiidae
    - Family Spondylidae
    - Family Entoliidae*
  - Superfamily ANOMIOIDEA
    - Family Anomiidae
    - Family Placunidae

Subclass PALAEOHETERODONTA

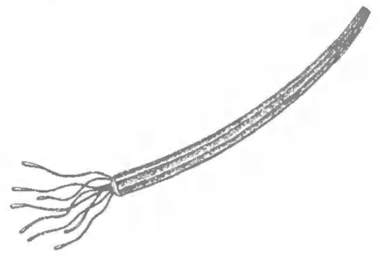
- Order TRIGONIOIDA
  - Superfamily TRIGONIOIDEA
    - Family Trigoniidae
- Order UNIONOIDA
  - Superfamily UNIONOIDEA
    - Family Margaritiferidae*
    - Family Unionidae*
    - Family Hyriidae
  - Superfamily MUTELOIDEA
    - Family Mutelidae*
    - Family Mycetopodidae*
    - Family Etheridae*

Subclass HETERODONTA

- Order VENEROIDA
  - Superfamily CHAMOIDEA
    - Family Chamidae
  - Superfamily LUCINOIDEA
    - Family Lucinidae
    - Family Fimbriidae
    - Family Thyasiridae
    - Family Ungulinidae
    - Family Mactromyidae
  - Superfamily GALEOMMATOIDEA
    - Family Galeommatidae
  - Superfamily CYAMIOIDEA
    - Family Cyamiidae
    - Family Neoleptonidae
    - Family Sportellidae
  - Superfamily CARDITOIDEA
    - Family Carditidae
    - Family Condylocardiidae
  - Superfamily CRASSATELLOIDEA
    - Family Crassatellidae
    - Family Astartidae*
  - Superfamily CARDIOIDEA
    - Family Cardiidae
    - Family Hemidonacidae
  - Superfamily TRIDACNOIDEA
    - Family Tridacnidae
  - Superfamily MACTROIDEA
    - Family Mactridae
    - Family Mesodesmatidae
    - Family Cardiliidae
  - Superfamily SOLENOIDEA
    - Family Solenidae
    - Family Pharidae
  - Superfamily TELLINOIDEA
    - Family Tellinidae
    - Family Semelidae
    - Family Psammobiidae
    - Family Solecurtidae
    - Family Donacidae
  - Superfamily ARCTICOIDEA
    - Family Trapeziidae
    - Family Kelliellidae
    - Family Vesicomyidae*
  - Superfamily GLOSSOIDEA
    - Family Glossidae
  - Superfamily CORBICULOIDEA
    - Family Corbiculidae
    - Family Sphaeriidae
  - Superfamily VENEROIDEA
    - Family Veneridae
    - Family Petricolidae
    - Family Glauconomidae
- Order MYOIDA
  - Superfamily MYOIDEA
    - Family Myidae
    - Family Corbulidae
  - Superfamily GASTROCHAENOIDEA
    - Family Gastrochaenidae
  - Superfamily HIATELLOIDEA
    - Family Hiatellidae
  - Superfamily PHOLADOIDEA
    - Family Pholadidae
    - Family Teredinidae

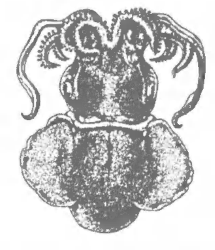
Subclass ANOMALODESMATA

- Order PHOLADOMYOIDA
  - Superfamily PHOLADOMYOIDEA
    - Family Pholadomyidae*
    - Family Parilimyidae
  - Superfamily THRACIOIDEA
    - Family Thraciidae
    - Family Periplomatidae
    - Family Laternulidae
  - Superfamily CLAVAGELLOIDEA
    - Family Clavagellidae
  - Superfamily PANDOROIDEA
    - Family Lyonsiidae*
    - Family Pandoridae
    - Family Myochamidae
    - Family Cleidothaeridae
  - Superfamily VERTICORDIOIDEA
    - Family Verticordiidae
  - Superfamily POROMYOIDEA
    - Family Poromyidae
  - Superfamily CUSPIDARIOIDEA
    - Family Cuspidariidae



CLASS SCAPHOPODA

- Order DENTALIIDA
    - Family Dentaliidae
    - Family Fustiariidae
    - Family Rhabdidae*
    - Family Laevidentaliidae
    - Family Gadilinidae
    - Family Omniglyptidae
- Order GADILIDA
  - Suborder ENTALIMORPHA
    - Family Entalinidae
  - Suborder GADILIMORPHA
    - Family Pulsellidae
    - Family Wemersoniellidae*
    - Family Gadilidae



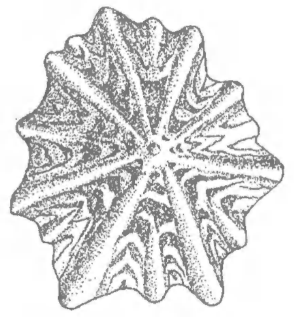
CLASS CEPHALOPODA

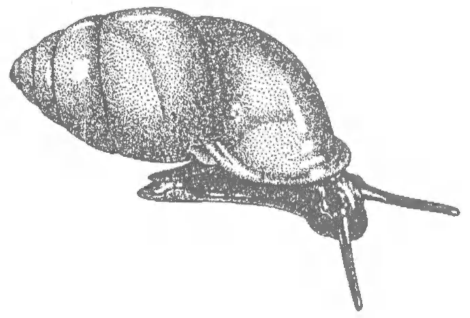
Subclass NAUTILOIDEA

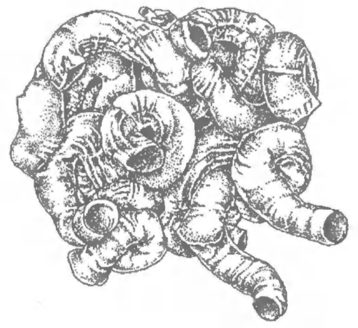
- Superfamily Nautiloidea
  - Family Nautilidae

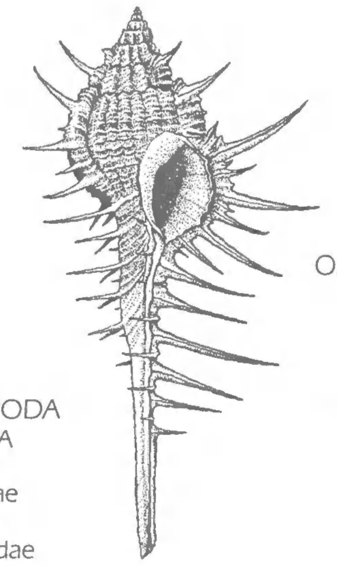
Subclass COLEOIDEA

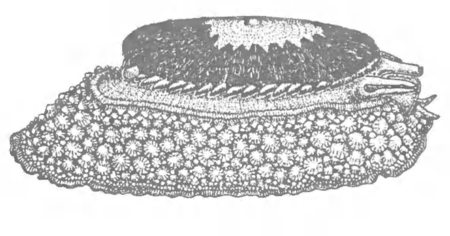
- Order SEPIOIDEA
    - Family Spirulidae
    - Family Sepiidae
    - Family Sepiadariidae
    - Family Sepiolidae
    - Family Idiosepiidae
- Order TEUTHOIDEA
  - Suborder MYOPSIDA
    - Family Pickfordiateuthidae*
    - Family Loliginidae
  - Suborder OEGOPSIDA
    - Family Lycoteuthidae
    - Family Enoploteuthidae
    - Family Octopoteuthidae
    - Family Onychoteuthidae
    - Family Walvisteuthidae*
    - Family Cycloteuthidae
    - Family Gonatidae*
    - Family Psychroteuthidae*
    - Family Lepidoteuthidae
    - Family Architeuthidae
    - Family Histioteuthidae
    - Family Neoteuthidae*
    - Family Bathyteuthidae
    - Family Ctenopterygidae
    - Family Brachioteuthidae
    - Family Batoteuthidae*
    - Family Ommastrephidae
    - Family Thysanoteuthidae
    - Family Chiroteuthidae
    - Family Mastigoteuthidae
    - Family Promachoteuthidae*
    - Family Grimalditeuthidae
    - Family Joubiniteuthidae
    - Family Cranchiidae
- Order VAMPYROMORPHA
    - Family Vampyroteuthidae
- Order OCTOPODA
  - Suborder CIRRATA
    - Family Cirroteuthidae*
    - Family Stauroteuthidae*
    - Family Opisthoteuthidae
  - Suborder INCIRRATA
    - Family Bolitaenidae
    - Family Amphitretidae
    - Family Idioctopodidae*
    - Family Vitreledonellidae
    - Family Octopodidae
    - Family Tremoctopodidae
    - Family Ocythoidae
    - Family Argonautidae
    - Family Alloposidae*

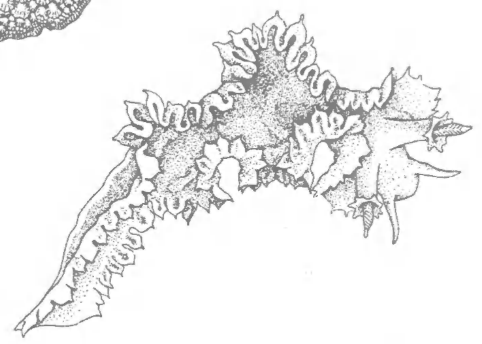


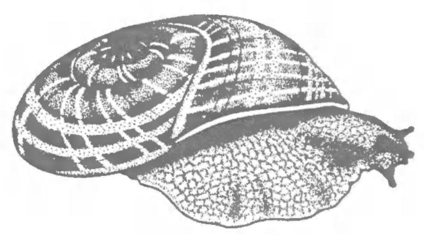












CLASS GASTROPODA

Subclass EOGASTROPODA

- Order PATELLOGASTROPODA
- Suborder PATELLINA
  - Superfamily PATELLOIDEA
    - Family Patellidae
- Suborder NACELLINA
  - Superfamily NACELLOIDEA
    - Family Nacellidae
  - Superfamily ACMAEOIDEA
    - Family Acmaeidae
    - Family Lepetidae
    - Family Lottiidae

Subclass ORTHOGASTROPODA

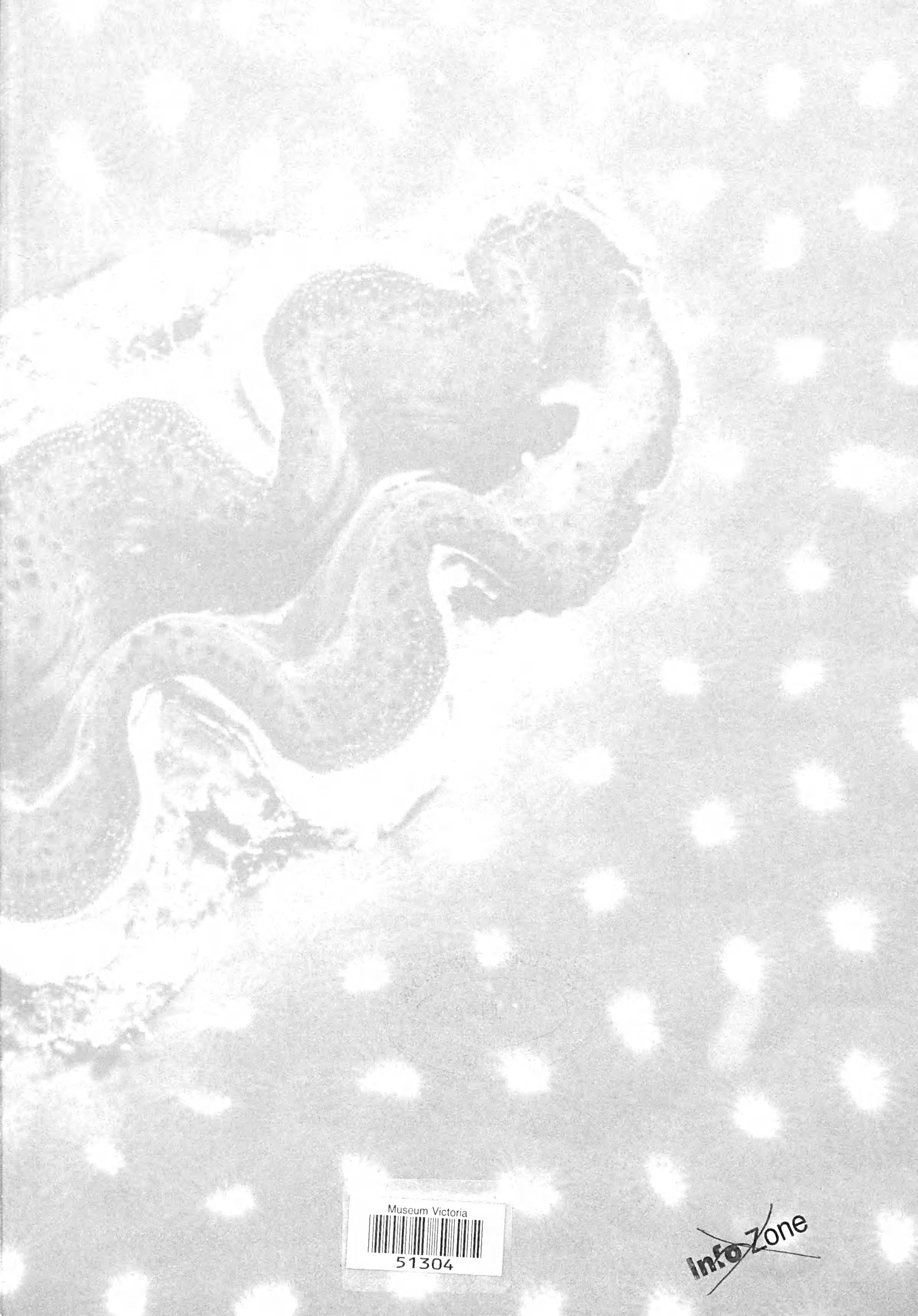
- Superorder COCCULINIFORMIA
  - Superfamily COCCULINOIDEA
    - Family Cocculinidae
    - Family Bathysciadiidae
  - Superfamily LEPETELLOIDEA
    - Family Lepetellidae*
    - Family Pseudococculinidae
    - Family Osteopeltidae*
    - Family Cocculinellidae
    - Family Choristellidae
- Superorder VETIGASTROPODA
  - Superfamily PLEUROTOMARIOIDEA
    - Family Pleurotomariidae
    - Family Scissurellidae
    - Family Haliotidae
  - Superfamily FISSURELLOIDEA
    - Family Fissurellidae
  - Superfamily TROCHOIDEA
    - Family Turbinidae
    - Family Trochidae
    - Family Skeneidae
    - Family Pendromidae
  - Superfamily SEGUENZIOIDEA
    - Family Seguenziidae
- Superorder NERITOPSINA
  - Superfamily NERITOIDEA
    - Family Neritopsidae
    - Family Neritidae
    - Family Phenacolepadidae
    - Family Titiscaniidae
    - Family Hydrocenidae
    - Family Helicinidae
- Superorder CAENOGASTROPODA
- Order ARCHITAENIOGLOSSA
  - Superfamily CYCLOPHOROIDEA
    - Family Cyclophoridae
    - Family Pupinidae
    - Family Diplommatinidae
  - Superfamily AMPULLARIOIDEA
    - Family Viviparidae
    - Family Ampullariidae (I)
- Order SORBEOCONCHA
  - Superfamily CERITHIOIDEA
    - Family Cerithiidae
    - Family Dialidae
    - Family Litiopidae
    - Family Turritellidae
    - Family Siliquariidae
    - Family Batillariidae
    - Family Planaxidae
    - Family Potamididae
    - Family Thiaridae
    - Family Diastomatidae
    - Family Modulidae
    - Family Scaliolidae
  - Superfamily CAMPANILOIDEA
    - Family Campanilidae
    - Family Plesiotrochidae
- Suborder HYPSOGASTROPODA
- Infraorder LITTORINIMORPHA
  - Superfamily LITTORINOIDEA
    - Family Littorinidae
    - Family Pickworthiidae
  - Superfamily CINGULOPSOIDEA
    - Family Cingulopsidae
    - Family Eatoniellidae
    - Family Rastodentidae
  - Superfamily RISSOOIDEA
    - Family Barleeidae
    - Family Anabathridae
    - Family Emblandidae
    - Family Rissoidae
    - Family Epigridae
    - Family Iravadiidae
    - Family Hydrobiidae
    - Family Pomatiopsidae
    - Family Assimineidae
    - Family Truncatellidae
    - Family Elachisinidae
    - Family Bithyniidae
    - Family Caecidae
    - Family Hydrococcidae
    - Family Vitrinellidae
    - Family Stenothyridae
  - Superfamily STROMBOIDEA
    - Family Strombidae
    - Family Struthiolariidae
  - Superfamily VANIKOROIDEA
    - Family Hipponicidae
    - Family Vanikoridae
    - Family Haloceratidae
  - Superfamily CALYPTRAEOIDEA
    - Family Calyptraeidae
  - Superfamily CAPULOIDEA
    - Family Capulidae
  - Superfamily XENOPHOROIDEA
    - Family Xenophoridae
  - Superfamily VERMETOIDEA
    - Family Vermetidae
  - Superfamily CYPRAEOIDEA
    - Family Cypraeidae
    - Family Ovulidae
  - Superfamily VELUTINOIDEA
    - Family Triviidae
    - Family Velutinidae
  - Superfamily NATICOIDEA
    - Family Naticidae
  - Superfamily TONNOIDEA
    - Family Bursidae
    - Family Cassidae
    - Family Ficidae
    - Family Laubierinidae
    - Family Personidae
    - Family Pisanianuridae
    - Family Ranellidae
    - Family Tonnidae
  - Superfamily CARINARIOIDEA
    - Family Atlantidae
    - Family Carinariidae
    - Family Pterotracheidae
- Infraorder PTENOGLOSSA
  - Superfamily TRIPHOROIDEA
    - Family Triphoridae
    - Family Cerithiopsidae
  - Superfamily JANTHINOIDEA
    - Family Janthinidae
    - Family Epitoniidae
    - Family Aclididae
  - Superfamily EULIMOIDEA
    - Family Eulimidae
- Infraorder NEOGASTROPODA
  - Superfamily MURICOIDEA
    - Family Muricidae
    - Family Turbinellidae
    - Family Buccinidae
    - Family Columbellidae
    - Family Nassariidae
    - Family Melongenidae
    - Family Fasciolariidae
    - Family Volutidae
    - Family Olividae
    - Family Harpidae
    - Family Marginellidae
    - Family Mitridae
    - Family Volutomitridae
    - Family Costellariidae
  - Superfamily CANCELLARIOIDEA
    - Family Cancellariidae
  - Superfamily CONOIDEA
    - Family Turridae
    - Family Terebridae
    - Family Conidae
- Superorder HETEROBRANCHIA
  - Superfamily VALVATOIDEA
    - Family Cornirostridae
    - Family Orbitestellidae
    - Family Xylodisculidae
  - Superfamily ARCHITECTONICOIDEA
    - Family Mathildidae
    - Family Architectonicidae
  - Superfamily RISSOELLOIDEA
    - Family Rissoellidae
  - Superfamily OMALOGYROIDEA
    - Family Omalogyridae
  - Superfamily PYRAMIDELLOIDEA
    - Family Pyramidellidae
    - Family Amathinidae
    - Family Cimidae
    - Family Donaldinidae
    - Family Ebalidae

OPISTHOBRANCHIA

- Order CEPHALASPIDEA
  - Superfamily ACTEONOIDEA
    - Family Acteonidae
    - Family Bullinidae
    - Family Hydatinidae
  - Superfamily RINGICULOIDEA
    - Family Ringiculidae
  - Superfamily CYLINDROBULLOIDEA
    - Family Cylindrobullidae*
  - Superfamily DIAPHANOIDEA
    - Family Diaphanidae
  - Superfamily PHILINOIDEA
    - Family Cylichnidae
    - Family Retusidae
    - Family Philinidae
    - Family Philinoglossidae*
    - Family Aglajidae
    - Family Gastropteridae
  - Superfamily HAMINOEOIDEA
    - Family Haminoeidae
    - Family Bullactidae*
    - Family Smaragdinellidae
    - Family Incertae sedis
  - Superfamily BULLOIDEA
    - Family Bullidae
  - Superfamily RUNCINOIDEA
    - Family Runcinidae
    - Family Ilbiidae
  - Superfamily INCERTAE SEDIS
    - Family Notodiaphanidae*
- Order ACOCHLIDEA
  - Superfamily ACOCHLIDIOIDEA
    - Family Acochlidiidae*
    - Family Hedylopsidae*
  - Superfamily MICROHEDYLOIDEA
    - Family Asperspinidae*
    - Family Microhedylidae
    - Family Ganatidae
- Order RHODOPEMORPHA
    - Family Rhodopidae
- Order SACOGLOSSA
  - Superfamily OXYNOOIDEA
    - Family Volvatellidae
    - Family Oxynoidae
    - Family Juliidae
  - Superfamily ELYSIOIDEA
    - Family Plakobranchidae
    - Family Elysiidae
    - Family Boselliidae*
    - Family Gascoignellidae*
    - Family Platyhedylidae*
  - Superfamily LIMAPONTIOIDEA
    - Family Caliphyllidae
    - Family Costasiellidae
    - Family Hermaeidae
    - Family Limapontiidae
- Order ANASPIDEA
  - Superfamily AKEROIDEA
    - Family Akeridae
  - Superfamily APLYSIOIDEA
    - Family Aplysiidae
- Order NOTASPIDEA
  - Superfamily TYLODINOIDEA
    - Family Tylodinidae
    - Family Umbraculidae
  - Superfamily PLEUROBRANCHOIDEA
    - Family Pleurobranchidae
- Order THECOSOMATA
    - Family Limacinidae
    - Family Cavoliniidae
    - Family Peraclididae
    - Family Cymbuliidae
    - Family Desmopteridae
- Order GYMNOSOMATA
- Suborder GYMNOSOMATA
    - Family Pneumodermatidae
    - Family Notobranchaeidae
    - Family Cliopsidae
    - Family Clionidae
- Suborder GYMNOPTERA
    - Family Hydromylidae
- Order NUDIBRANCHIA
- Suborder DORIDINA
  - Superfamily ANADORIDOIDEA
    - Family Corambidae
    - Family Goniodorididae
    - Family Onchidorididae
    - Family Polyceridae
    - Family Gymnodorididae
    - Family Aegiretidae
    - Family Vayssiereidae
  - Superfamily EUDORIDOIDEA
    - Family Hexabranchidae
    - Family Dorididae
    - Family Chromodorididae
    - Family Dendrodorididae
    - Family Phyllidiidae
- Suborder DENDRONOTINA
    - Family Tritoniidae
    - Family Bornellidae
    - Family Marianinidae
    - Family Hancockiidae
    - Family Dotidae
    - Family Scyllaeidae
    - Family Tethydidae
    - Family Phylliroidae
    - Family Lomanotidae
- Suborder ARMININA
    - Family Arminidae
    - Family Doridomorphidae
    - Family Charcotiidae
    - Family Madrellidae
    - Family Zephyrinidae
    - Family Pinufiidae
- Suborder AEOLIDINA
    - Family Flabellinidae
    - Family Eubranchidae
    - Family Aeolidiidae
    - Family Glaucidae
    - Family Embletoniidae
    - Family Tergipedidae
    - Family Fionidae

PULMONATA

- Order SYSTELLOMMATOPHORA
  - Superfamily OTINOIDEA
    - Family Smeagolidae
  - Superfamily ONCHIDIOIDEA
    - Family Onchidiidae
  - Superfamily RATHOUISIOIDEA
    - Family Rathouisiidae
    - Family Veronicellidae (I)
- Order BASOMMATOPHORA
  - Superfamily AMPHIBOLOIDEA
    - Family Amphibolidae
  - Superfamily SIPHONARIOIDEA
    - Family Siphonariidae
  - Superfamily LYMNAEOIDEA
    - Family Lymnaeidae (I)
    - Family Ancylidae
    - Family Planorbidae (I)
    - Family Physidae (I)
  - Superfamily GLACIDORBOIDEA
    - Family Glacidorbidae
- Order EUPULMONATA
- Suborder ACTOPHILA
  - Superfamily ELLOBIOIDEA
    - Family Ellobiidae
- Suborder TRIMUSCULIFORMES
  - Superfamily TRIMUSCULOIDEA
    - Family Trimusculidae
- Suborder STYLOMMATOPHORA
- Infraorder ORTHURETHRA
  - Superfamily ACHATINELLOIDEA
    - Family Achatinellidae
  - Superfamily CIONELLOIDEA
    - Family Cionellidae (I)
  - Superfamily PUPILLOIDEA
    - Family Pupillidae
    - Family Pleurodiscidae (I)
    - Family Valloniidae (I)
  - Superfamily PARTULOIDEA
    - Family Enidae
- Infraorder SIGMURETHRA
  - Superfamily ACHATINOIDEA
    - Family Ferrussaciidae (I)
    - Family Subulinidae
    - Family Megaspiridae
    - Family Achatinidae (I)
  - Superfamily STREPTAXOIDEA
    - Family Streptaxidae (I)
  - Superfamily RHYTIDOIDEA
    - Family Rhytididae
  - Superfamily ACAVOIDEA
    - Family Caryodidae
  - Superfamily BULIMULOIDEA
    - Family Bulimulidae
  - Superfamily ARIONOIDEA
    - Family Punctidae
    - Family Charopidae
    - Family Helicodiscidae
    - Family Arionidae (I)
  - Superfamily LIMACOIDEA
    - Family Limacidae (I)
    - Family Milacidae (I)
    - Family Zonitidae (I)
    - Family Trochomorphidae
    - Family Helicarionidae
    - Family Cystopeltidae
    - Family Testacellidae (I)
  - Superfamily SUCCINEOIDEA
    - Family Succineidae
    - Family Athoracophoridae
  - Superfamily POLYGYROIDEA
    - Family Corillidae
  - Superfamily CAMAENOIDEA
    - Family Camaenidae
  - Superfamily HELICOIDEA
    - Family Helicidae (I)
    - Family Bradybaenidae (I)



InfoZone

MOLLUSCA

The Southern Synthesis

Bronwyn M. Bancroft. **The Living Sea** circa 1992. *Gouache on archival paper* (25.5 x 35.8 cm)
Collection: Australian Biological Resources Study, Canberra

Back cover: Yangarriny Dalwangu (1932-) Northeast Arnhem Land, Northern Territory
Ancestors of the Yirritja moiety circa 1979. Ochres on *Eucalyptus bark* (155.0 x 56.0 cm)
Collection: Australian National Gallery, Canberra

Australian Biological Resources Study, Canberra

MOLLUSCA

The Southern Synthesis

Part A

Fauna of Australia Volume 5

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Department of the Environment

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AUSTRALIA

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Endpapers. Like a jewel in a star-studded sky, an embedded giant clam, *Tridacna crocea*, displays its mantle to the light, used by symbiotic algae to photosynthesise nutrients shared with their host. [L. Newman & A. Flowers]

Plate 1. The vivid colours of chromodoridid nudibranchs, such as *Chromodoris westraliensis*, may advertise the defensive glands, which exude a powerful deterrent to predators. [G. Bell/Ocean Wide Images]

Plate 2. Young cranchiid squids, *Teuthowenia pellucida*, are abundant in the upper 600 m of eastern Australian waters. As they mature, they descend gradually to depths exceeding 2400 m, where they spawn once before dying. [G. Bell/Ocean Wide Images]

Plate 3. The egg cowry, *Calpurnus verrucosus* (Ovulidae), lives, feeds and broods its young on a species of the fleshy soft coral *Lobophyllum*. [G. Bell/Ocean Wide Images]

Plate 4. The extensive array of cerata, or gills, of the nudibranch *Pteraeolidia ianthina* (Glaucidae) maximises the exposure to light of symbiotic dinoflagellates within these organs, to the mutual benefit of both organisms. [G. Bell/Ocean Wide Images]

Plate 5. Doughboy scallops, *Mimachlamys asperrima* (Pectinidae), gape while filtering suspended matter from water passing over their gills. Mantle tentacles exclude large particles and blue pallial eyes may warn of potential predators. [G. Bell/Ocean Wide Images]

Plate 6. Superb camouflage has evolved in many molluscs. This egg cowry, a species of *Prionovolva* (Ovulidae), closely matches the form and colour of its coral prey. [G. Bell/Ocean Wide Images]

Plates 7-37, background. The superabundant cardiid *Fragum erugatum*, the primary component of Shell Beach, Shark Bay, Western Australia. [M. Fagg]

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PREFACE

From many perspectives, the phylum Mollusca is one of the most significant components of biodiversity in the Australian region. With an estimated 19 000 species, molluscs rank among the largest and most diverse groups, and are important components of the ecological communities throughout the region, from desert outcrops, mound springs and montane rainforest to the depths of the ocean.

Among non-marine molluscs, camaenids, charopids and hydrobiids in particular have radiated enormously, and comprise the major portion of an estimated 2000 terrestrial and freshwater species. Endemism in non-marine species is extremely high (98.6% of 1040 described species), more so than any other well-known Australian groups (reptiles, 89%; vascular plants, 85%; mammals, 82%). The geographical ranges of many are also very small (about 20 km^2 or less) and are highly susceptible to the effects of human intervention, especially land clearance and deforestation. Australian non-marine molluscs rate strongly as the flagship group for the conservation of the region's invertebrates as a whole.

Molluscs have always been important economic resources for Australian communities, as evidenced by their dominance in middens across Australia. More recently, molluscs have assumed great economic significance in a number of spheres. Most prominent are the fisheries, in which abalone, scallops and cultured pearls contribute some A$400 million annually to the national economy. Several other groups are farmed; the successful mariculture of giant clams, using techniques pioneered in Australia, simultaneously provides a valuable export commodity, permits re-stocking of reefs, and reduces the impact of over-exploitation of wild populations. Less obvious economic issues are the annual costs of controlling livestock and human diseases transmitted via freshwater molluscs (A$200 million), and minimising the destruction of crops by introduced species of slugs and snails (A$50 million). Both aspects emphasise the necessity for adequate quarantine procedures. Some freshwater species have considerable potential as bioindicators of the health of Australian water bodies.

Australian malacology has grown enormously from William Dampier's simple descriptions of Australian molluscs in 1699, and the first significant scientific collections made during exploratory voyages, such as those of James Cook and Nicholas Baudin. Currently, research relevant to Australian Mollusca adds several hundred papers to the primary scientific literature each year, posing a daunting task for any non-specialist trying to stay informed on this group.

The primary role of the *Fauna of Australia* series is to provide authoritative syntheses of primary zoological literature on all taxa in the fauna, to the level of family, for the benefit of a broad, non-specialist clientele. The *Mollusca* is an excellent example of the success of this approach, comprising contributions from 70 authors, in which some 7700 papers in the primary literature are cited; 50% of these were published after 1980.

This volume comprises a series of overviews at one or more levels for the phylum and six classes, which serve to introduce treatments for the 423 molluscan families presently recognised in the region. At each level, available information on Morphology & Physiology, Natural History and Biogeography & Phylogeny is presented. The glossary in this volume has been limited to those terms generally necessitating reference to specialist literature. The numerous illustrations, almost all commissioned for this volume, are based on Australian material unless indicated otherwise.

This volume has benefitted enormously from the contributions of numerous individuals and organisations, to all of whom unreserved thanks are due. The most significant contributions are those of the authors – see overleaf – and the illustrators. Reviews of all text and technical advice were provided throughout production by W.F. Ponder, F.E. Wells and A.J. Underwood. Specialist reviews of chapters or sections were undertaken by R.C. Bullock, C. Carlson, D.J. Eernisse, K. Emberton, J.M. Healy, P.A. Hutchings, K. Jensen, K. Lamprell, T. Okutani, P.A. Maxwell, M.C. Miller, L. Newman, L.v. Salvini-Plawen, J. Stanisic, R.C. Willan and B.R. Wilson. Editorial work on several sections was contributed by P.A. Maxwell, D.F. McMichael, W.F. Ponder, A. Rowell and B.R. Wilson. Author's contributions are listed with pagination on *p. xi*, and suggestions for citation of sections at four different levels are provided on *p. iv*, to ensure that each contributor receives due recognition when cited in future publications. The high quality artwork in this volume is one of its most outstanding features, and represents the combined talents of 24 illustrators: S.P. Collin, C. Eadie, R. Evans, I. Grant, I. Hallam, A.J. Hill, K. Hollis, A.M. Jones, P. Kaas, H. Lewis, L. Newman, G. Parker, R. Plant, M. Ryan, M.A. Saul, B. Scott, A. Solem, G. Steiner, M.E. Taylor, T.E. Thompson, R.D. Turner, C. Vachelot, D. Wahl and S. Weidland. We give special thanks to: W.F. Ponder for his staunch support personally and as an Editorial Committee member; S.E. Boyd, J.M. Healy, K. Lamprell, P. Maxwell, L. Newman and B.R. Wilson for their outstanding support at all times; C. Wallace, and D. Wahl and C. Eadie for their valuable contributions as initial editor and graphic designers for the volume, respectively; C. Jordan and staff of the Biodiversity Group and CSIRO Black Mountain libraries; A. Hallam, H. Thompson and C. Eadie for their willing assistance in the final hours of preparation, and; Marta Veroni, CSIRO Publishing, who carefully nurtured the volume through the process of publication.

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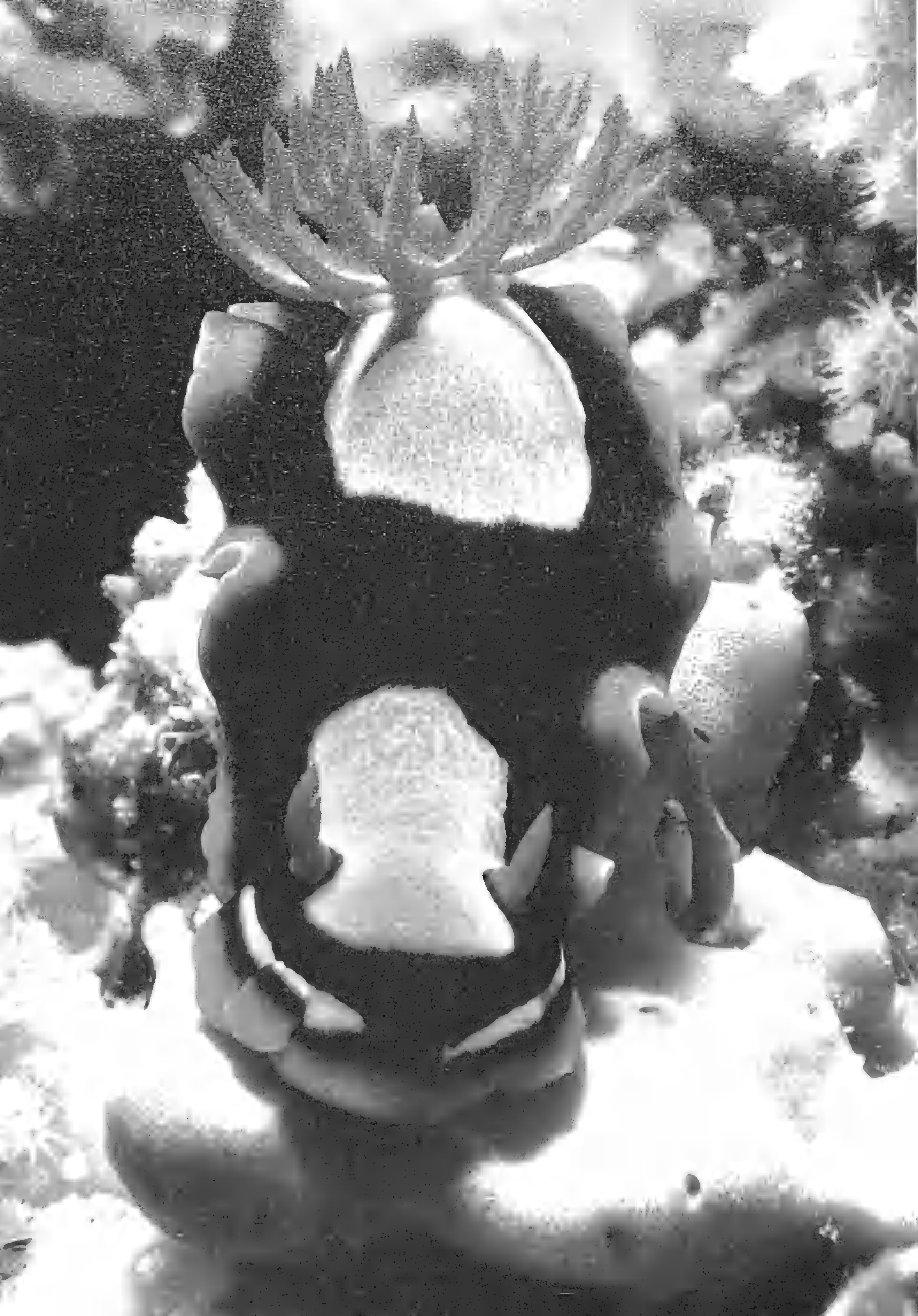

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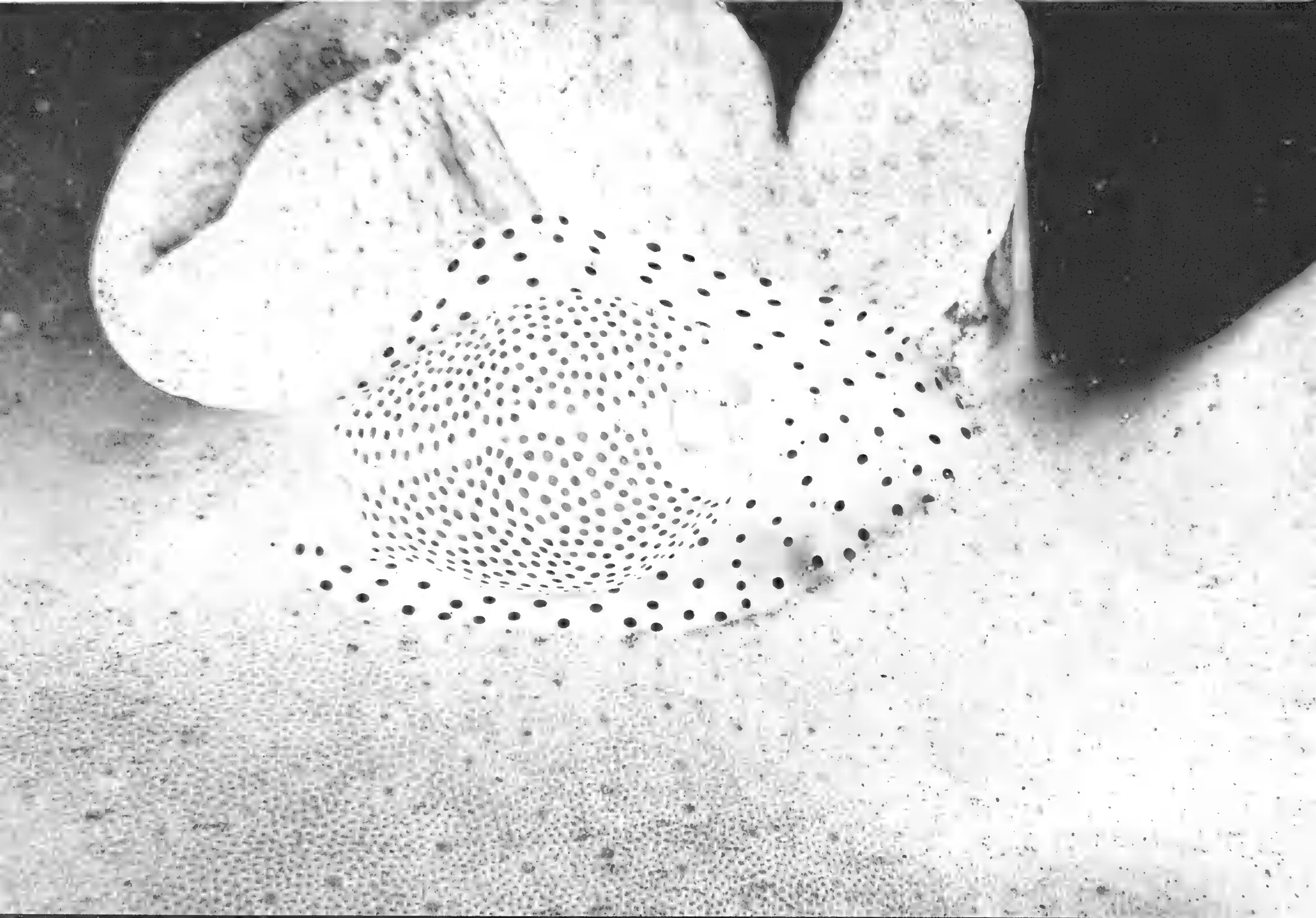
CONTENTS

PART A

PART B



AUTHORS' CONTRIBUTIONS

Authors' contributions are listed here with page numbers as a ready source of reference for purposes of citation. Its primary purpose is to ensure that authors receive due recognition for their contribution. Examples of citations covering four different levels are provided on page iv.

PART A

1 Phylum MOLLUSCA **1–144**

Definition and General Description by Don T. Anderson	1
Classification of Mollusca by Winston F. Ponder	1–6
History of Discovery by J. Hope Black	6–11
Morphology and Physiology of the Mollusca by Bronwen J. Scott & Ron Kenny	11–23
Molluscan Life Histories by Colin Little	23–29
Molluscs on Rocky Shores by A.J. Underwood	29–32
Molluscs on Coral Reefs by Carla Catterall	33–36
Molluscs in Marine and Estuarine Sediments by Charles H. Peterson & Fred E. Wells	36–46
Pelagic Molluscs by Rudolf S. Scheltema, Leslie Newman & Lu Chung Cheng	46–55
Holopelagic Gastropods by Leslie Newman *Cephalopods by Lu Chung Cheng* *Meroplankton by Rudolf S. Scheltema*	
Molluscs on Land by Colin Little	55–59
Molluscs of Inland Waters by Keith F. Walker	59–65
Economic Significance by Joe Boray & John L. Munro	65–77
Molluscs and Parasitic Diseases, Molluscs as Plant Pests by Joe Boray *Fisheries and Mariculture by John L. Munro*	
Distribution and Relationships of Marine and Estuarine Fauna by Winston F. Ponder & Fred E. Wells	77–80
Distribution and Affinities of Non-Marine Molluscs by Winston F. Ponder, Fred E. Wells & Alan Solem	80–88
Non-Marine Zoogeographical Regions by Fred E. Wells *The Freshwater Molluscan Fauna by Winston F. Ponder* *The Terrestrial Molluscan Fauna by Alan Solem*	
The Fossil Record by Peter A. Jell & Thomas A. Darragh	88–101
Introduction by Peter A. Jell & Thomas A. Darragh *Palaeozoic Era, Mesozoic Era by Peter A. Jell* *Cainozoic Era by Thomas A. Darragh*	
Methods and Techniques in Malacology by Winston F. Ponder	101–104
Quantitative Ecological Sampling of Molluscs by A.J. Underwood	104–105
Conservation by Winston F. Ponder	105–115

2 Class APLACOPHORA **145–159**

by Amélie H. Scheltema

3 Class POLYPLACOPHORA **161–194**

Introduction by Piet Kaas, Allan M. Jones & Karen L. Gowlett-Holmes	161–177
Definition and General Description, History of Discovery, Morphology and Physiology, Natural History (Life History, Ecology and Behaviour, Economic Significance), Classification by Piet Kaas & Allan M. Jones *Natural History (Biogeography), Fossil Record by Karen L. Gowlett-Holmes*	
Suborder Lepidopleurina by Piet Kaas	178
Family Lepidopleuridae by Karen L. Gowlett-Holmes	178–179
Family Hanleyidae by Karen L. Gowlett-Holmes	179–180
Suborder Choriplacina by Karen L. Gowlett-Holmes	180
Family Choriplacidae by Karen L. Gowlett-Holmes	180
Suborder Ischnochitonina by Piet Kaas	180
Family Ischnochitonidae by Tonia Cochran	180–183
Family Schizochitonidae by Karen L. Gowlett-Holmes	183–184
Family Mopaliidae by Karen L. Gowlett-Holmes	184–185
Family Chitonidae by Karen L. Gowlett-Holmes	185–188
Suborder Acanthochitonina by Piet Kaas	188
Family Acanthochitonidae by Karen L. Gowlett-Holmes	188–189
Family Cryptoplacidae by Karen L. Gowlett-Holmes	189

4 Class BIVALVIA **195–234**

by Brian Morton, Robert S. Prezant & Barry Wilson

Definition and General Description, Morphology and Physiology (External Features and Shells), Biogeography, Fossil History and Phylogeny, Classification by Robert S. Prezant

History of Discovery, Morphology and Physiology (Mantle and Body Cavities, Musculature and Locomotion, Feeding and Digestion, Excretion, Respiration, Sense Organs and Nervous System, Reproduction, Embryology), Natural History by Brian Morton

Barry Wilson revised the chapter and added Australian material

5 Subclass PROTOBRANCHIA **235–247**

by Robert G.B. Reid

6 Subclass PTERIOMORPHIA **249–288**

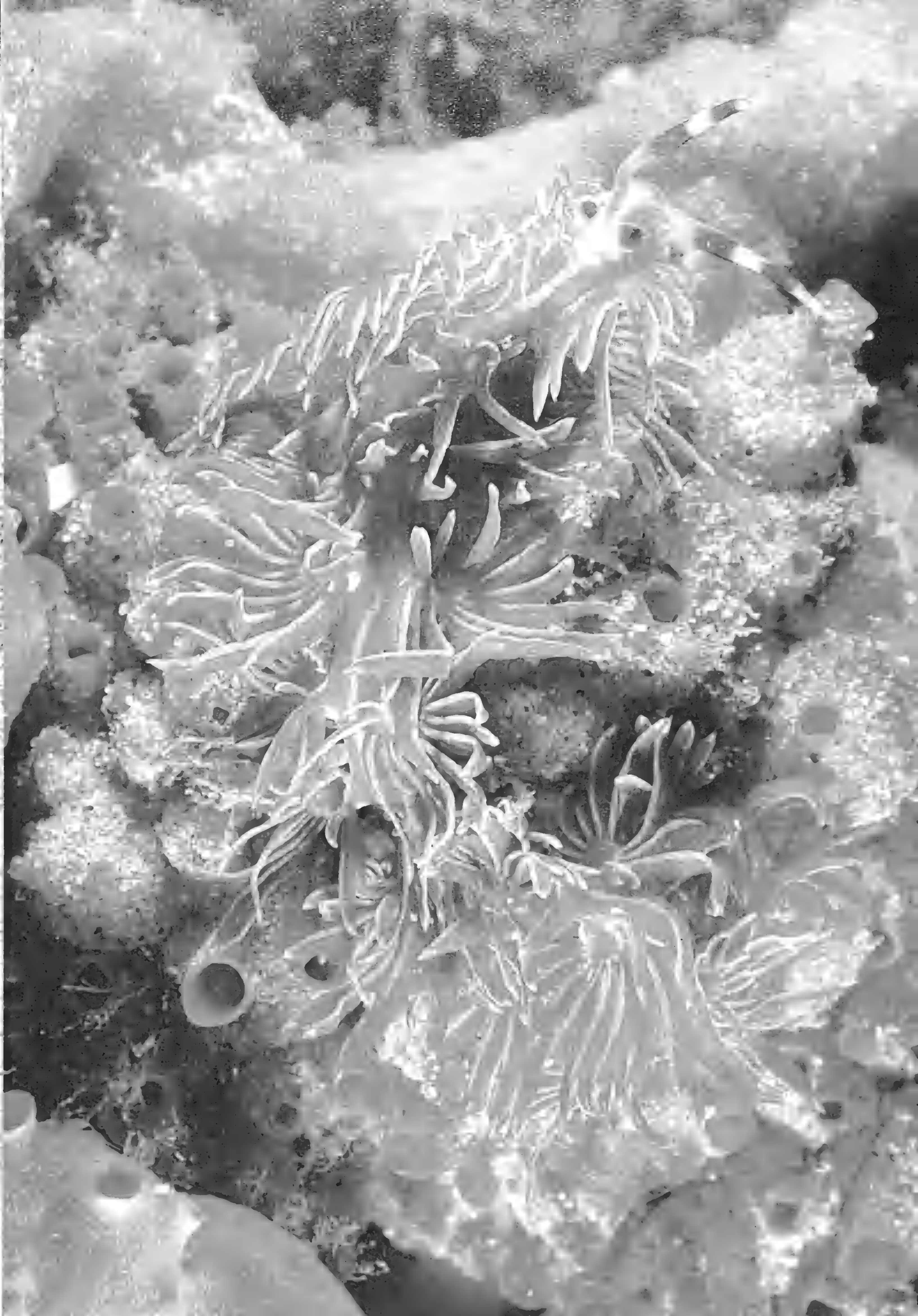
Introduction by Barry Wilson	249–250
Order Mytiloida by Barry Wilson	250–253
Order Arcoida by Suzanne E. Boyd	253–261
Order Pterioida by Alan J. Butler	261–267
Order Limoida by Alan J. Butler	267–268
Order Ostreoida by Shirley M. Slack-Smith	268–282

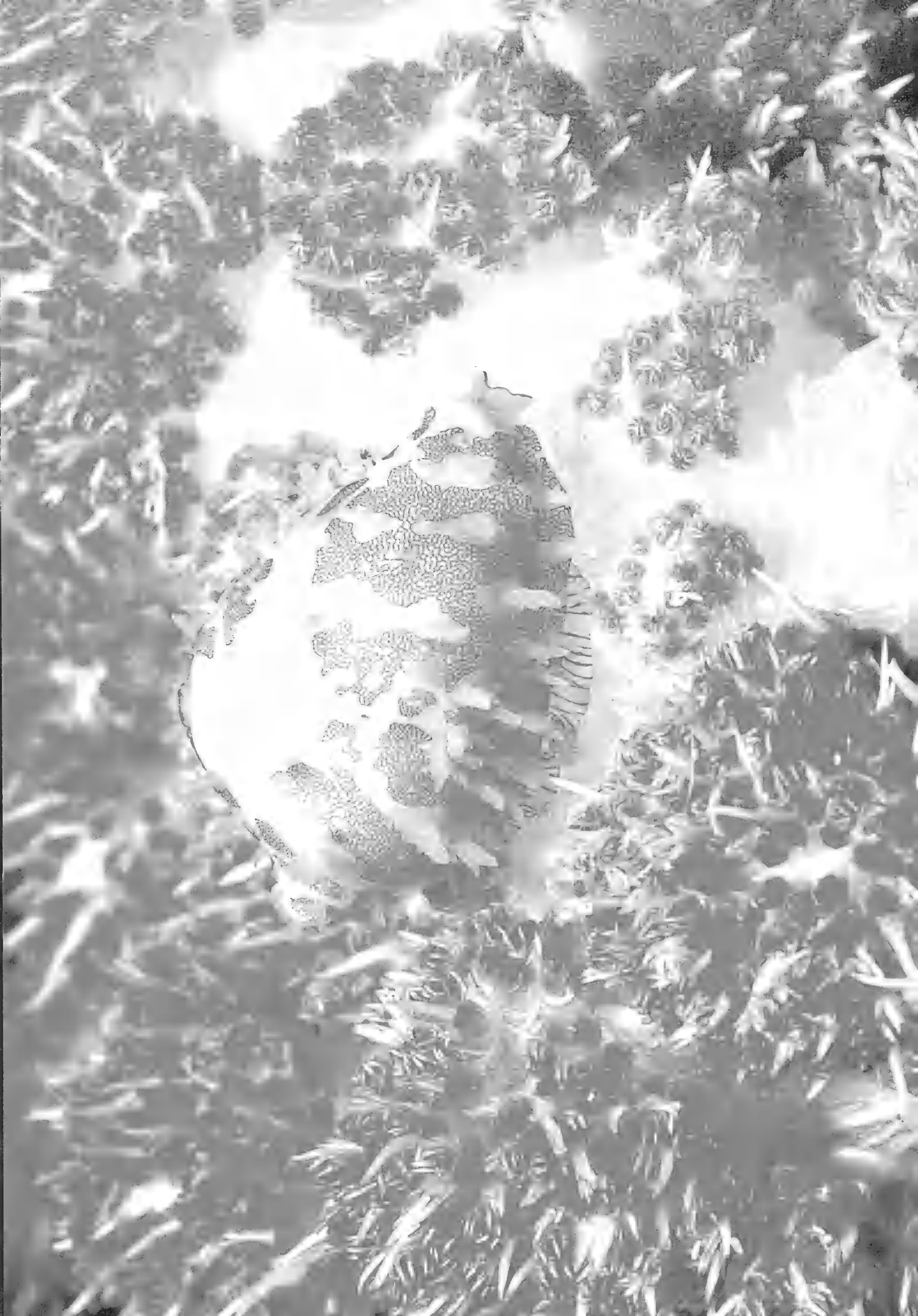
7 Subclass PALAEOHETERODONTA **289–300**

Introduction by Robert S. Prezant	289–294
Order Trigonioida by Thomas A. Darragh	294–296
Order Unionoida by Brian J. Smith	296–298

8 Subclass HETERODONTA **301–396**

Introduction by Robert S. Prezant	301–307
Order Veneroida by Brian J. Smith	306–307
Superfamily Chamoidea by Shirley M. Slack-Smith	307–309
Superfamily Lucinoidea by Robert G.B. Reid & Shirley M. Slack-Smith	309–315
Superfamily Galeommatoidea by Winston F. Ponder	316–318
Superfamily Cyamioidea by Winston F. Ponder & Roger G. de Keyzer	318–322





PHYLUM MOLLUSCA

CHAPTER 1

DEFINITION AND GENERAL DESCRIPTION

Molluscs are unsegmented coelomate animals that have an anterior head, a ventral foot, and a dorsal visceral mass covered by a mantle. The mantle secretes a calcareous shell and encloses a mantle cavity containing paired ctenidia or gills. The anus, excretory pores and genital pores open into the mantle cavity. Internally, the coelom is reduced and the body cavity is an expanded blood space or haemocoel.

Molluscs are a very diverse group of animals. Although some groups are so modified that they no longer have a dorsal shell or a mantle cavity, for example, nudibranch sea slugs, all molluscs retain the basic head-foot-visceral mass morphology diagnostic of the phylum. The head carries out sensory and feeding functions and contains, except in bivalve molluscs, a characteristic buccal mass incorporating a toothed, ribbon-like radula. The foot is basically a muscular structure which functions as a locomotory organ. The visceral mass comprises the major internal organ systems – dorsal heart, gonads, kidneys, digestive system. The cavities surrounding the gonads and kidneys, and the pericardial cavity surrounding the heart, are coelomic cavities. The general internal body cavity is a haemocoel. The circulation of blood through the haemocoelic system is maintained by the pumping action of the heart and by the general muscular contractions of the soft body wall.

Behind the buccal mass, the digestive system continues as an oesophagus, stomach and intestine. Complex digestive glands open into the stomach. Cilia are important agents in the movement and sorting of food in the gut. Cilia are also important in generating a respiratory current through the mantle cavity and in the removal of sediment and debris from the mantle cavity and gills. The comb-like ctenidia contain blood vessels which carry a flow of oxygenated blood to the heart. A respiratory current passes through the mantle cavity, traversing the ctenidia and flushing the discharge from the anus, kidneys and, in more primitive molluscs, the gonads. Many molluscs have more elaborate reproductive systems, which incorporate copulation and internal fertilisation. Sexes are usually separate, although hermaphrodites are typical of some groups, such as many terrestrial snails and the marine opisthobranchs.

The head-foot-visceral mass organisation of molluscs is further reflected in the nervous system, which is centred on three pairs of ganglia – cerebral, pedal and visceral – located in the three main parts of the body. Associated with their unsegmented structure, lack of a jointed skeleton and use of a unitary muscular foot as an organ of crawling and attachment, molluscs are basically slow moving animals. Many have become sessile. The speed and agility of cephalopods is the result of an extreme evolutionary modification consequent on the transformation of the respiratory current into a jet propulsion mechanism.

In spite of their distinctive adult morphology, molluscs have long been considered to be close relatives of two phyla of worm-like coelomate animals, the non-segmented Sipuncula and the segmented Annelida. This relationship is evident in the pattern of embryonic and early larval development shared by these phyla (Anderson 1982; Nielsen 1995).

In all, cleavage is spiral. The blastula has a distinctive array of presumptive areas – rudiments of the future components of the embryo – including a mesodermal area formed by a single postero-dorsal cell, 4d. The first hatched larval stage of development is a trochophore propelled by cilia on the prototroch, an equatorial band of large ciliated cells (Fig. 1.1). Only after this stage do the diagnostic molluscan, sipunculan or annelidan features begin to develop.

The close relationship of the Mollusca to the Annelida adduced from comparative embryology has been confirmed by Eernisse, Albert & Anderson (1992) in their cladistic analysis of metazoan morphology. Molecular biological analyses also support this close relationship, as shown by Field *et al.* (1988) in comparisons of ribosomal RNA sequences, and Wheeler, Cartwright & Hayashi (1993), who compared ribosomal DNA and the protein ubiquitin in a wide range of annelid, onychophoran and arthropod taxa, with molluscs as an outgroup.

CLASSIFICATION OF MOLLUSCA

No unique characters define the entire Phylum Mollusca, which shows great structural and ecological variability, and members of the group can only be separated from other animals by the possession of a combination of characters.

The debate over the origin of Mollusca is not yet resolved, but the outcome has major implications for the construction of the early phylogeny of molluscs. A.H. Scheltema (1988) and Salvini-Plawen (1990), representing the two main schools of thought, have discussed the matter at length, the latter favouring a mesenchymate, flatworm-like ancestor and the former a coelomate, possibly segmented, ancestor. This matter has also been discussed at length by Haszprunar (1996). The discovery of living monoplacophorans in the 1950s (Lemche & Wingstrand 1959) rekindled the idea refuted previously by Hoffmann (1937) that the ancestral mollusc was segmented. However, the serial repetition of organs seen in monoplacophorans was re-established by Wingstrand (1985) who suggested an 8-metameric molluscan ancestor. Molecular evidence to date has not resolved the issue unequivocally (Salvini-Plawen 1990; Haszprunar 1996), some results favouring a coelomic, segmented ancestor (Ghiselin 1988), as outlined in the previous section.

Unlike the normal textbook ancestral or 'archetype' mollusc (Fig. 1.2A; see for example, Barnes 1968; Morton, J.E. 1979), which was essentially based on an untorted gastropod, it is now generally agreed that the first molluscs had neither a shell, nor a distinct division into a head, foot and visceral mass (Fig. 1.2B; Salvini-Plawen 1972, 1980, 1990; Haas 1981; Scheltema, A.H. 1988; Haszprunar 1992, 1996). Their very small size was a feature of early molluscs (Chaffee & Lindberg 1986; Haszprunar 1992).

Within the assemblage of animals sharing the molluscan ground plan, several very distinct groups can be recognised (Fig. 1.3). Some of these are markedly different, including the familiar snails, octopuses and squids, and bivalves. Six to eight classes of living molluscs have been recognised. Additional classes have been erected for extinct groups, though the inclusion of some of these in the Mollusca is disputed. Not all of the classes are equally distinct, their relationships being reflected in groupings at subphylum level. Whereas there is now some general agreement on this level of classification, the names abopve the class level are referred to infrequently. These groups are briefly discussed below. Such schemes should reflect the evolution of the group in a classification based on phylogenetic relationships and one such scheme is shown in Figure 1.4. However, the relationships of the classes of molluscs are by no means settled, as for example is evident from the varying schemes adopted by various authors in the *Origin and Evolutionary Radiation of the Mollusca* edited by J.D. Taylor (1996).

Three main grades of organisation are generally recognised within the Mollusca – aplacophoran, polyplacophoran and conchiferan. In the usually accepted classification, the first two groups comprise the subphylum Auculifera, equivalent to the old class-level grouping of 'Amphineura', and the remaining groups are included in the subphylum Conchifera. The shell probably evolved independently in these two groups (Haas 1981). A brief diagnosis of each subphylum and class is given below; more detail can be found under the sections dealing with the classes.

Subphylum Auculifera (Amphineura)

Class Aplacophora. The Aplacophora, previously considered to comprise a single class or subclass of the Amphineura, are now often divided into two classes, Neomeniomorpha and Chaetodermomorpha (= Solenogastres and Caudofoveata, respectively) (Salvini-Plawen 1972, 1990; Boss 1982; Salvini-Plawen & Steiner 1996), although these have been treated as subclasses by some other workers (for example, Scheltema, A.H. 1978, 1988; see Chapter 2). Salvini-Plawen (1972, 1985, 1990) argued that these two groups cannot be maintained in a single class because they have separate origins (that is, they are paraphyletic, or as shown in Figure 1.4, polyphyletic) but this was disputed by A.H. Scheltema (1988, 1996). As monophyly of each group is undisputed, they are defined separately below but are not ranked.

Salvini-Plawen (1990) used Aplacophora as the name for the earliest grade of molluscan evolution, encompassing the molluscan archetype, as well as the Chaetodermomorpha and Neomeniomorpha. The aplacophoran cuticle contains aragonitic spicules, the gut is straight, and paired gonads shed gametes via the pericardium to the exterior. In Salvini-Plawen's (1990) view, within this grade two quite separate lines have evolved from the ancestral mollusc that moved, presumably by gliding using cilia and mucus. One line – the Scutopoda, which contains only the Chaetodermomorpha – took up sediment burrowing, became elongate and worm-like, and developed a reduced gliding surface by mid-ventral fusion of the mantle margins. In the other line (Adenopoda), from which the Neomeniomorpha evolved, and the rest of the Mollusca according to Salvini-Plawen (1972, 1985, 1990), an anterior pedal gland and a mantle cavity developed, and became restricted to the ventral foot. Developmental data provide additional evidence for a common ancestor of Polyplacophora and neomenioids (Salvini-Plawen 1972, 1985, 1990). A.H. Scheltema (1988; Chapter 2) argued that the Aplacophora is monophyletic, defined by several autapomorphies, and that the adenopods arose independently from a coelomate ancestor. Lindberg & Ponder (1996) reviewed the evidence for these views.

The Chaetodermomorpha, also termed the Caudofoveata, are worm-shaped, cylindrical, and covered by a cuticle and aragonitic scales. The posterior mantle cavity contains one pair of ctenidia. The ventral gliding area is reduced and lacks a distinct pedal groove. Chaetoderms burrow in muddy marine sediments, and feed on micro-organisms. A radula is present, ventrally separated sacs occur along the midgut and the sexes are separate.

The Neomeniomorpha, or Solenogastres, are worm-shaped and laterally compressed. The gliding sole, or foot, lies in a distinct ventral groove, the mantle has a cuticle bearing aragonitic scales or spicules, and the modified mantle cavity lacks ctenidia. A radula is present and the midgut is straight, usually with lateral pouches. These marine carnivores are epibenthic or epizoic on cnidarians (coelenterates), on which they feed. Aplacophorans are hermaphrodites.

Class Polyplacophora (Placophora, Loricata). Chitons, or coat of mail shells, have a flattened body and a broad foot, a mantle covered with cuticle and spicules or scales and a shell of eight (primitively seven in an extinct fossil group) valves. The shell valves bear sensory papillae or aesthetes. The head is simple, lacking eyes or tentacles. The mantle cavity surrounds the foot (peripedal) and supports multiple pairs of ctenidia. The gut includes a radula and a tasting, or subradular, organ, oesophageal and midgut (= digestive) glands, a stomach and a looped intestine. Most chitons are grazing herbivores, some feed on colonial organisms, such as sponges, and one group captures small prey. The sexes are separate in most chitons. These marine animals usually occur on hard substrata. Runnegar, Pojeta, Taylor & Collins (1979), Runnegar & Pojeta (1985) and Eernisse & Reynolds (1994) discussed the origins of the group as indicated by the fossil record.

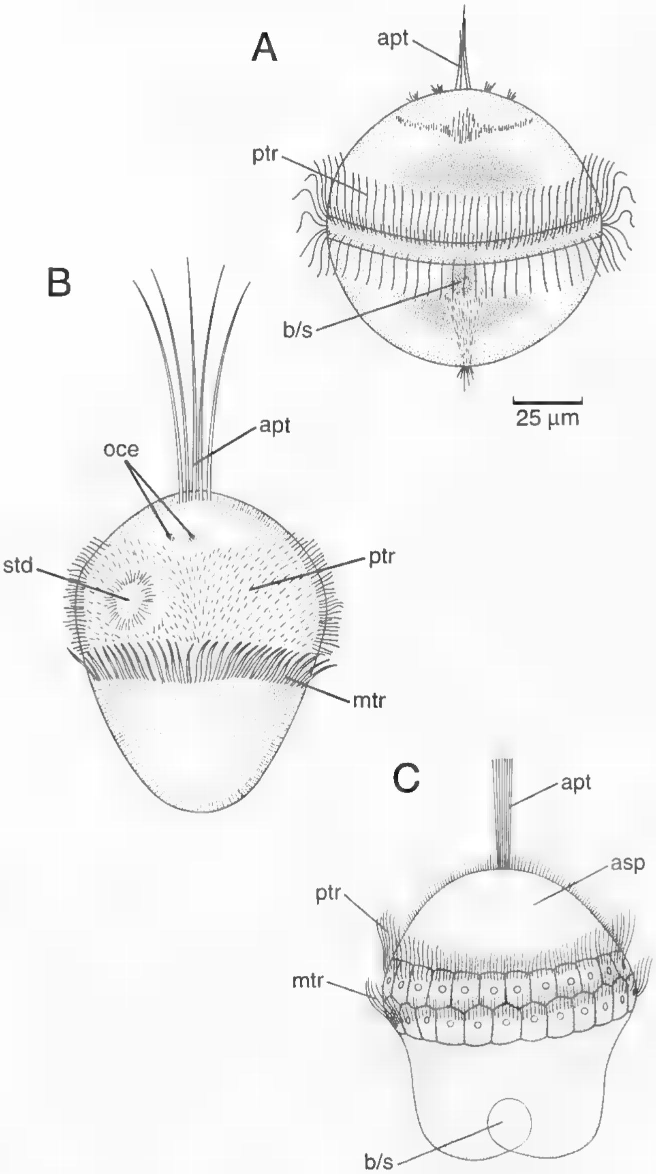


Figure 1.1 Early trochophore larvae. **A**, a polychaete annelid. **B**, a sipunculan. **C**, a gastropod mollusc. **A**, *Anaitides williamsi* (Phyllodocidae). **B**, *Golfingia* sp. (Golfingiidae). **C**, *Patella* sp. (Patellidae). **apt**, apical tuft; **asp**, apical sensory plate; **b/s**, blastopore/stomodeum; **mtr**, metatroch; **oce**, ocelli; **ptr**, prototroch; **std**, stomodeum; scale bars not available for B and C. (A, after Blake 1975; B, after Hyman 1959; C, after Hyman 1967)
[A, B, I. Hallam; C, C. Eadie]

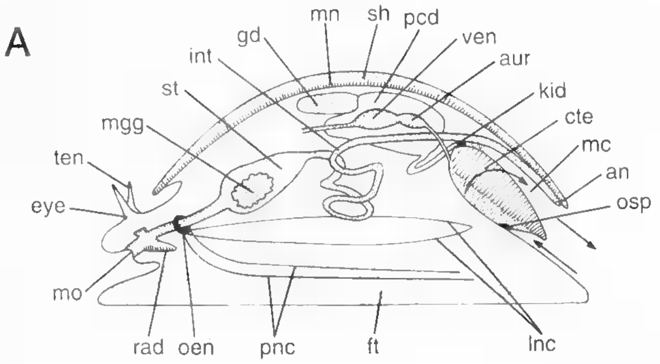
Subphylum Conchifera

The single shell of the members of this group and the multiple shell plates of the Polyplacophora were probably derived independently (Haas 1981), although Salvini-Plawen (1990) argued that two bundles of shell muscles are attached to each polyplacophoran shell valve and these multiple muscles are retained in monoplacophorans, suggesting fusion of the shell valves of a polyplacophoran ancestor. Autapomorphies of the Conchifera include the presence of appendages on the head, jaws in the buccal cavity, a protostyle region of the stomach, statocysts and a subrectal commissure in the nervous system. However, the monophyly of the Conchifera has been questioned by Lindberg & Ponder (1996).

Two main groups have been recognised. Members of one burrow into soft bottoms by means of an anterior, elongate foot and have a shell that envelops the entire body. This group comprises the extinct Rostroconchia, the Bivalvia and the Scaphopoda and has been named Loboconcha, Diasoma or Ancyropoda. The second group became more mobile, developed a free head with photoreceptors (eyes) and the shell became restricted to the increasingly conical visceral body and the mantle to a posterior cavity. This group has been termed the Visceroconcha, Rhacopoda or Cyrtosoma.

Class Monoplacophora (Tryblidiida, Galeroconcha). Monoplacophorans are covered with a cap-shaped shell. The head bears two pairs of appendages and the peripedal mantle cavity supports five to six pairs of modified ctenidia. There are five to six pairs of excretory organs, and two pairs of (heart) auricles and gonads. The gut includes a radula and a protostyle sac region of the stomach. The animals are marine detritus feeders, attached to hard substrata. The sexes are separate. Detailed comparisons of polyplacophorans with monoplacophorans were made by Lemche & Wingstrand (1959) and Wingstrand (1985). If the many divergent fossil groups often referred to it are included, the Monoplacophora is undoubtedly paraphyletic (as in Fig. 1.4) or polyphyletic (for example, Salvini-Plawen 1980, 1990; Harper & Rollans 1982). Another monoplacophoran-like group, the Cyclomya, is extinct. Runnegar & Pojeta (1985) discussed the evolution of the group and how coiled and even bivalved shells have apparently evolved in the group.

This class is not treated in the present volume as most of its members inhabit very deep water, and none is yet recorded from Australian waters. Living monoplacophorans have, however, been found in Antarctica (Warén & Hain 1992) and New Zealand (Marshall 1990).



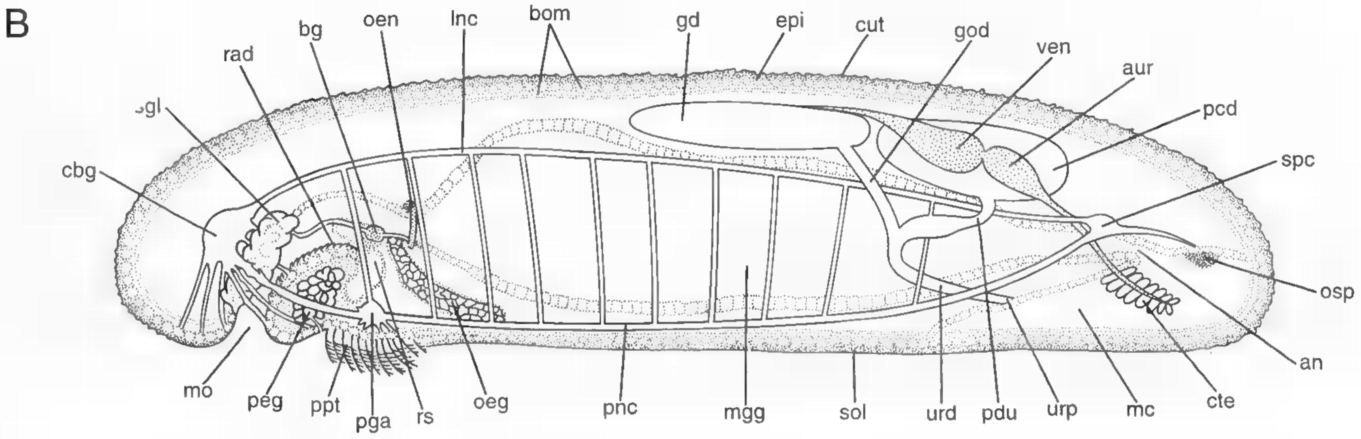


Figure 1.2 Hypothetical ancestral molluscs. **A**, initial concept, showing differentiation of the head, foot and visceral mass, and presence of a shell. **B**, recent concept of a small animal with a cuticle and no distinct regionalisation. **an**, anus; **aur**, auricle; **bg**, buccal ganglion; **bom**, body musculature (outer circular, inner longitudinal); **cbg**, cerebral ganglion; **cte**, ctenidium; **cut**, cuticle with embedded scales; **epi**, epidermis; **eye**, eyespot; **ft**, foot; **gd**, gonad; **god**, gonoduct; **int**, intestine; **kid**, kidney; **lnc**, lateral nerve cord; **mc**, mantle cavity; **mgg**, midgut gland; **mn**, mantle; **mo**, mouth opening; **oeg**, oesophageal gland; **oen**, oesophageal nerve ring; **osp**, osphradium; **pcd**, pericardium; **pdu**, pericardial duct; **peg**, pedal gland; **pga**, pedal ganglion; **pnc**, pedal nerve cord; **ppt**, pedal pit and cirri; **rad**, radula; **rs**, radula sac; **sgl**, salivary gland; **sh**, shell; **sol**, pedal sole; **st**, stomach; **spc**, suprarectal commissure; **ten**, tentacle; **urd**, urinogenital duct; **urp**, urinogenital pore; **ven**, ventricle. (A, after Barnes 1963; B, after Haszprunar 1992) [I. Hallam]

Class Gastropoda (Univalvia). In all gastropods, including snails, slugs and limpets, the mantle cavity is rotated from its posterior position during the developmental process of torsion, so that it comes to be at the anterior end. Secondarily, this may be laterally or posteriorly re-positioned through detorsion. The larval shell is coiled, and usually has an operculum; the adult shell may be limpet-like, rudimentary or lost; the operculum may also be lost in adults. The head is free, and bears a pair of photoreceptors (eyes) and, usually, two lateral tentacles. A radula and a midgut (digestive) gland are present consistently in the gut; an oesophageal gland is often present, and a subradular organ occurs in primitive forms. The stomach varies from complex to simple, and typically has a (proto)style sac. The intestine may be looped to almost straight. Gastropods may be dioecious or hermaphroditic, and the left reproductive organs are reduced. Gastropods use a wide variety of feeding methods and occur in many types of terrestrial, freshwater and marine habitats, including the pelagic zone. This class is by far the largest group of Mollusca.

Linsley & Kier (1984) proposed a new class, Paragastropoda, to accommodate some Palaeozoic taxa with left-handed coiled shells that were included in the gastropods. In addition the status of another large fossil group, the Bellerophontida, is disputed, as there is disagreement about whether or not its members are torted. They are regarded as untorted and included in the Monoplacophora by some recent writers (for example, Salvini-Plawen 1980, 1990; Runnegar & Pojeta 1985), but others regard at least some as gastropods (see Ponder & Lindberg 1996, 1997).

Class Cephalopoda (Siphonopoda). Octopuses, squids, cuttlefish and *Nautilus* are conchiferans with a dorso-ventrally elongated body. When present, the shell is coiled to straight, typically chambered, and pierced by a siphuncular tube. The head is free, and bears a pair of eyes, and one or two circles of eight to ten (or up to about 90 in *Nautilus*) tentacles surrounding the mouth. The

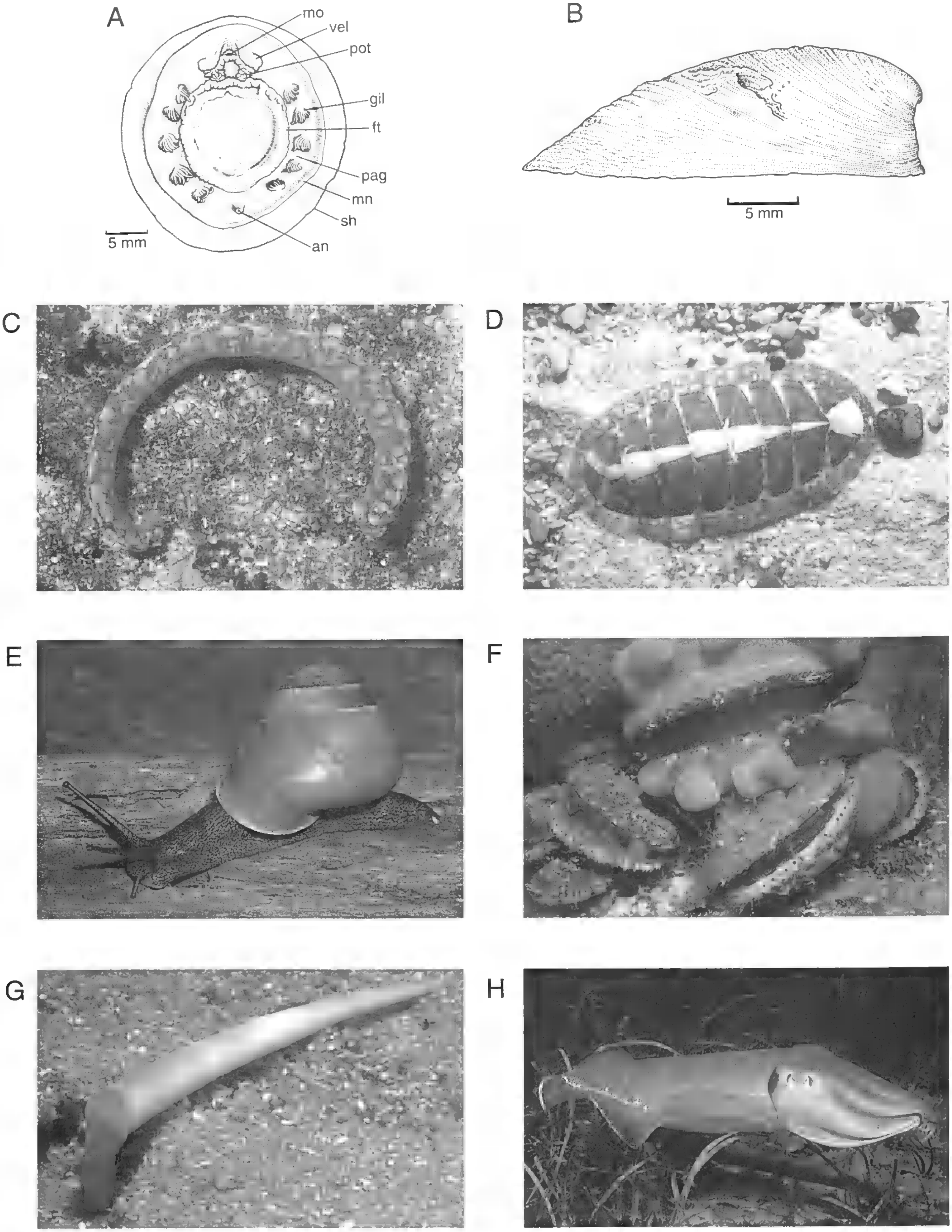


Figure 1.3 Representatives of each extant class in the Phylum Mollusca. **A**, the monoplacophoran *Neopilina galatheae*, ventral view. **B**, the shell of *Neopilina galatheae*, lateral view. **C**, the neomenioid aplacophoran *Epimenia australis* (Epimeniidae), from Madang, New Guinea. **D**, a polyplacophoran, *Ischnochiton contractus* (Ischnochitonidae), from Yorke Peninsula, South Australia. **E**, *Sphaerospira incei* (Camaenidae), a terrestrial pulmonate gastropod from Queensland. **F**, the bivalve, *Mimachlamys asperrimus* (Pectinidae), from Yorke Peninsula, South Australia. **G**, a scaphopod, *Laevidentalium* species (Dentaliidae), from Shark Bay, Western Australia. **H**, the cephalopod, *Sepia apama* (Sepiidae), at Rapid Bay, South Australia. **an**, anus; **ft**, foot; **gil**, gill; **mn**, mantle; **mo**, mouth; **pag**, pallial groove; **pot**, postoral tentacles; **sh**, shell; **vel**, velum. (A, B, after Lemche & Wingstrand 1959)

[A, B, C. Eadie; C, R. Willan; D, F, K. Gowlett-Holmes; E, Queensland Museum; G, C. Bryce/WA Museum; H, F. Bavendam] foot is modified as a funnel for jet propulsion. The mantle cavity is restricted to the posterior part of the body, with two ctenidia (four in *Nautilus*). Strong beak-like jaws arm the beginning of the alimentary tract. A rectal ink sac provides fluid used in defence. The sexes are separate in most groups. The nervous system is very concentrated. Among these marine, benthic or pelagic carnivores are the largest molluscs, with body sizes up to 8 m (arms up to 22 m), including the extinct Ammonoida.

Class Bivalvia (Lamellibranchia, Pelecypoda, Acephala). Bivalves, such as clams, oysters, scallops, cockles and mussels, are laterally compressed conchiferans covered with a shell composed of two valves joined dorsally by a ligament. The mantle cavity surrounding the body contains a single pair of enlarged ctenidia, and the posterior mantle is often extended into siphons. The foot is laterally compressed and often bears a byssal gland. The head bears labial palps and the mouth; the buccal apparatus, including the radula are lacking, as are the eyes and cephalic tentacles. The gut includes a complex stomach. Most bivalves are ciliary suspension-feeders, although some are deposit-feeders; a few are micro-carnivores and some others gain most or all of their nutrition from symbiotic bacteria in their gills. Bivalves are dioecious or hermaphroditic. They are benthic, often burrowing, or may be epiphytic or, rarely, epizoic, and they occupy a wide variety of marine and freshwater habitats.

Class Scaphopoda (Solenoconcha). The tusk shells are conchiferans in which the mantle is fused mid-ventrally and the tubular shell is open at both ends. The head bears a long snout and two groups of slender tentacles, termed captacula, and the foot is cylindrical and pointed. Ctenidia, distinct blood vessels and auricles are lacking. The sexes are separate. These marine micro-carnivores burrow in sediment.

Extinct classes

Class Rostroconchia. This is the only extinct class about which there is general agreement and that is indisputably molluscan (Runnegar & Pojeta 1985). This diverse group has bivalved adult shells derived from a single larval and juvenile shell. Most were probably deposit-feeders but some were suspension-feeders and looked and behaved rather like modern bivalves. They ranged from the earliest Cambrian to the latest Permian (Runnegar & Pojeta 1985).

Other extinct groups. Some groups were included in the Mollusca in the past just because they have a shell. For example, Brachiopoda, which have long been regarded as a separate phylum, were once regarded as molluscs, as were barnacles, which are shell-bearing crustaceans. Most fossil groups are recognised only from their hard parts, such as shells. Many groups acquired shelly hardparts in the early Cambrian (Rozanov 1992). Some of these groups were undoubtedly molluscan but others were not. There has been controversy over the inclusion of two extinct groups, the Hyolitha and the Conodonta, in the Mollusca.

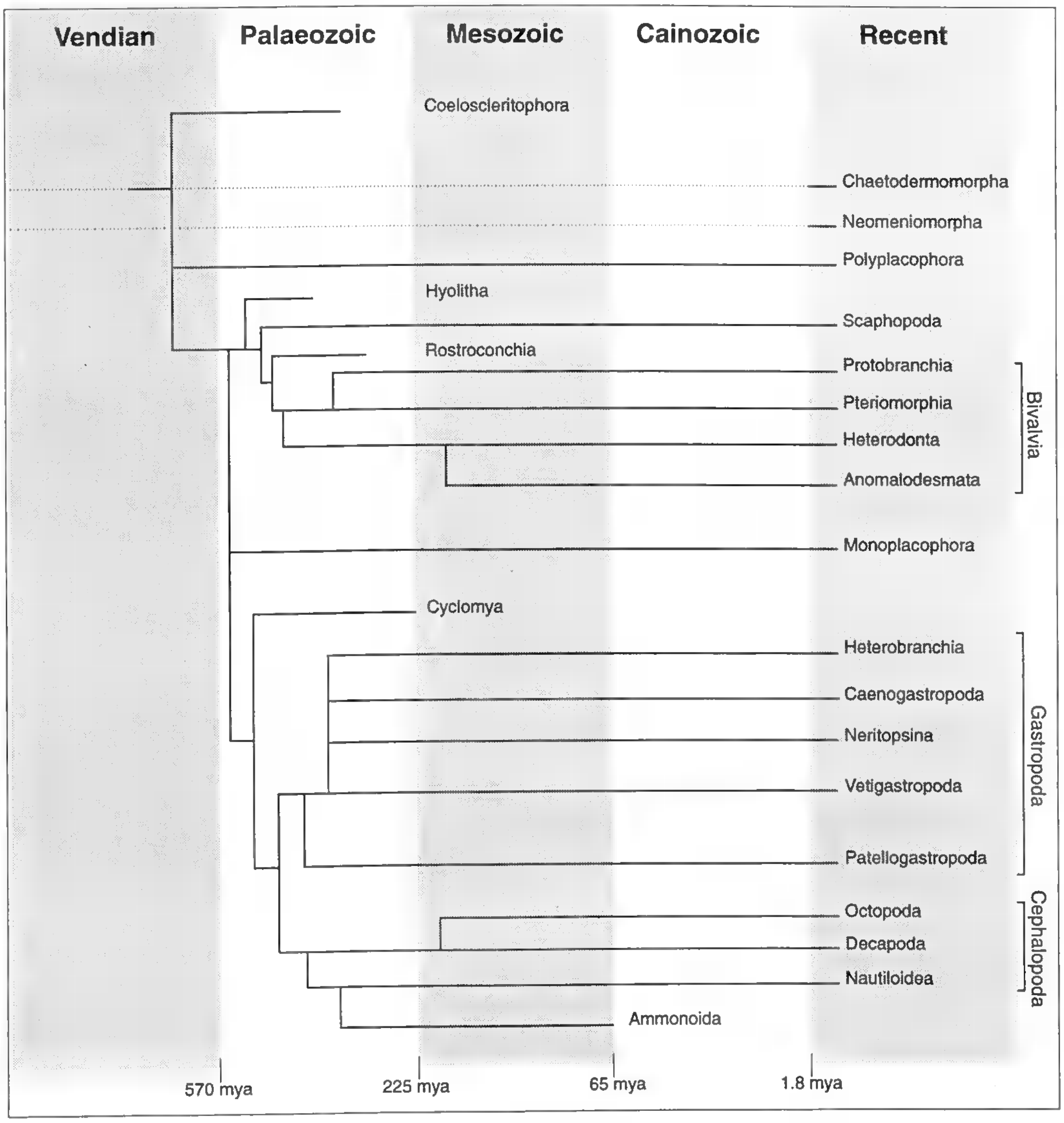


Figure 1.4 A phylogeny of the phylum Mollusca, compiled from various sources. mya, millions of years ago.

Figure 1.5 François Péron. An engraving by Chabard, based on a drawing by Lesueur. [Muséum d'Histoire Naturelle – Le Havre – no. 06105]

The Hyolitha is sometimes regarded as a class of molluscs (for example, Marek & Yochelson 1976; Yochelson 1984) but Runnegar (1980) and Runnegar & Pojeta (1985) have argued that this group was probably derived independently from molluscs and should be placed in a separate phylum.

Tillier & Cuif (1986) suggested that the Conodonta, a very large and diverse but enigmatic group, were aplacophorans but this has been disputed strongly (for example, Briggs, Aldridge & Smith 1987). More recent studies of fossilised soft-parts indicate that conodonts were probably a major group of vertebrates (Briggs 1992; Sansom, Smith, Armstrong & Smith 1992).

HISTORY OF DISCOVERY

The history of molluscan science is part of the history of Australian exploration. The present account summarises the activities and contributions of the early malacologists up to the mid 1900s. The extensive works of subsequent researchers are synthesised in more detail elsewhere in this volume.

The earliest records of Australian molluscs were those of the personnel of Dutch vessels that made unscheduled or deliberate landings on the coast of New Holland on their way to the Dutch East Indies.

In 1606, the crew of Captain William Janszoon's ship, the *Duyfken* went ashore at Batavia River, near Cape Keerweer in the Gulf of Carpentaria. There they collected and ate large numbers of a 'delicious large green snail', possibly a species of *Turbo*. Van Roosenbergh, supercargo on *Het Hapenvan Hoorn*, recorded cuttlebones near Shark Bay in 1629, as did Francis Pelsart, whose ship *Batavia* was wrecked on Houtman Abrolhos in the same year. In 1697 Willem de Vlamingh of the *Geelwink* recorded oysters in the same area. He also collected a nautilus and a baler shell which were drawn by a crew member, Victorsoon. The account of this voyage and the drawings were sent by Nicholas Witsen, a former director of the Dutch East India company, to the naturalist physician Martin Lister who published part of Witsen's letter in 1698.

The English seafarer William Dampier of *Cygnet* made landfall on the Kimberley coast of Western Australia in 1686. He recorded Aborigines collecting cockles, mussels and periwinkles (Dampier 1697). The authorities were so impressed with his account of this voyage they provided HMS *Roebuck* for an exploring expedition to New Holland in 1698. On his return Dampier wrote a second book, in which he illustrated fish and a cuttlefish (Dampier 1703, reproduced in Stanbury 1987). He also recorded mussels, periwinkles, limpets, pearl and edible oysters, long oysters and cockles, and noted that the shore was lined with many other sorts of very strange and beautiful shells.

James Cook's voyage on the *Endeavour* (1768) was the first expedition planned and equipped as a scientific voyage of observation and discovery. In the course of the voyage, the geology, flora and fauna of the lands visited were to be recorded by the scientific party, which included Joseph Banks and Carl Solander.

The official collections of the expedition all went to Banks' house in Soho and from there some zoological specimens were dispersed to personal contacts of Banks. The major portion of the molluscan material remained unworked for many years (Whitehead 1969; Stanbury 1987) through lack of interest – Banks was interested mainly in botany and Solander had died early – and the collection was deposited finally in the British Museum (Wilkins 1955). As a consequence, specimens in private collections, such as those of Dr John Fothergill and the Duchess of Portland, provided the earliest knowledge of many Australian shells. These collections were often assembled from shells collected by crew members, and sold to dealers such as George Humphrey and Thomas Martyn, who supplied the growing and lucrative European market. John Marra, a gunner's mate on *Resolution* during Cook's second voyage, sold his collection of shells to Humphrey along with most of the other shells collected on the voyage.

In his discussion of the contribution to conchology of the Cook voyages, Dance (1971) listed the shells collected on all three voyages, with their country of origin.

Some of the molluscs collected on these voyages became part of the collection of Elizabeth Bligh, wife of William, master of the *Resolution* on Cook's third voyage. The collection was sold in 1822. The catalogue of the auction listed a wide variety of Australian shells and in its appendix, William Swainson described a number of new species including *Haliotis gabra*, *Mitra carbonaria*, *M. nivosa* and *Voluta maculata*.

John Hunter (1793), captain of the *Sirius* of the First Fleet, illustrated three undescribed shells from New South Wales, which were probably the specimens on which Perry (1811) based the names *Septa rubicunda* and *S. spengleri*.

Following the Dutch and English expeditions to New Holland, a number of French voyagers visited the region in the late 18th Century (Stanbury 1987). Because of various misfortunes or delays, however, the results of these early expeditions were not published.

Nicholas Baudin's expedition to Australia between 1800 and 1804, on the vessels *Le Géographe* and *Le Naturaliste*, assembled one of the most significant biological collections for this region to date, comprising over 100 000 specimens. Most were collected through the efforts of the naturalist François Péron (1807, 1816) (Fig. 1.5) and artist Charles-Alexandre Lesueur along Australian shores (Laissus 1988). Landfall was made at Cape Leeuwin, Western Australia, and the vessels then turned north to explore the western coast. Péron made shore collections at Shark Bay, Barrier Island and at the Barren Islands where a number of fossil shells were found. They made dredge hauls at Geographe Bay and Dupache Island.

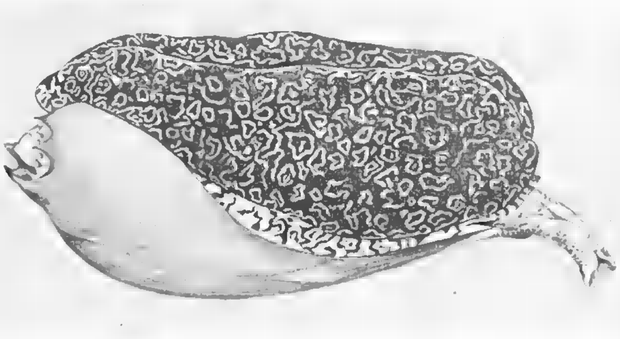


Figure 1.6 The volute, *Melo miltonis*, collected by Péron on the Western Australian coast in 1801 (Bonnemains *et al.* 1988) and painted by Nicolas Martin Petit. This species occurs in the intertidal and sublittoral zones.
[Muséum d'Histoire Naturelle – Le Havre – no. 72067]

Several of these specimens were painted by Nicolas-Martin Petit and Lesueur, both promoted to artists from assistant gunners during the expedition, following the resignations of the three official artists (Figs 1.6, 1.7; Bonnemains 1988).

After visiting Timor, the expedition sailed to Van Diemen's Land where Péron recorded a giant squid with tentacles two metres long. Sailing into the D'Entrecasteaux Channel, Péron again made collections including mussels and other molluscs (Fig. 1.7). At Bruny Island, he found a number of new or rare species and genera, including *Trigonia*, known previously only from fossil specimens. After a stay at Port Jackson Baudin continued his exploration south and west to King Island, Kangaroo Island, King George Sound, Rottnest Island, Shark Bay and Melville Island, and thence to France. The fossil material collected by the expedition was put aside until Christian Von Buch (1814) published his notes.

The molluscan specimens collected by the expedition were sent to the great French biologist, Jean Baptiste de Lamarck (1818–1823). In 1804 he drew attention to the similarity between the *Trigonia* collected at various localities around Van Diemen's Land and European fossil species. In his seven volume *Histoire Animaux sans Vertébrés*, Lamarck laid the foundation of the science of malacology and recorded more than fifty European fossil genera still living in Australia.

Louis Duperrey's expedition in *La Coquille* reached Port Jackson in early 1824. The surgeon-naturalist René Primevere Lesson collected many new species including land shells taken during several inland excursions arranged by the botanist, Allan Cunningham (Lesson & Garnot 1826–1830).

Perhaps the most important of the French expeditions was that of *l'Astrolabe* (1826–1827) under the command of Jules Dumont d'Urville. There were several naturalists, including Jean René Constant Quoy and Joseph Paul Gaimard, amongst the ship's complement. Extensive collections were made of molluscs and other marine invertebrates on the coasts of south-eastern Australia and Tasmania. Descriptions of these were published in two volumes (Quoy & Gaimard 1839).

The final French Expedition of *l'Astrolabe* and *Le Zelée* between 1837 to 1840 was again under the command of Dumont d'Urville with Charles Hector Jacquinot as captain of *l'Astrolabe* and Jacques Bernard Hombron as surgeon-naturalist. The expedition made extensive collections in Torres Strait (Rousseau 1854).

Coastal Marine Surveys

From the time of settlement, the British government realised the need for a survey of the coast. Several vessels were commissioned for this purpose and either had naturalists assigned to them or the ships surgeons acted as naturalists. One of the earliest of these survey vessels was HMS *Investigator* (1801–1803) under the command of Lieutenant Matthew Flinders. The naturalist of the voyage was the botanist Robert Brown. Although there is no official record of a molluscan collection, Brown sent fossil and Recent shells to George Humphrey and fossils to William Buckland, a well-known geologist and a trustee of the British Museum.

Lieutenant Phillip King made four expeditions, three on HMS *Mermaid* and the fourth on HMS *Bathurst* to survey the northern coast of New Holland between 1818 and 1822, with Allan Cunningham as naturalist. He published a journal of the voyages, in which John Edward Gray described 111 molluscs in an appendix on the flora and fauna (King 1827).

Between 1830 and 1850 there were a number of visits by survey vessels. The most noteworthy of these were HMS *Beagle* (1831–1836), commanded by Robert Fitzroy, with Charles Darwin as naturalist, and HMS *Sulphur* (1836–1842) with Edward Belcher as captain and Richard Hinds (1844–1845) as surgeon-naturalist. Belcher was also the captain of HMS *Samarang* when it visited northern Australia and many countries of the Indonesian Archipelago during 1843–1846. The surgeon naturalist was the gifted artist, Arthur Adams (1850), who edited and illustrated the zoology of the voyage. The molluscs were described by Adams and Reeve. Adams and his brother Henry published the three-volume *Genera of Recent Mollusca* (1853–1858).

Francis Blackwood, captain of HMS *Fly*, surveyed the Queensland coast during 1843–1845. Two noted naturalists, John MacGillivray and Joseph Jukes were on board. Jukes (1847) wrote the narrative in which Gray described six species and noted 'the collection contains several others, but would require more time than I can bestow on the subject'. The extensive collections were divided between the British Museum and Hugh Cuming. The fossils collected were described by Jukes (1847, 1850). This survey was continued by Captain Owen Stanley on HMS *Rattlesnake* in 1847 and 1848, with MacGillivray as naturalist, and Thomas Henry Huxley as assistant surgeon. Molluscs collected on the expedition were listed by Forbes (1851), and the shell collection was sent to Cuming by MacGillivray.

The United States Exploring Expedition of 1838–1842 under Charles Wilkes (1844–1874) arrived in Sydney in 1839. Fossils were described by James Dana, naturalist on board, and included specimens collected in the Wollongong district. The molluscan collections were described by August Addison Gould (1856).

No history of the discovery of molluscs would be complete without the mention of the dealers who were prepared to pay the 18th and 19th Century voyagers for their exotic finds and so stimulated many ordinary seamen and officers to make collections in the lands they visited.

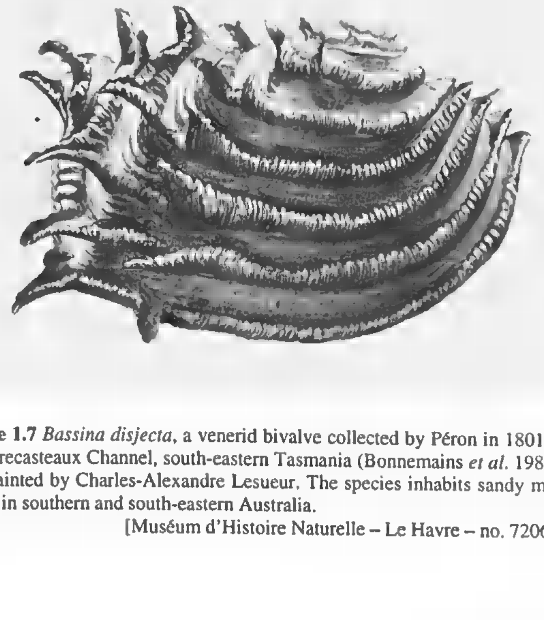


Figure 1.7 *Bassina disjecta*, a venerid bivalve collected by Péron in 1801 in D'Entrecasteaux Channel, south-eastern Tasmania (Bonnemains *et al.* 1988), and painted by Charles-Alexandre Lesueur. The species inhabits sandy mud banks in southern and south-eastern Australia.
[Muséum d'Histoire Naturelle – Le Havre – no. 72067]

Figure 1.8 George French Angas, Secretary to the Australian Museum from 1853 to 1861, published numerous papers on molluscs of Queensland and New South Wales. [Australian Museum]

Thomas Martyn bought the bulk of the shells from Cook's second and third voyages. His interest was partly trade, but more particularly he required new species to illustrate his very fine opus *The Universal Conchologist* issued between 1784 and 1789. George Humphrey bought shells collected on Cook's second voyage and also from many of the early colonists, including his son, Adolarius Humphrey, who was appointed mineralogist in 1803 to David Collins' expedition to found a colony in southern Australia.

Hugh Cuming, perhaps the greatest shell collector and dealer of all time, devoted his life to acquiring a magnificent worldwide collection. Initially, collecting was subsidiary to his business, but by the age of 35 he retired and devoted his time to acquiring and maintaining his collection. He travelled extensively, and paid collectors or bought specimens collected by voyagers. Although Cuming did not publish, his collection was made available to a number of leading conchologists and was the source of many of the exotic shells described by Lovell Reeve, the three generations of George Brettingham Sowerby and the Adams brothers.

All the early collecting of marine molluscs was carried out in shallow water, usually in the intertidal zone, except for some offshore dredging by the French scientists. The first deep-water sampling was undertaken by HMS *Challenger*, with Professor Charles Thomson (1880–1895) as director of scientific staff. In 1874, a number of dredge hauls were made to depths of 4680 m off the south-eastern coast of Australia, netting a large number of deep-water molluscs, many of them previously unknown. Later, 223 specimens of molluscs were recorded from hauls made off the tip of Cape York. The extensive mollusc collections were described in the Expedition Reports by Edgar Albert Smith (1885), Robert Boog Watson (1886), Alfred Cort Haddon (1866) and Paul Pelseneer (1888a, 1988b). Later collections in Torres Strait by Haddon in 1888 were described by James Comstock Melvill and Robert Standen in 1899.

Terrestrial Exploration

The crossing of the Blue Mountains in 1813 opened up the Western Plains for exploration. Allan Cunningham was one of several resident naturalists who systematically combed the settled region and extended his collecting to newly discovered territories. With John Oxley, the Surveyor General, Cunningham explored the Lachlan River in 1817 and between the Hunter River and the Darling Downs in 1827. Hugh Cuming received most of the specimens from Cunningham's fifteen years of collecting in Australia.

Charles Sturt collected Recent and fossil molluscs on his expeditions along the Macquarie and Darling Rivers in 1828, and down the Murray River to its mouth in 1829 to 1830. Described by James Sowerby, these specimens provided the first evidence of Tertiary rocks in Australia (Sturt 1833). Thomas Mitchell completed Sturt's work, collecting along the northern rivers which join the Darling, Lachlan, Murrumbidgee and Murray Rivers, and in western and north-eastern Victoria. Mitchell's invertebrate fossils including molluscs were sent to James Sowerby (Mitchell 1838).

Several European migrants to Australia in the first half of the 18th Century made valuable fossil and Recent collections. Paul de Strzelecki collected molluscan fossils through south-eastern Australia and Tasmania. His specimens were described by John Morris in Strzelecki's report (1845). Others of note were Ludwig Leichardt and John Lhotsky. Most of their specimens were sent to institutions or dealers in Europe.

One of the most important collectors in this category was Johan Preiss who reached the Swan River, Western Australia, in December 1828. He made extensive collections and also purchased material. His molluscan collection went to a German malacologist, Karl Theodor Menke in 1843.

Frederick Waterhouse, curator of the South Australian Museum, was a member of John Stuart's expedition that made a successful crossing of the continent from south to north in 1862. His collection of freshwater shells was described by Adams and Angas (1863).

Colonial Scientists

The next phase of malacology in the colony began in the 1820s and 1830s with the establishment of scientific societies, museums and libraries. While marine exploration and surveys after colonisation encompassed the entire Australian coastline, terrestrial exploration was initiated from the centre of settlement on the east coast and results were brought back to Sydney. Later, residents of the new settlements in Hobart, Melbourne and Adelaide supported their own scientific institutions. In the much smaller and more dispersed populations of Western Australia and Queensland this development was slower and later. In Sydney this phase coincided with the arrival of the Macleay family and the Reverend William Branwhite Clarke, author of over 180 scientific papers (Grainger 1892). He was commissioned by the government to make a geological exploration of the southern districts of the colony. Lacking comparative material, he sent Palaeozoic fossils to Sedgwick in 1844 and the upper Palaeozoic forms to Frederick McCoy.

Further collections were sent to Cambridge and were described by Professor Laurent de Koninck, in a two volume report in 1876–1877, translated by David, David & Dun (1898). The material was returned to Clarke, but was lost in the Garden Palace fire in Sydney in 1882.

Alexander Macleay and his family were very prominent in the establishment of the Linnean and Royal Societies and the Australian Museum (Stanbury 1987). William, Alexander's nephew, inherited the Macleay collection, expanded it and then donated it to the Sydney University in 1890. He mounted a major expedition to Torres Strait and New Guinea in the *Chevert* in 1875, with George Masters, John Brazier and William Petterd as naturalists. Brazier described and catalogued the gastropods (Iredale 1956).

Brazier took part in the earlier expeditions of HMS *Curacoa* in 1865, and the *Eclipse* expedition to the Great Barrier Reef in 1871. In the 1870s he sent many specimens for description to

George French Angas (Fig. 1.8) who named a number of species for him. Employed by the Australian Museum in 1880, later Brazier became the first official conchologist. Though retrenched in 1883, he continued to write, and had published over 150 papers by 1905 (Iredale 1956). After this he lost interest and sold most of his collection to Charles Hedley who gave it to the Australian Museum.

William Petterd, a Tasmanian scientist and boot importer, was a keen collector of natural history specimens and visited many parts of the eastern coast of Australia and New Guinea. He wrote 26 papers on molluscs including a *Monograph of the Land Snails of Tasmania* (Petterd 1879).

No discussion of New South Wales 19th Century scientists would be complete without reference to Macleay's contemporary, James Cox M.D. He made an extensive shell collection, sending specimens to the British Museum and latterly to Henry August Pilsbry. He published three major works on land snails (Cox, J.C. 1864, 1868, 1909), based largely on his own collection, and drawing on collections of others including John MacGillivray and George Masters.

Initially based in Melbourne, George Masters collected in Tasmania and sent insects to Macleay. He moved to Sydney in 1863, becoming a collector for Macleay and subsequently assistant curator and collector of the Australian Museum in 1864, travelling extensively throughout Australia. He was curator of the Macleay Museum from 1874 to 1912, and moved with the collections to the University of Sydney in 1890 (Ponder & Stansbury 1972).

Frederick McCoy was appointed Melbourne's first professor of natural history in 1847, soon after becoming palaeontologist to the Geological Survey of Victoria and Honorary Director of the newly established National Museum of Victoria. McCoy was an academic rather than an explorer. His writing included the unfinished *Prodromus of Palaeontology of Victoria* Volumes 1 to 7, 1876–1882 and the *Prodromus of Zoology* Volumes 1 to 12, 1878–1890. The first paper exclusively on Victorian Recent molluscs was published by the naturalist, Charles Maplestone (1872).

The Natural History Society of South Australia, formed in 1838, asked for donations of specimens for a museum. In 1856 the Museum was established (Stanbury 1987: 221) and the collections were built up by donations and purchases, the first being a large collection of molluscs. By 1863 the curator, Frederick Waterhouse, had recorded 2000 molluscan specimens (Hale 1956).

George French Angas (Figs 1.8, 1.9), son of George Fife Angas, can be called the 'Father of Australian Conchology'. He published over fifty papers on molluscs (Iredale 1959). He arrived in South Australia in 1843 and spent three years travelling with Sir George Grey, explorer and administrator, making sketches and recording natural history. In 1853 Angas was appointed Secretary to the Australian Museum where he remained until his retirement in 1861. During this time he collected in Queensland and in New South Wales, between Port Stephens and Jervis Bay. His collection was sold in 1869. Most type specimens are held by the British Museum, though those of many land shells are in the Hancock Museum, Newcastle-on-Tyne.

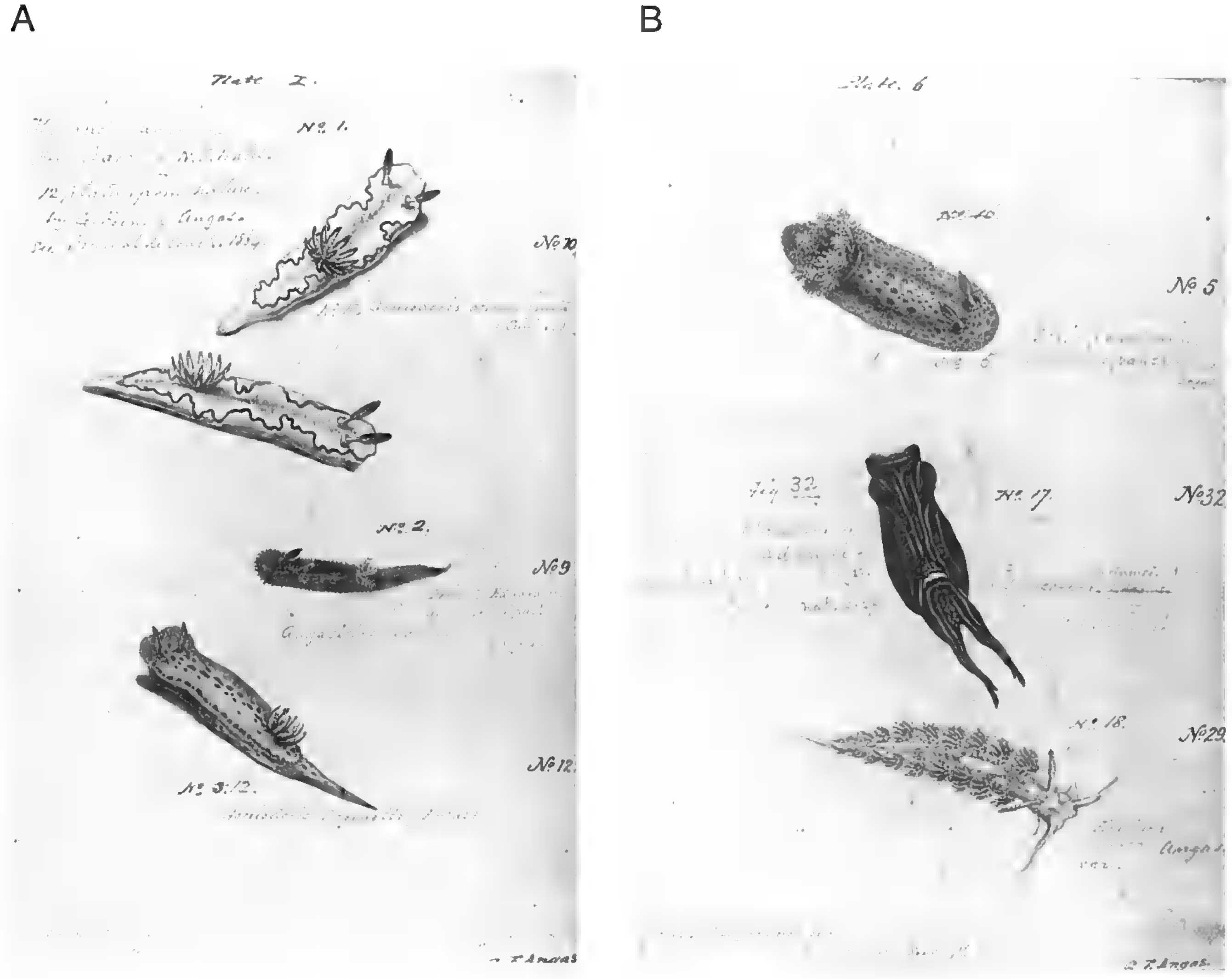


Figure 1.9 Two of 12 plates portraying the nudibranchs of Port Jackson, painted in watercolour and described by George French Angas. **A**, plate 2, including *Goniodoris atromarginata*, *Angasiella edwardsi* and *Goniodoris bennetti*. **B**, plate 6, showing *Doris pantherina*, *Chelidonura adamsii* and *Flabellina ornata*.
[Australian Museum]

Figure 1.10 Robert Etheridge Junior was palaeontologist to both the Geological Survey of New South Wales and the Australian Museum from 1887 to 1895, and subsequently Curator of the latter until 1920. He made a major contribution to knowledge of Australian stratigraphy, and showed clearly the significance of Australian fossil mollusc faunas in a global context. [Australian Museum]

The W. Michaelson and R. Hartmeyer expedition from the Hamburg Museum collected extensively in south-western Australia in 1905. The results were published in three volumes by Johannes Thiele (1911, 1930; Polyplacophora, Gastropoda, Bivalvia), Werner Meyer (1909; Cephalopoda) and William Hoffman (1930; Pulmonata). The material is held in the Humboldt University Museum, Berlin.

An Independent Science

The third phase of malacology in Australia began with the appointments of Ralph Tate to the foundation Elder Chair of Natural Sciences at Adelaide University in 1874 and Robert Etheridge Junior (Fig. 1.10) as palaeontologist to the New South Wales Geological Survey in 1887. Tate published numerous papers on both Recent and fossil molluscs, and described 225 of the 380 species in Harris' (1897) *Catalogue of Tertiary Mollusca in the Department of Geology British Museum.* Tate's fossil collection is in the University of Adelaide. He inspired other workers, such as John Dennant and Albert Kitson who compiled a catalogue of the Tertiary fossils of Australia (Dennant & Kitson 1903). Etheridge and Tate's work provided a fresh perspective on Australian fossil faunas, and 'freed Australian palaeontology from the bondage of Europe' (Vallence 1978).

Tasmania's first major resident conchologist and geologist was Julian Tenison Woods. Arriving in Tasmania in 1854, he wrote numerous papers on both the Recent and fossil Tasmanian molluscan faunas as well as those of Victoria, New South Wales and Queensland (Stephens 1890).

Other contributors to knowledge of Tasmanian molluscs were Robert Johnston, Government Statistician and Registrar-General, who published on Recent Mollusca (Anon 1919), William Legrand (1871), who wrote on land shells, and Mary Lodder, who issued a list of Tasmanian shells in 1900. Lodder was an enthusiastic naturalist; her collection and library were left to the Queen Victoria Museum, Launceston. She also contributed specimens to the Tasmanian Museum. William May collaborated with Tate on the *Revised Census of the Marine Mollusca of Tasmania* (Tate & May 1901). A competent artist, May illustrated his own papers, such as *The Illustrated Index of Tasmanian Shells* (May 1923). His collection is now in the South Australian Museum (Macphail & Zeidler 1977, 1978).

During William Bednall's curatorship at the South Australian Museum from 1886 to 1914, the conchological collections were enlarged by donations from many sources. Of special note were the Winnecki Collection of land shells from the Kimberley, Alligator Rivers and Fowler Bay districts, and the large collection made in 1906 by Amandus Zeitz and his son Frederick in the scrub areas of the Clarence and Richmond Rivers.

From 1900 the Museum's chief benefactor was Joseph Verco who enlarged the collections continually by his own dredging expeditions and by purchase of other collections which he donated to the Museum (Cotton 1933a). In 1894 he presented the Bednall Collection consisting of shells and other material collected by Police Inspector Pairt Foelsche.

One of the most important collections donated (in 1921) was that of Ralph Tate's land shells, including 25 type specimens. Verco purchased the Agnes F. Kenyon worldwide collection of cowries and cones, which included John Brazier's types, the Elijah Matthews collection of South Australian and Torres Strait shells, and the May Collection. He encouraged his friends, such as Edwin Ashby and William Torr, to donate their collections to the Museum. Ashby had written a number of papers on chitons (Iredale & Hull 1927a; Winckworth 1942) and Dr William Torr had collected in Europe and New Zealand as well as Australia and was the author of several papers (Iredale & Hull 1927a). After Verco's death, he arranged and edited his diary of collecting activities (Cotton 1935a).

On Bednall's retirement in 1914, Verco was appointed honorary Curator of Molluscs (Cotton 1933a). In 1923 Bernard Cotton was chosen as a cadet and in 1928 became assistant conchologist and photographer under Verco. Cotton was appointed Curator of Molluscs in 1934 after Verco's retirement. He was the author of numerous papers on South Australian molluscs (Laws & Mincham 1968), including the *Molluscs of South Australia* (Cotton & Godfrey 1940).

Robert Etheridge Junior (Fig. 1.10) returned to Australia in 1887 as palaeontologist to the Geological Survey of New South Wales and the Australian Museum. In 1895 he was appointed Curator of the Museum and its Director from 1917 to his retirement in 1920. Many of his 400 papers were important contributions on fossil molluscs (Dunn & Rainbow 1926), including a Monograph on the Cretaceous Mollusca of South Australia and the Northern Territory (Etheridge 1902a).

Charles Hedley, a self-taught naturalist of independent means, was appointed scientific assistant to the Australian Museum in 1881, conchologist in 1895 and assistant curator (Director) in 1908. His many papers on molluscs include those on material collected by the Shackleton Expedition (1907 to 1909) and the first Australian (1907 and 1914) Antarctic Expeditions (Iredale 1958). Hedley participated in the Royal Society of London Expedition to Funafuti in the Ellice Islands in 1896 (Hedley 1899a, 1899b, 1899c), the deep-sea trawling expedition of the *Thetis* in 1898 (1902, 1903), and in the MV *Endeavour* dredging expedition to the Great Australian Bight during August and September 1909 (Hedley 1911, 1914). After a distinguished career, he resigned from the Museum in 1924.

Tom Iredale (Fig. 1.11) succeeded Hedley as conchologist in 1924. Iredale published over 400 papers, including biographies of naturalists, studies in ecology and zoogeography, as well as taxonomy (Whitley 1972). His special interests were conchology and ornithology, but because of a wide knowledge of zoological literature, Iredale had a profound influence on the thinking of most of the taxonomic zoologists with whom he came in contact.

Joyce Allan was appointed 'girl sorter' to Charles Hedley in 1917. She became a permanent member of the staff of the Australian Museum in 1920 and was appointed conchologist when Iredale retired in 1944. She was a capable artist and illustrated papers for Hedley, Iredale, Whitley and others. She published a number of papers and two books on molluscs which she illustrated (Allan 1950, 1956; Whitley 1968).

Thomas Sargeant Hall, the first Australian-born palaeontologist, had studied under McCoy. He collaborated with George Pritchard in his studies of molluscs. Their study of Tertiary fossils led Pritchard to an interest in Recent marine species (Colliver 1947). In 1898 Pritchard published the first of a number of joint papers with John Gatliff, including a *Catalogue of Marine Molluscs of Victoria* in nine parts (Smith, B.J. & Black 1969). On his death the Gatliff collection and library were purchased by the Museum of Victoria.

John Gabriel's interests in natural history were encouraged by his father, Joseph Gabriel, and his interest in marine molluscs was fostered by Gatliff, with whom he collaborated in many publications. He published also on terrestrial molluscs, initially with Hedley (Macpherson 1963). Appointed the first honorary conchologist to the Museum in 1933 and an honorary member of staff until his death, he contributed many specimens to the collection, and all of his types after the appointment of a full time curator in 1945. On his death, Gabriel's large collection and library were left to the Museum.

Sydney Jackson, one of the last of the independent collector naturalists, accumulated large collections of bird eggs and land snails. Iredale (1937) was allowed access to the latter while working on the terrestrial molluscs and Jackson donated type specimens, designated by Iredale, to the Australian Museum. The remainder of the collection was purchased by the Museum of Victoria in 1946.

Frank Alexander Cudmore, naturalist and palaeontologist, made a very large and important collection of Australian Tertiary marine fossils which he donated to the Museum of Victoria in 1937. This collection incorporated that of T.S. Hall, and with those of the Museum and the Geology School of the University of Melbourne, formed the basis for Frederick Singleton's very significant publications on Tertiary molluscs.

Figure 1.11 Tom Iredale, conchologist at the Australian Museum from 1924 to 1944, published extensively in malacology and ornithology.
[Australian Museum]

As the 20th Century draws to a close, Australian malacology has developed and expanded into a wide variety of disciplines. Evidence of this progress is clear in the wealth of detail described for each class or subclass of the phylum, which comprises the bulk of this volume.

MORPHOLOGY AND PHYSIOLOGY OF THE MOLLUSCA

General Features

Members of the major classes of molluscs demonstrate a wide adaptive radiation within the scope of the anatomical and physiological limits set by each class pattern. Some forms are extremely well organised with a high level of nervous coordination. Two classes (Gastropoda, Bivalvia) have evolved features which allow colonisation of fresh waters, but only gastropods have emerged onto dry land. There is no marked correlation between the level of organisation and habitat: relatively primitive groups of gastropods include terrestrial members, whereas the wholly marine cephalopods have developed the most complex coordination and behaviour patterns.

Several morphological features characterise molluscs in general. All molluscs are non-segmented, that is, the body wall and its musculature are not divided into units arranged along the length of the body. Thus molluscs are quite distinct from the annelid worms and arthropods which have definitive patterns of metameric segmentation. However, the presence of a trochophore larva suggests that Annelida and Mollusca have a common ancestry. Metamerism is not evident at any developmental stage, except in the monoplacophorans. Whether the apparent metamerism seen in monoplacophorans is the primitive condition for the Mollusca or is a specialised secondary development has been the subject of much discussion (Wingstrand 1985; Ghiselin 1988; Scheltema, A.H. 1988; Salvini-Plawen 1990; Haszprunar 1996).

Molluscs are coelomate. A body cavity develops within the mesoderm – the middle primary layer – and separates the major organ systems from the body wall. Molluscs are also primarily bilaterally symmetrical, although their basic morphological systems are often highly modified.

The general structure of a mollusc typically includes a muscular foot associated with locomotion or attachment, an anterior head region carrying light-responsive, chemical and tactile sense organs, and a dorsal visceral mass in which most organs of the major functional body systems are housed.

The mantle is formed from extensions of the body wall, and cells capable of secreting a structurally rigid shell are usually present on its outer surface layer. The mantle usually forms a mantle cavity, a pouch which typically encloses the gills. It may also be a vestibule between the organism and its external environment, with apertures opening from the alimentary tract, excretory ducts, and in some instances the reproductive organs.

The shell, if present, may consist of one, two or eight units. It is usually calcified, and external, but it may be reduced or internal as a result of mantle overgrowth in many forms, or absent. The shell may be simple or coiled. Shell characters are often used in classification.

Typically gills form the respiratory structures, although these may be altered, reduced or lost, and their respiratory functions may be taken over by other structures. In some taxa, the gills perform secondary functions, such as the protection of eggs, feeding and removal of excretory products. The position and arrangement of the basic molluscan gills, or ctenidia, are diagnostic, and are major keys to the pattern of evolution within the phylum.

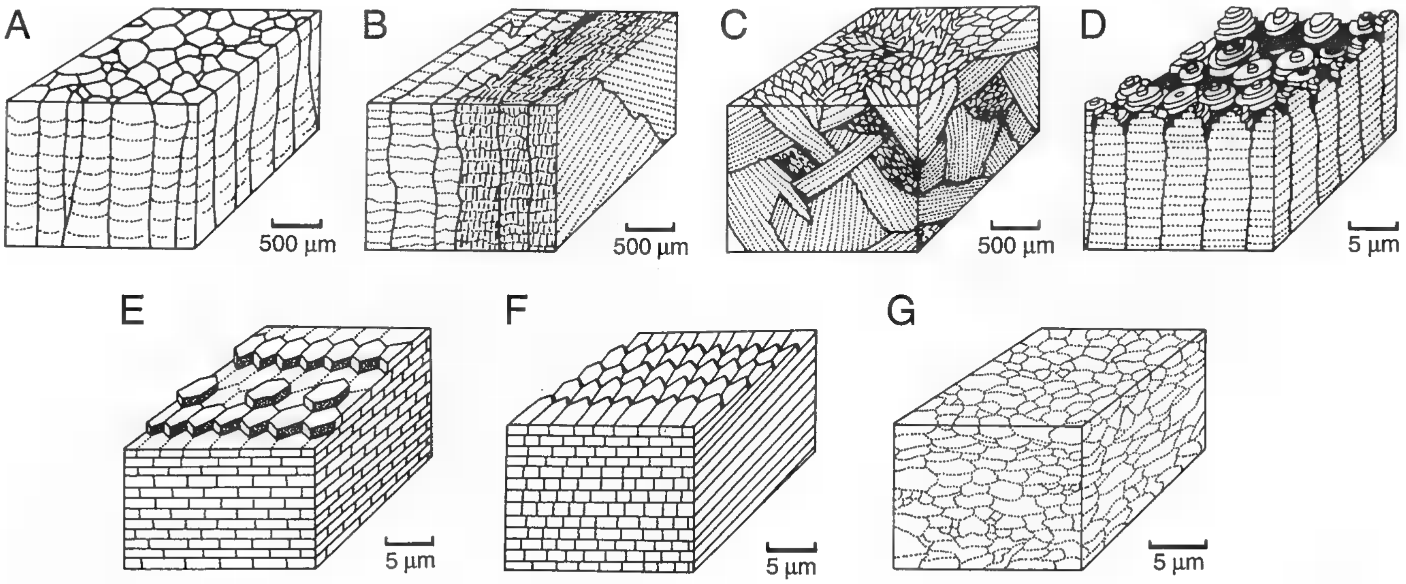


Figure 1.12 Microstructural arrangements in the molluscan shell, shown in the vertical faces of blocks cut through the shell. **A**, prismatic structure, comprising columnar calcitic or aragonitic crystals. **B**, crossed-lamellar structure, formed of non-aligned layers, each composed of similarly aligned aragonitic needles. **C**, complex crossed-lamellar structure, in which crystals of lamellae interdigitate strongly with those of other lamellae. **D**, columnar nacre, formed by tablet-shaped aragonite crystals arranged in columns. **E**, sheet nacre, comprising layers of tablet-shaped crystals which overlap like brickwork in overlapping sheets. **F**, foliated nacre, elongate overlapping calcite crystals forming lamellae. **G**, homogeneous structure, an integrated mass of small aragonitic crystals. (After Currey & Taylor 1974) [C. Eadie]

Molluscan hearts are well developed and typically consist of two auricles and a ventricle, an arrangement termed diotocardian. The monotocardian arrangement, in which one auricle is present, occurs only in some gastropods.

The digestive tract may be straight, U-shaped or coiled. Most taxa have a radula, which is a file-like ribbon of chitinous teeth used for rasping food.

The nervous system varies from simple to highly complex. Usually, it has cross connectives and at least three pairs of ganglia. The Mollusca demonstrate strong trends towards concentration of nerve clusters to form major ganglia. Well-developed sense organs, including eyes, statocysts and osphradia occur in most groups.

Fertilisation may be external or internal, sometimes with specialised organs for copulation and egg and sperm storage. Cleavage is spiral and unequal. All molluscs are triploblastic. The first larval stage for many forms is the trochophore, followed by the veliger. Some bivalves (Unionoidea) have a parasitic glochidium larva. Direct development occurs in some members of all groups and in all Cephalopoda.

There are many variations on this generalised pattern and the seven classes of the phylum (see classification section above for more detail) show the suite of adaptations that have evolved.

The Aplacophora include marine benthic forms with no shell, a reduced foot, and minute spicules scattered throughout the body wall. They are hermaphroditic or the sexes are separate. Some have a pair of ctenidia. Polyplacophorans have a shell of eight plates surrounded by a girdle, and six or more pairs of gills set in rows in the groove between the girdle and foot. The sexes are usually separate. They are marine, and most occur on rocks in shallow water. The Monoplacophora is a deep-water marine group with a single shell and several pairs of ctenidia. The sexes are separate.

In gastropods, the shell is often spiral and the head region is distinct; the visceral mass, usually protected by the shell, is typically rotated 180° relative to the main body axis, bringing the mantle cavity to the front from its normally posterior position. A pair of ctenidia represents the primitive state, but one or both of these may be lost. The sexes are separate or hermaphroditism occurs. Gastropods occur in terrestrial, freshwater, and both benthic and planktonic marine habitats.

Scaphopoda have a tubular, slightly curved shell open at both ends, lack gills, and are dioecious. They burrow in marine sediments.

The shell in the Bivalvia is composed of two lateral valves, symmetrical or nearly symmetrical, and hinged dorsally. The mantle forms two lateral chambers, and gills (ctenidia) are paired. A head and radula are lacking. Bivalves may be protandrous hermaphrodites or dioecious. They occur in marine and freshwater habitats.

The shell of the Cephalopoda may be external, internal or lost; the head and eyes are well developed. The eyes are complex with superficial similarities to vertebrate eyes. A chitinous beak or jaws, a siphon, and a foot divided into eight or 10 arms are present. Two to four pairs of ctenidia are present. Most of the nerve ganglia are grouped as a brain in a cartilage-like skull. Cephalopods are dioecious. All are marine.

Shell Structure

The molluscan shell is secreted by the outer surface of the mantle. It is constructed from crystals of calcium carbonate in the form of aragonite or calcite bound in a protein matrix of conchiolin, which constitutes about 5% by mass (Currey & Taylor 1974). The crystals are arranged in a number of distinct microstructures (Fig. 1.12).

In most molluscs the shell is arranged in three distinct layers: the periostracum or outer layer, the outer ostracum or prismatic layer, and the inner ostracum or nacreous layer. In the Polyplacophora this organisation is modified and the shell is formed from two different layers lying beneath the periostracum: the tegumentum, which contains both calcium carbonate and conchiolin, and the hypostracum/articulamentum which is entirely calcareous (Haas 1981). Molluscs of other classes may have reduced shells, but the structural components remain the same.

The periostracum is a thin protective sheet of quinone-tanned conchiolin secreted by the mantle edge (Hunt & Oates 1978). It is the first layer to be formed as the shell increases in size and juvenile shells often have a fragile, transparent margin of periostracum projecting beyond the ostracum. Old shells may lose this organic covering. Terrestrial pulmonates in particular display a variety of periostracal sculpture patterns including ribs, pustules and hairs. Some taxa lack the periostracum, for example, the Cypraeidae which have a vitreous shell, enveloped by mantle lobes when the animal is active.

The outer ostracum is also secreted by the edge of the mantle. It is composed of columnar prisms of calcite or aragonite packed together in a network of conchiolin. Material is added to the forward margin as the animal grows. Growth is not constant and each period of shell-forming activity results in growth lines, usually overlain by ostracal sculpture. In some groups the mantle is reflected onto the outer surface of the shell, where localised deposition of the prismatic layer forms a callus or rib.

The whole mantle surface is involved in the secretion of the inner ostracum. It is produced continuously and is the only part of the shell which can be repaired successfully if damaged. Like the outer ostracum, it is formed of calcite or aragonite crystals in a conchiolin matrix. The crystals are arranged in horizontal layers or laminae separated by sheets of protein. The shell lining may be porcellaneous if the laminae are thick and regular, or nacreous if they are thin and irregular. A particle or fragment lodged between the shell and mantle may become encased in nacre, forming a pearl. Commercial pearls are harvested from bivalves, mainly from tropical Indo-Pacific pearl oysters of the genus *Pinctada* (Pteriidae).

Materials for shell production are obtained through food and the immediate environment. As molluscs have no ability to concentrate calcium, levels in an animal's body tissues reflect ambient levels. The abundant calcium and carbonate in seawater allow marine shells to be large and ornate, whereas terrestrial and freshwater shells are frequently reduced, particularly in areas of high acidity.

Calcium ions may enter the mantle directly or via metabolic channels and the circulatory system, whereas carbonate is provided by the mantle and body fluids. These materials are released into the extrapallial fluid between mantle and shell, and are deposited onto the shell surface.

Shell formation begins during the larval stage of most molluscs, and a shell is nearly always present in the veliger larva. In bivalves, the shell begins as a single dorsal plate which folds in half and separates to become the characteristic umbones of the adult shell. Subsequent growth occurs along the forward and lateral margins of the shell, and can be divided into radial, transverse and tangential components. The radial component increases the overall size of the shell as material is added to the outer edge, and can be seen clearly as radial growth lines in most bivalves. Transverse growth occurs at right angles to the previous component and determines the curvature and separation of the valves. Tangential growth may occur in any direction parallel to and away from the umbones and determines the adult shape of the shell.

The larval shell of a gastropod is known as the protoconch and forms the apical whorl of the adult shell. This region can usually be distinguished from the later whorls by a difference in colour and surface sculpture. Asymmetrical growth about the central axis or columella and the overlapping of consecutive whorls result in the helical shape typical of most gastropods, although in many limpet-shaped forms conspicuous coiling is present only in the protoconch.

Musculature and Locomotion

The molluscan body is attached to its shell by muscles, which may vary in number from eight pairs in the Monoplacophora to a single muscle in many Gastropoda. These muscles are responsible for the withdrawal of the soft parts into the sanctuary of the shell, and are generally very powerful. Muscles leave a conspicuous 'scar' at their point of insertion on the inner ostracum, most easily seen in bivalves, limpets and other molluscs with simple shells. The shape and position of these scars can be a useful diagnostic tool.

The valves of a bivalve are held closed by the adductor muscles (Fig. 1.13A). Although these muscles are strong, they have little staying power, and continual antagonistic pressure, for example, from the tube feet of a starfish on the outside of the shell, can quickly fatigue them. In the smaller bivalves the adductor muscles can contract rapidly. The propulsive effect of ejected water as the valves slam shut is used as a means of locomotion by some non-attached epifaunal species, such as some scallops (Pectinidae) and members of the Limidae.

Infaunal bivalves use the muscular foot to burrow into the substratum. Hydrostatic pressure, combined with contraction of the paired pedal protractor muscles, causes the foot to extend. Simultaneous contraction of the adductor muscles pushes water out of the shell, loosening the sand and assisting the foot to push into the substratum. Increased hydrostatic pressure dilates the tissues of the foot, providing an anchor against which the anterior and posterior pedal retractors work, drawing the shell into the sand (Trueman 1966; Gould 1969; Tevesz 1975; Gilbert 1977). In some infaunal bivalves, one pair of pedal retractors contracts before the other pair, generating a rocking motion which facilitates burrowing. Repetition of this sequence enables the bivalve to descend a long way into the sand. Many of the boring bivalves use the edge of the shell in a similar manner to grind away a burrow in wood or stone. The animal returns to the surface by pushing against the anchored foot. Less commonly the animal pivots round and burrows upwards. A third method of locomotion employed by bivalves can be seen in the cockles (Cardioidea). When threatened, the cockle swiftly extends its foot, which is folded in the shell, and levers itself off the substratum in a leaping movement.

The body wall musculature of the shell-less aplacophorans comprises three muscle layers – an outer circular layer, an inner longitudinal layer and an oblique middle layer. One or more of these layers are absent in some taxa. Chaetoderm aplacophorans use hydrostatic pressure to move the head forward followed by contraction of the longitudinal muscles of the body wall (Scheltema, A.H., Tscherkassky & Kuzirian 1994).

The foot is the primary organ of locomotion in chitons (Fig. 1.13B), monoplacophorans and most gastropods (Fig. 1.13C), and is typically ciliated and covered in glandular cells. When moving across a hard substratum, direct or retrograde waves of contractions pass either forwards or backwards, respectively, along the length of the foot. At the crest of the wave, the foot is lifted from the substratum, then replaced a short distance ahead of its previous position. Movement is assisted by the secretion of mucus which reduces friction. Locomotory waves may extend for the whole width of the foot (monotaxy), or the foot may be divided longitudinally into two, with waves passing alternately along either side (ditaxy).

Gastropods which move over soft substrata often travel by ciliary propulsion. Those that burrow do so much in the manner of bivalves, and extend the foot through hydrostatic pressure, drawing the shell in by muscular contraction of the single columellar muscle. Scaphopods also use this method. Members of the Strombidae can leap like cockles, using the serrated operculum as a lever.

Heteropods and some opisthobranchs have adopted a free-swimming pelagic habit, their shells commensurately reduced in size or weight. The foot of a heteropod is laterally compressed to form a ventral fin, and the shell is thin and transparent. Heteropods swim upside down and actively pursue their planktonic prey near the water's surface. Thecosome and gymnosome opisthobranchs swim elegantly through the water, driven by the foot which is modified into a pair of expanded parapodia. The delicate nature of the parapodia and their fanciful resemblance to wings have led to the group's common name of 'sea-butterflies'. Other swimming opisthobranchs use similar parapodial folds, different specialised structures, or lateral or dorso-ventral undulations.

Cephalopods are highly organised and are the most active of all molluscs, adapted entirely for a swimming existence; some forms are secondarily sedentary. Most cephalopods move rapidly by suddenly contracting the mantle and expelling water through the siphon (Fig. 1.13D). Cuttlefish and squid are adept at this method of jet propulsion, and capable of both high speed and rapid changes of direction. The muscle fibres of the mantle are arranged in both radial and annular patterns (Ward & Wainwright 1972). When the annular fibres relax, the radial fibres contract, pulling the mantle edge tight against the head and forcing water out through the siphon. Octopods can also use this method of locomotion, but most frequently move across the substratum using their arms which are lined with adhesive suction discs. Some deep-water octopods have membranes between the arms which form a bell like that of a jellyfish, and motion is achieved by rhythmic contraction of the bell.

Feeding and Digestion

Molluscan diets are very diverse. Almost every available food source has been exploited and many different adaptations have developed taking the greatest advantage of those food sources. Some groups are fairly restricted in their diets, but many eat a wide range of animal and plant matter.

The morphology of the molluscan alimentary tract varies markedly between some classes. In general, a terminal or ventral mouth is present anteriorly and opens into the buccal cavity. In many classes the buccal cavity contains the odontophore or 'tongue' which is overlain by the radula, a flexible chitinous ribbon covered with numerous transverse rows of teeth. The number of teeth varies from very few to more than a hundred thousand. Food scraped up by the radula passes down the oesophagus to the stomach, sometimes via a crop. Once in the stomach, particles are sorted by ciliary action and eventually pass through the intestine to the anus.

Many polyplacophorans feed on encrusting algae. The mouth is anterior and ventral, and the buccal cavity is lined with chitin (Salvini-Plawen 1983). When feeding, chitons protrude the subradular organ on the ventral surface of the odontophore, and then protract the odontophore and radula (Fretter 1937). Salivary glands release a non-enzymatic lubricant, and the mucus and food mixture passes into the oesophagus. The oesophageal (or sugar) glands secrete amylase, which breaks down starch. Food passes into the crop, and thence to the stomach, where it is stirred by cilia and directed to the digestive diverticula, while cellulose-splitting enzymes are released from the digestive gland. Digestion is largely extracellular and takes place in the stomach and anterior intestine, the latter also being the site of absorption.

Gastropod feeding and digestion reflect the wide-ranging adaptive radiation in this group, which includes herbivores, carnivores, scavengers, ciliary-feeders and parasites (reviewed by Purchon 1977). Furthermore, some of the adaptive forms have arisen more than once in different groups within the Gastropoda.

The radula is always used in feeding, except in some opisthobranchs and caenogastropods, where it has been lost. Digestion is always at least partially extracellular, and the extracellular digestive enzymes are produced by salivary, oesophageal and digestive glands, singly or in combination. The stomach is the site of extracellular digestion, and the digestive gland the site of intracellular digestion, if any, and absorption. There are always some ciliary tracts for moving food through the gut.

The basic plan of each transverse row of a radula is a central, or rachidian, tooth flanked by lateral teeth and, in turn, by marginal teeth. Examples of five basic arrangements of radula teeth are shown in Figure 1.14. In groups of prosobranch gastropods, the arrangment of the radula has been used for classification, expressed as a formula. In such formulae, the central tooth, 'R', is flanked on each side by the number of lateral and marginal teeth; 'D' indicates the position of the largest lateral tooth. Formulae given by Fretter & Graham (1962) for the arrangements in Figure 1.14 are: docoglossate, 3 + D + 2 + R + 2 + D + 3; rhipidoglossate, many to 1 + 4 + R + 4 + 1 to many; taenioglossate, 3 + R + 3 or 2 + 1 + R + 1 + 2; rachiglossate, 1 + R + 1; toxoglossate, D + 0 + D or 1 + 0 + 0 + 0 + 1. The formula for the ptenoglossate radula is many + 0 + many.

A pattern of gut morphology suited to herbivory is considered the most primitive. In this pattern, the radula is constructed of a large number of very small, fairly uniform teeth, adapted for grazing. Primitively two lateral jaws are present, but in pulmonate snails the radula rasps against a median chitinised jaw on the upper lip.

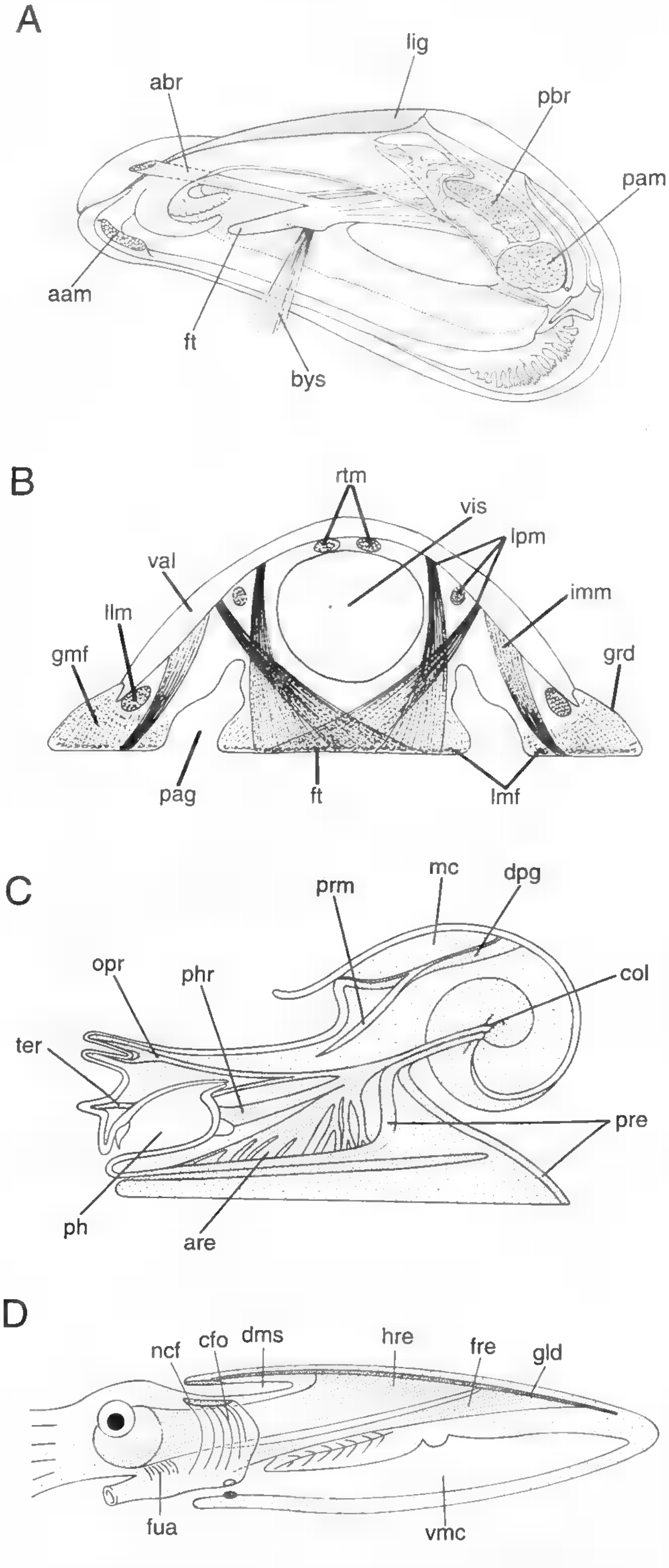


Figure 1.13 Pedal and shell musculature. **A**, view of *Xenostrobus*, (Bivalvia: Mytilidae), with right valve removed, to show musculature. **B**, muscular arrangement of a chiton sectioned through an intermediate valve. **C**, retractor muscle system of a typical pulmonate snail – the pharyngeal, optic and tentacular retractors act together to retract the head. **D**, mantle cavity and associated muscles in a squid. **aam**, anterior adductor muscle; **abr**, anterior byssal retractor muscle; **are**, anterior retractor muscle; **bys**, byssus; **cfo**, collar fold; **col**, columella; **dms**, dorsal mantle space; **dpg**, diaphragm; **fre**, funnel retractor; **ft**, foot; **fua**, funnel adductors; **gld**, gladius; **gmf**, girdle muscle fibres; **grd**, girdle; **hre**, head retractor; **imm**, inner mantle muscle; **lig**, ligament; **llm**, lateral longitudinal muscle; **lmf**, longitudinal muscle fibres in foot and girdle wall; **lpm**, latero-pedal muscles; **mc**, mantle cavity; **ncf**, nuchal cartilage; **opr**, optic retractor muscle; **pag**, pallial groove; **pam**, posterior adductor muscle; **pbr**, posterior byssal retractor muscle; **phr**, pharyngeal retractor; **ph**, pharynx; **pre**, posterior retractor muscle; **prm**, penial retractor; **rtm**, rectus muscles; **ter**, tentacular retractor muscle; **val**, valve; **vis**, visceral sinus; **vmc**, ventral mantle cavity. (A, after Wilson, B.R. 1967; C, after Solem 1974a; D, after Wells, F.E. 1988)
[A, R. Plant; B, P. Kaas; C, D, C. Eadie]

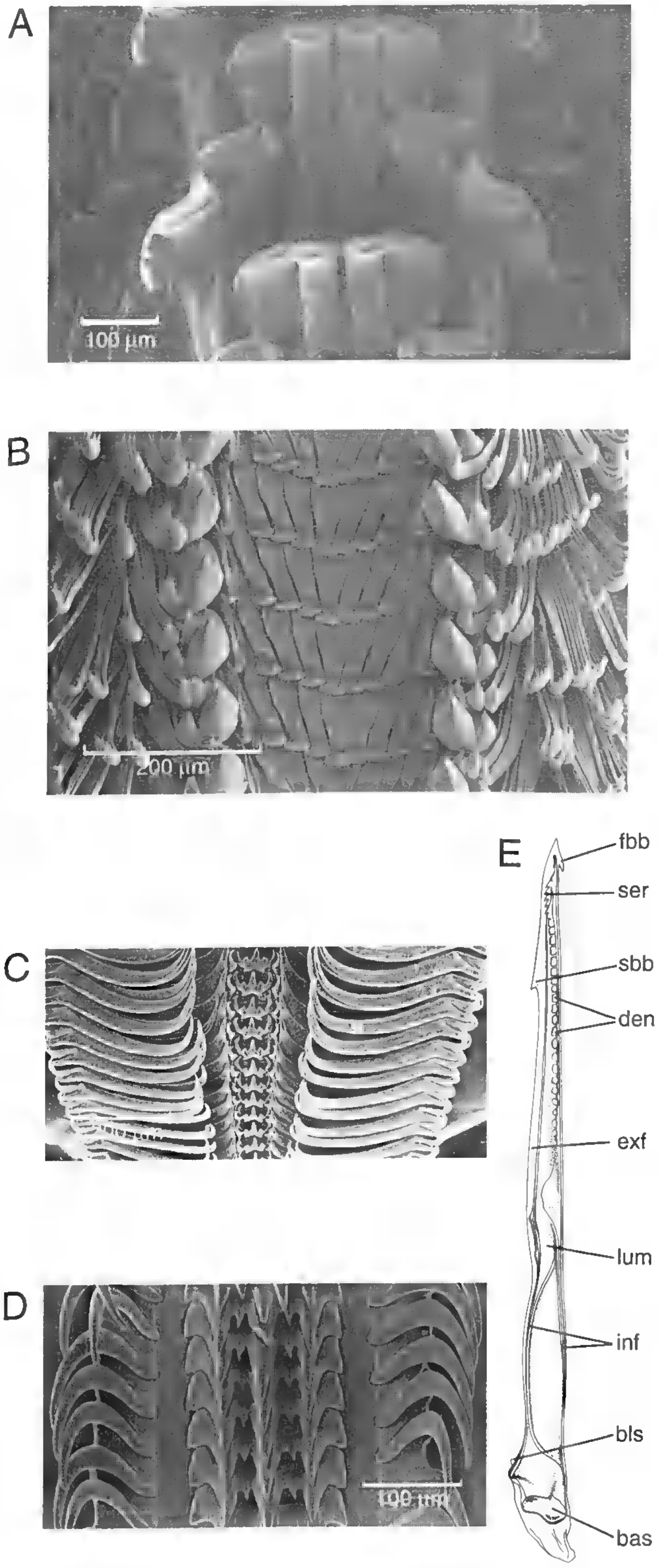


Figure 1.14 Gastropod radulae. **A**, limpets, such as *Scutellastra longicosta* (Patellidae), use the few robust, rasping teeth in each row of the docoglossate radula to feed on tough fucoid and encrusting algae. **B**, the central, smaller lateral and numerous fine marginal teeth in each row in the rhipidoglossate radula of the vetigastropod *Montfortula rugosa* are suited to algal grazing. **C**, the taenioglossate radula of *Oxygyrus keraudreni* (Atlantidae), comprising a large central, a pair of lateral and two pairs of marginal teeth, is used to rasp algae directly off the substratum. **D**, the rachiglossate radula of most neogastropods, as seen in the fasciolariid *Phos senticosus*, is formed of a large central tooth flanked by a pair of lateral teeth, and is suited to carnivory. **E**, as in other *Conus* species (Conidae), one large specialised tooth filled with venom forms half of each row of the toxoglossate radula of *Conus anemone*. **bas**, base; **bls**, basal spur; **den**, denticles; **exf**, external fold; **fbb**, first barb; **inf**, internal fold; **lum**, lumen; **sbb**, second barb; **ser**, serration.
[A, C. Hickman; B, D. Lindberg; C, L. Newman; D, G. Harasewych/Smithsonian Institution; E, R. Henderson/WA Museum]

In many herbivores the oesophagus is enlarged to form a crop, which, in the opisthobranchs, may include chitinous grinding plates and thus act as a gizzard (Howells 1942).

Enzymatic action commences in the crop in some species. A crystalline style and style sac are found in some neotaenioglossans and in all bivalves. The style is a flexible rod formed of a digestive amylase adsorbed onto the protein of the gelatinous matrix. It lies in the style sac with one end protruding towards the oesophageal end of the stomach. Ciliary action rotates the style, drawing food from the oesophagus and stirring the stomach contents. The stomach wall near the head of the style is protected by a chitinous gastric shield; the rest of the wall is thrown into folds and some of it acts as a ciliary sorting area. Large particles detached from the style are carried directly to the intestine, and finer particles are moved by ciliary action to the digestive diverticula.

The radulae of carnivorous gastropods typically have fewer, larger teeth than the herbivorous species, and the teeth are usually aculeate in shape. In the neotaenioglossan caenogastropods, however, there is little differentiation between the radulae of carnivorous and herbivorous species. Many predatory caenogastropods carry the radula on a protrusible proboscis formed by the invaginated snout.

Some carnivorous gastropods feed almost exclusively on bivalve molluscs. Many muricids and naticids use the radula to drill a small hole in the shell of their prey, through which the body tissues are extracted. Muricids evert a special gland (accessory boring organ) on the anterior margin of the foot and apply it to the area to be drilled. The proboscis of naticids bears a similar gland. The secretion in muricids is not acid, but is thought to be a calcium-chelating agent. Drilling and secretion alternate. Following drilling, the proboscis is inserted and the radula is used to break up tissue (Carriker 1961).

In some carnivores (not only molluscs), intermittent feeding has led to extensive crop development, often with a lining of plates, allowing food to be swallowed whole.

Ciliary-feeding is used by some gastropods, including the planktonic thecosomes (Opisthobranchia). A mucous gland on the mantle and ciliary currents on the parapodia enable thecosomes to trap foraminiferans, diatoms, and other small planktonic organisms (Yonge 1926). The oesophagus acts as a pump, and chitinous plates crush the protective shells (Morton, J.E. 1953). Other gastropods use the gill to filter suspended material (Orton 1914; Cook, P.M. 1949) and some vermetids feed with a mucous net (Morton, J.E. 1951).

Most land pulmonates are herbivores. The large crop is the site of extracellular digestion, including some breakdown of cellulose by crop bacteria. Some carnivorous pulmonates, which feed mainly on earthworms and other snails, possess large, sabre-like teeth used to shred soft-bodied prey. At least one species of the carnivorous Rhytididae may be secondarily herbivorous (Smith, B.J. 1979a).

Parasitism in various degrees has developed among the gastropods. The Pyramidellidae are ectoparasitic on various invertebrates, sucking the host's body fluids through a long proboscis, much in the manner of mosquitoes. Their main adaptations to a parasitic existence are the loss of the radula and the development of a buccal pump (Fretter & Graham 1949). The Eulimidae are ectoparasites and endoparasites on echinoderms. The extreme body modifications of some eulimids make systematic relationships difficult to determine. Some are so specialised that only the presence of the veliger stage and a late larval spiral shell identify them as gastropods at all.

Cephalopods are exclusively carnivorous, preying on fish, crustaceans and other marine invertebrates. Prey are caught in the arms, and, in decapods, also with the long, extendable tentacles. The tentacular suckers of some squid are armed with barbs or are produced into hooks. The food is transferred to the mouth which lies within the ring formed by the bases of the arms. Cephalopods have a parrot-like beak and a radula. One of two pairs of salivary glands opens into the buccal cavity and secretes mucus and digestive enzymes. The second opens behind the lower jaw and secretes a narcotising poison. The bite of some species of the blue-ringed octopus genus, *Hapalochlaena*, is known to be dangerous to humans (Sutherland, S.K. & Lane 1969). The pancreatic and hepatic sections of the digestive gland both produce enzymes. Digestion is extracellular and commences in the stomach. Food passes into the caecal sac where an elaborate series of ciliated folds sort and conduct the particles. Absorption takes place in the caecum walls and possibly in the intestine.

In the protobranch bivalves, which are predominantly detritus-feeders, the food is gathered mainly by the labial palps. There is a simple, ciliated sorting region and a faecal protostyle (Morton, J.E. 1953). Digestion is extracellular, the digestive gland having a purely secretory function (Owen 1956). Faeces are formed in the intestine and the exhalant current sweeps them from the anus to the exterior.

In filibranch and eulamellibranch bivalves, the respiratory gills have assumed a second role, that of gathering fine, planktonic food particles (Fig. 1.15C–E). The pattern of the ciliary beat moves channels of mucus towards the food grooves, which are variously positioned. Food is passed along the tracts towards the mouth, where the labial palps are involved in sorting rather than food gathering. Rejected particles are carried forward to the mantle edge and then back along the mantle edge to the area of the inhalant siphon, and are periodically ejected by closing of the valves (Atkins 1937a, 1937b). The stomach has a ciliated sorting area. A crystalline style is present and some extracellular digestion of carbohydrates takes place. Particles are then moved into the ducts of the digestive gland where protein digestion is intracellular. In many intertidal species the style is regenerated between tides (Nelson 1925).

Giant clams in the genus *Tridacna* (Tridacnidae) culture symbiotic zooxanthellae in the mantle tissue. Special crystalline vesicles in the mantle concentrate sunlight, increasing the potential for photosynthesis by the algae within them. Specialised blood cells engulf and digest some of the algae but clams may also derive nutrients from plankton and other suspended material. Zooxanthellae also occur in some nudibranch opisthobranchs.

Septibranch bivalves are predominantly carnivorous and scavenge. Water currents generated by movements of the muscular septum (Fig. 1.15C) bring organisms such as small crustaceans into the mouth, from which they pass to the crushing gizzard (Purchon 1956).

Scaphopods feed on microscopic organisms such as foraminiferans. Fine tentacles (captacula) with adhesive papillae extend into the substratum and bring back food to the mouth. A well-developed radula with flattened teeth is present. The intestine leads anteriorly from the stomach then turns laterally midway to open into the central mantle cavity. The digestive processes remain largely unknown (Morton, J.E. 1959).

Circulatory System

The circulatory system is simple. In many molluscs the heart, enclosed by the pericardium (haemocoel), circulates blood through the body tissues. The molluscan heart is well developed and is typically diotocardian in arrangement. The monotocardian arrangement is found in some gastropods only. Blood passes from the auricle(s) to the ventricle, and carries oxygen to the head, foot, mantle and visceral mass via anterior and posterior aortas. An auriculo-ventricular valve prevents backflow (Duval & Runham 1981). The main arteries branch into smaller arteries which ramify through the body tissue. As there are no true capillaries (except in the cephalopods), blood drains into lacunae and sinuses, eventually returning to the heart, probably assisted by movement of the foot. In some species at least, blood flow is controlled by muscular sphincters or ostioles (Carriker 1946). Cephalopods have a main median heart and two accessory branchial hearts, which maintain blood pressure in the ctenidia.

The heart is absent in a number of molluscs. Some small opisthobranchs circulate blood by contraction of the body wall or movement of the cerata (Evans, T.J. 1953), and scaphopods, lacking both a well-defined heart and defined blood vessels, move blood in a similar way.

Two respiratory pigments are found in molluscs – haemocyanin and haemoglobin. Both occur in solution; respiratory pigments are not carried in cells in molluscs. Haemocyanin, which is prevalent in cephalopods and gastropods, is a copper-containing protein, with a molecular weight of 300 000 to 8 900 000 Da (Ghiretti 1966). Each haemocyanin molecule is built of 180 subunits, which in turn comprise two copper atoms attached to the side chains of histidine amino acids (Wood, Salisbury & Bannister 1968). In terrestrial slugs, haemocyanin is synthesised in interstitial cells in the tentacular and subdermal connective tissue (Reger 1973).

Gastropods which live in poorly oxygenated environments often have the widespread, respiratory pigment, haemoglobin. It is particularly useful in oxygen concentrations of 1 to 7% (normal oxygen concentrations are approximately 7 to 15% in water and 18 to 20% in air). The buccal mass muscles often employ the haemoglobin-like myoglobin, which may store oxygen while the muscles are active. Some bivalves which live in muddy, poorly oxygenated substrata have haemoglobin in their blood, but otherwise no respiratory pigment is present. Oxygen diffuses into the blood across the lamellae of the ctenidia, providing adequately for the requirements of sedentary bivalves.

Excretion

The molluscan kidneys and associated excretory organs extract nitrogenous waste from the blood and expel it from the body. They lie within the coelom and communicate with the pericardial coelom through the renopericardial ducts. Kidneys may take a variety of forms, particularly in gastropods. In polyplacophorans, lower gastropods, bivalves and cephalopods the kidneys are paired. In more advanced gastropods, the right kidney may have become incorporated into the genital tract or has disappeared altogether.

Accessory renal organs include the pericardial glands. In many bivalves, these glands are attached to the auricular or pericardial wall, and in some they form the Keber's organs, which arise at the pericardium and penetrate the mantle tissues. The kidneys and pericardial glands of cephalopods are closely associated with the accessory hearts and the afferent branchial vessels.

The renal system initially forms an ultrafiltrate of the blood, virtually identical in composition to the blood but lacking proteins. Once mixed with secretions from the pericardial glands, it passes from the pericardium to the kidneys. Nitrogenous wastes are secreted into it, and biologically valuable substances such as glucose, amino acids and inorganic ions are selectively absorbed. Nitrogenous wastes are the breakdown products of proteins and nucleic acids. Metabolised amino acids form ammonia, which may either be excreted unchanged, or first synthesised to urea or uric acid. Nucleic acids (purines and pyrimidines) may be excreted as such or as uric acid, allantoin, urea, beta-amino acids or ammonia.

In freshwater molluscs the kidney retains most of the salts, and produces a hypotonic urine which is excreted almost continually. Up to 65% of the extracellular fluid is voided daily. Ammonia is either directly or partially converted to amines and urea, and released. Ammonia is highly toxic, but diffuses extremely rapidly in water, and is therefore a suitable excretory product for aquatic molluscs. Urea is also highly soluble and is less toxic. Animals which excrete ammonia and urea are termed ammonotelic and ureotelic, respectively.

Land molluscs must conserve water. In these, the kidney, not the pericardium, is the principal site of ultrafiltrate production. The primary and secondary ureters recover water, salts and other material, and differ in structure and function (Garner 1974). Resorption of water and ions occurs in the primary ureter, producing a hypotonic urine, and further water is removed in the secondary ureter. Land molluscs are uricotelic, that is, they

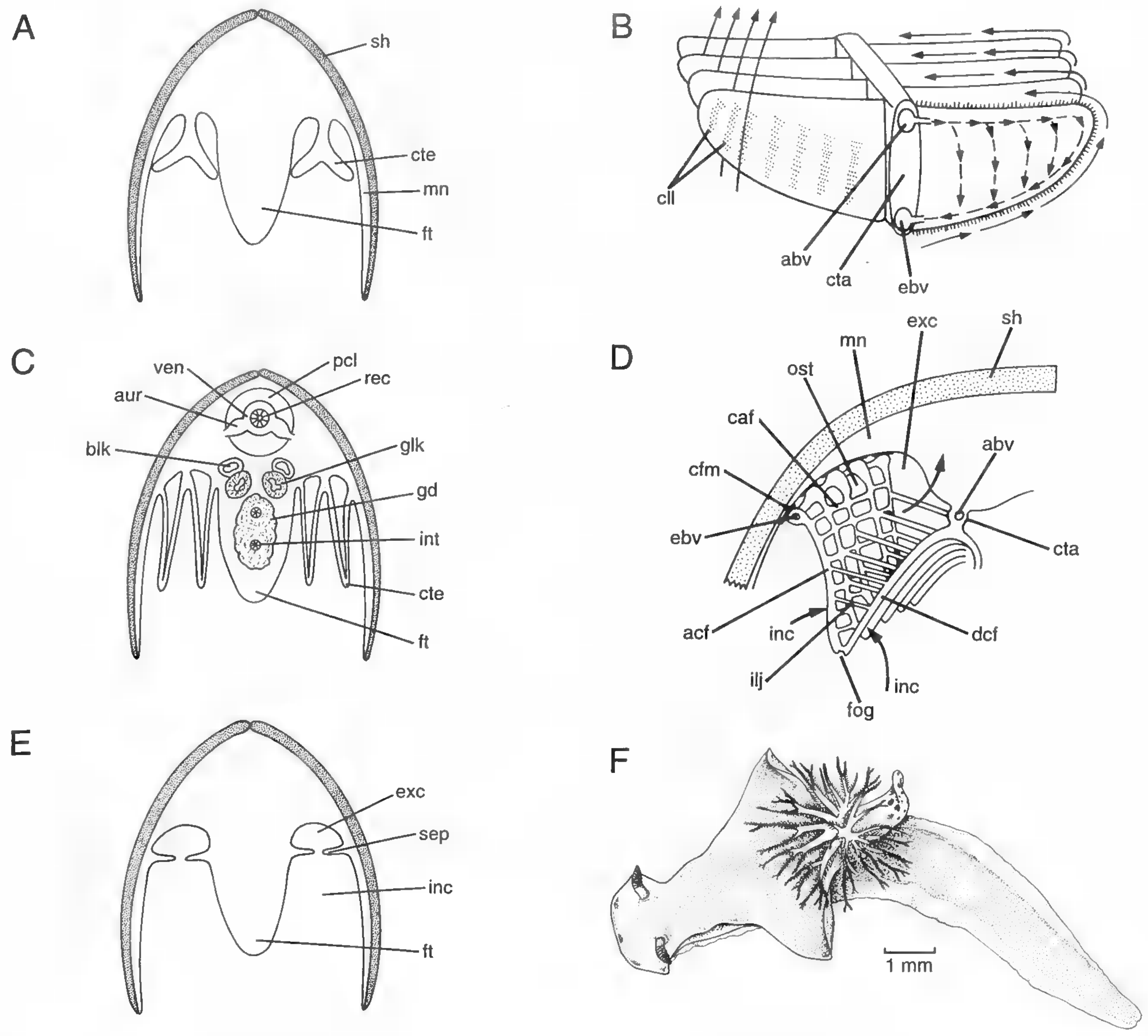


Figure 1.15 Some respiratory arrangements in molluscs. **A**, simple arrangement of the ctenidia in protobranch bivalves. **B**, true gill, or ctenidium, of a protobranch bivalve, showing its basic bipectinate form and alternation of gill leaflets, or filaments, on gill axis. **C**, W-shaped ctenidia in eulamellibranch bivalves, adapted to suspension-feeding. **D**, arrangement of gill filaments in eulamellibranch bivalve. **E**, modified ctenidia forming septa in the septibranch anomalodesmatan bivalves. **F**, the nudibranch *Ceratosoma trilobata* (Chromodorididae), showing secondary dorsal gill of cerata. **abv**, afferent branchial vessel; **acf**, ascending arm of ctenidial filament; **aur**, auricle; **blk**, bladder portion of kidney; **caf**, connection between adjacent filaments; **cfm**, connection of filament to mantle; **cll**, lateral cilia; **cta**, ctenidial axis; **cte**, ctenidium; **dcf**, descending arm of ctenidial filament; **ebv**, efferent branchial vessel; **exc**, exhalant chamber; **fog**, food groove; **ft**, foot; **gd**, gonad; **glk**, glandular portion of kidney; **ilj**, interlamellar junction; **inc**, inhalant chamber; **int**, intestine; **mn**, mantle; **ost**, ostium; **pcl**, pericardial coelom; **rec**, rectum; **sep**, muscular septum; **sh**, shell valve; **ven**, ventricle; large arrows indicate the direction of water flow; short arrows show cleansing ciliary currents. (A, C, E, after Barnes 1963; B, D, after Brusca & Brusca 1990) [A, C, E, C. Eadie; B, D, I. Hallam; F, S. Weidland]

excrete uric acid, which is virtually insoluble. Removal of water results in its precipitation in the kidney, where it is stored, sometimes for prolonged periods during hibernation or aestivation, and then periodically expelled. Selective resorption is also demonstrated for marine molluscs, and various substances may be conserved or excreted, depending on the requirements of the animal. Marine molluscs are usually in complete osmotic equilibrium with their environment, but have limited abilities to adjust the blood concentration to match higher or lower salinities.

Marine molluscs are ammonotelic. Cephalopods in particular excrete a great amount of ammonia, with associated amines, purines, urea and occasionally uric acid. The gills and digestive gland are also involved in the release of ammonia.

Respiration

Most molluscs are aquatic and all but two classes are wholly marine. The Bivalvia are confined to aquatic environments and only the Gastropoda have terrestrial members. Respiratory organs are commensurately conservative. Virtually all aquatic molluscs have ctenidia (Fig. 1.15). Almost all terrestrial gastropods have a diffusion lung, formed from the highly vascularised lining of the mantle cavity. There are exceptions to this. Aquatic pulmonates have lungs and a few semi-terrestrial caenogastropods have reduced ctenidia.

Ctenidia, the 'original' gills of molluscs, are protected within the mantle cavity. In some gastropods ctenidia have been lost and replaced by secondary gills. The surface of secondary gills may be folded repeatedly to increase the area over which diffusion may occur. Ctenidia may be regular in form, such as in bivalves (Fig. 1.15A) and cephalopods, or irregular, as in Monoplacophora. Chitons have from six to 70 pairs of gills, arranged in a single row on each side of the animal between the girdle and the foot. Water is drawn into the mantle cavity via the incurrent chamber between the girdle and gills, and passes out posteriorly through the excurrent chamber between the gills and the foot.

Few gastropods retain the primitively paired ctenidia in adult life. Some groups of vetigastropods, such as the Fissurellidae, have a pair of ctenidia. These are situated anteriorly, and the shell has become secondarily conical and bilaterally symmetrical, with the exhalant opening placed anteriorly as a groove or slit in fissurellids, but below a marginal row of holes in haliotids.

Among other more primitive gastropods, the true limpets (Patelligastropoda) have a conical shell. In the Lottiidae, the single ctenidium lies across the front of the animal. A secondary development of lateral gills has occurred in the Patellidae.

In other 'prosobranchs', the gills have either been reduced to a single unit or have undergone further reduction, and are simply respiratory filaments on one side only. The axis of the gill is attached to the body wall of the mantle cavity. In this situation, the water current is drawn in at one side of the head and the exhalant current leaves at the other side. In many taxa the anus opens near the exhalant current aperture.

Opisthobranchs do not have a ctenidium and demonstrate a variety of alternative gas exchange surfaces. Nudibranchs have secondary posterior gills surrounding the anus, or have cerata, which are lateral and/or dorsal projections. In many taxa, the cerata contain ramifications of the digestive gland and are not specifically respiratory in function. In most nudibranchs, in fact, gaseous exchange seems to occur all over the body surface (see Circulation and Respiration, Chapter 16).

Pulmonates successfully invaded the terrestrial habitat, developing specialised adaptations which free them from dependence on water. The floor of the vascularised pulmonary cavity is muscular and acts as a diaphragm: contraction causes active inspiration, the pneumostome closes and the diaphragm relaxes, causing air pressure to increase. Oxygen diffusion to the blood is thus facilitated.

Not all pulmonates are terrestrial. Many are aquatic, occurring in a range of freshwater to marine habitats. Air breathing is retained by some of these secondarily aquatic forms, and others have developed methods of extracting oxygen from water. Freshwater pulmonates, such as the Ancylidae and Planorbidae, have secondary gills, or pseudobranchs (Hubendick 1978).

Gill structure in bivalves is more conservative than that of gastropods. The gills of protobranchs are thought to represent the most primitive condition. They are small and bipectinate and function only in gas exchange. More elaborate structures, such those of bivalves with filibranch, pseudolamellibranch and eulamellibranch gills, function both in gas exchange and food collection. The gill filaments of these groups are much longer than those of the protobranchs and are reflexed in the middle. Each filament is doubled into a V (demibranch), each side of the gill axis. The ascending and descending limbs of the filaments are connected and held in place by supporting tissue. Tufts of cilia lock adjacent filaments together in filibranchs. In eulamellibranchs, the ciliary connections have been replaced by the fusion of tissue to form flat or corrugated sheets, and the interlamellar junctions divide the space between the lamellae into a series of tubes. The tips of the ascending limbs of the filaments are fused with the mantle, completely separating the inhalant and exhalant chambers.

Some respiration occurs across the mantle surface in all bivalves in addition to respiration across the gills. In septibranch bivalves, however, the gills no longer function as respiratory organs, but are modified to form a septum dividing the mantle cavity into separate inhalant and exhalant areas. Rhythmic movements of the highly muscular septum generates a respiratory current, and gas exchange occurs principally across the mantle.

Nervous System and Sense Organs

Molluscan nervous systems range from a very simple pattern of paired nerve cords and sparse ganglia innervating few muscles and sense organs, to the highly complex, cartilage-encased brains of cephalopods, which are capable of learning and rapid identification of prey.

The primitive nervous system of Polyplacophora may be similar to that of the earliest molluscs (Fig. 1.16A). The circum-oesophageal nerve ring forms two functional areas – the dorsal cerebral commissure and the ventral labial commissure. Buccal ganglia, connected to the labial commissure, innervate the odontophore, which has an intricate arrangement of muscles. Paired pallial nerve cords lie at the sides of the body, and paired pedal cords run along the foot. The nerve cords are connected by multiple cross commissures.

Polyplacophoran sense organs are unusual. Tactile organs on the snout and a subradular organ beneath the odontophore test the substratum for food. The plates of the shell and the girdle which protect the entire dorsal surface of the body are the primary sites of most of the sense organs. There are two types: large optical megalaesthetes and smaller, more numerous tactile micraesthetes. Megalaesthetes are light sensitive, and in some species have a lens, retina, optical pigments, and an elementary cuticular cornea. Clustered about them, the micraesthetes are epidermal papillae, sensitive to touch. There are no cephalic eyes.

Gastropods demonstrate a higher level of organisation. Nerve cells are clustered into several ganglia responsible for innervation of specific areas, such as the visceral mass, foot and gills (Fig. 1.16B). The visceral loop (formerly the pallial cords) becomes twisted as a result of torsion, so ganglia in this loop originally lying on the left are now situated on the right and vice versa. This condition is termed chiastoneury. As the complexity of the animals increases, the figure-of-eight arrangement becomes obscured and all ganglia are linked in a simple nerve ring.

Gastropods usually have at least one pair of cephalic tentacles, and in pulmonates there is often a second pair formed from extensions of the oral lappets. Cephalic tentacles are tactile, probably chemosensitive, and generally bear the eyes at their bases. In the slower-moving forms, the eyes are simple, but in the more active or predatory groups they are highly developed. Heteropods, which hunt in the surface waters of the oceans, have large eyes and find their prey solely by sight. Advanced pulmonates have eyes at the tips of the cephalic tentacles; the lower tentacles are tactile and chemosensory.

The osphradium is a chemoreceptor which tests water entering the mantle cavity. It is widespread among gastropods and may be a small area of cells or a large bipectinate gill-like organ, as in the Neogastropoda. Yonge (1947) suggested the osphradium may also function as a mechanoreceptor which senses the amount of sediment entering the mantle cavity.

In most Bivalvia the cerebral and pleural ganglia are fused and quite separate from the visceral ganglia. However, in some groups the cerebral ganglia have joined with the visceral ganglia to form a 'visceral brain'.

Bivalves have paired osphradia which are controlled by the cerebro-pleural ganglia. Some bivalves have concentrations of photoreceptors distally on the siphon, whereas others have sophisticated eyes. Individual eyes in the Arcidae are clustered together, and in many active forms, such as *Spondylus* species, eyes are on tentacles distributed along the edge of the mantle. The eyes in *Spondylus* and related genera are intricate, with retinal rods and cones, though they are incapable of producing sharp images.

The cephalopod nervous system is the most highly organised nervous system of any invertebrate (Fig. 1.16C). It is controlled by a brain, composed of several lobes, enclosed in a cartilaginous 'skull'. Cephalopods are active predators, and much of the nervous system is devoted to sensory organs and the coordination of locomotory muscles. Some cephalopods have giant nerve cords which radiate from the giant fibre lobe of the pleuro-visceral centre. They control the contractions of the mantle and are capable of very rapid transmission of impulses, resulting in quick movements.

The predatory cephalopods rely on sight to locate prey. In some respects, cephalopod eyes resemble those of vertebrates. The rigid lens is held in place by ciliary muscles and is focused by changing its distance from the retina. The iris controls the amount of light entering and has a slit-shaped pupil. It is unlikely that cephalopods form sharp images, but they seem to have the ability to determine vertical and horizontal movements and shapes. It is also thought that they have colour vision.

Reproduction

Many molluscs are dioecious, that is, the sexes are separate and remain either male or female throughout life. Others are hermaphrodites and may have female and male tracts which mature and are functional simultaneously, or may start life as one sex and change to the other as they grow older. Simultaneous hermaphroditism is widespread among the Heterobranchia.

Protandrous consecutive hermaphroditism is common in many groups. In this state, an animal begins life as a male and develops into a female. The best-known case is that of the slipper limpet *Crepidula fornicata* (Calyptraeidae), which forms chains of individuals. The animal at the base is a large mature female, and that at the summit is a small male. Those in between are in varying stages of hermaphroditism.

This form of protandry involves major reorganisation of the reproductive organs as those of the male are broken down and replaced with those of the female. It is markedly different from the protandry found among the higher Gastropoda, such as the Arionidae (Pulmonata) in which the male and female tracts become active consecutively, without any major structural changes (Parivar 1978).

Rhythmic consecutive hermaphroditism, in which there are repeated changes of gender, is uncommon. Some oysters (Ostreidae) change sex periodically, but the transformation of individuals is often out of phase, so males and females are always present in a population (Mackie 1984).

Parthenogenesis is also uncommon, but it is well documented in the freshwater hydrobiid *Potamopyrgus antipodarum*, in which males are rare (Wallace, C. 1978), Thiaridae (Jacob 1957) and the European arionid slug *Deroceras laeve* (Nicklas & Hoffman 1981).

Reproduction in the Aplacophora and Monoplacophora is little known. Sexes are generally separate, with paired, but usually fused gonads. In the Aplacophora, the gametes pass through the pericardium and pericardial ducts to the exterior. Some forms have

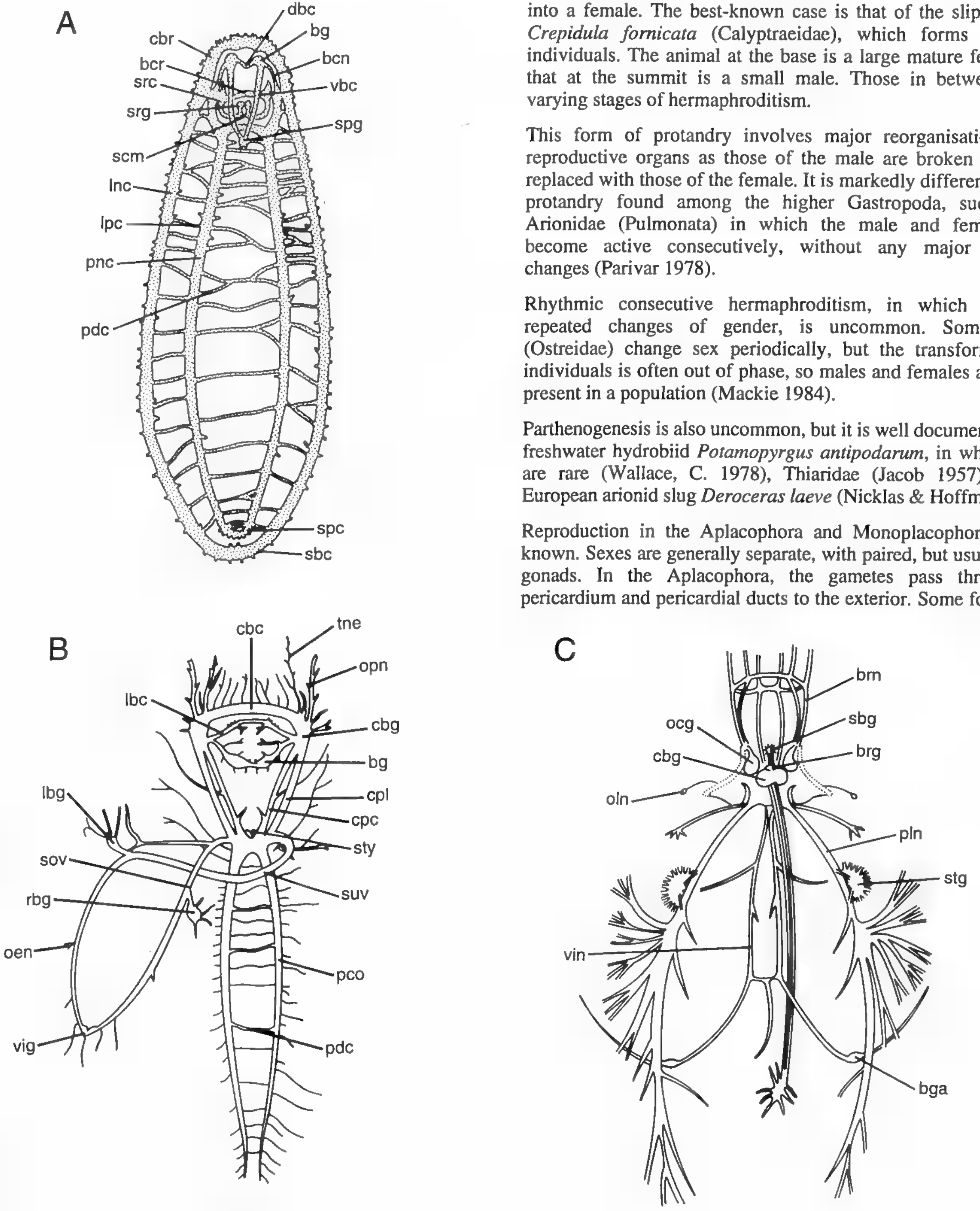


Figure 1.16 Molluscan nervous systems. **A**, a chiton, *Lepidochitona monterosatoi* (Lepidochitonidae). **B**, a vetigastropod, *Haliotis tuberculata* (Haliotidae). C, a coleoid cephalopod, *Sepia* species (Sepiidae). **bcn**, buccal connective; **bcr**, buccal part of cerebrobuccal ring; **bg**, buccal ganglion; **bga**, branchial ganglion; **brg**, brachial ganglion; **brn**, brachial nerves; **cbc**, cerebral commissure; **cbg**, cerebral ganglion; **cbr**, cerebrobuccal ring; **cpc**, cerebropedal connective; **cpl**, cerebropleural connective; **dbc**, dorsal buccal commissure; **lbc**, labial commissure; **lbg**, left branchial ganglion; **lnc**, lateral nerve cord; **lpc**, latero-pedal commissure; **ocg**, optic ganglion; **oen**, oesophageal nerve; **oln**, olfactory nerve; **opn**, optic nerve; **pco**, pedal nerve cord; **pdc**, pedal commissure; **pln**, pallial nerve; **pnc**, pedal nerve cord; **rbg**, right branchial ganglion; **sbc**, subrectal commissure; **sbg**, superior buccal ganglion; **scm**, subradular commissure; **sov**, suboesophageal part of the visceral loop; **spc**, suprarectal commissure; **spg**, supraradular ganglion; **src**, subradular connective; **srg**, subradular ganglion; **stg**, stellate ganglion; **sty**, statocyst; **suv**, supra-oesophageal part of visceral loop; **tne**, tentacular nerve; **vbc**, ventral buccal commissure; **vig**, visceral ganglion; **vin**, visceral nerve. (A, after Eernisse & Reynolds 1994, modified from Gantner 1987; B, after Fretter & Graham 1962; C, after Barnes 1963) [A, C. Eadie; B, C, I. Hallam]

seminal receptacles and copulatory stylets. Monoplacophorans have lobed gonads which lie ventrally in the peri-intestinal blood sinus. They have two pairs of short gonoducts through which the reproductive products travel before being expelled via the excretory pores. There are no copulatory organs.

Most Polyplacophora are dioecious, although at least two species of American *Lepidochitona* are hermaphrodites (Eernisse 1984). A single median gonad lies in the anterior of the pericardial cavity. The gonoducts open directly to the exterior, in the pallial grooves in front of the nephridiopores. There are no copulatory organs and fertilisation is external. Eggs are released into the sea, though in a few taxa they are brooded in the mantle cavity. Chiton eggs are rich in yolk and are surrounded by a thick outer layer or chorion, which is sculptured. Work by Eernisse (1984) indicates that the patterns of ornamentation of the eggs are constant within species, and thus are useful taxonomic features.

The gastropods exhibit a wide range of reproductive strategies. 'Prosobranch' gastropods are predominantly dioecious. In the most primitive forms (Patellogastropoda, Vetigastropoda) the reproductive tracts are simple and the differences between the male and female systems are minimal. Gametes pass down a gonoduct to the functional right kidney, and are then shed through the nephridopore. Fertilisation is external.

More complex arrangements exist in the neritopsines and caenogastropods, which include specialisation of the female tract to receive and store sperm, and the development of an intromittent organ in the male.

The structure of fertile euspermatozoa, also termed eupyrene or 'typical' sperm, varies widely in molluscs. The simplest form is that of ect-aquasperm, typical of groups with external fertilisation, such as the chaetoderms (Aplacophora), monoplacophorans, chitons, scaphopods and bivalves. Within the Gastropoda, patellogastropods and most vetigastropods also have ect-aquasperm (Fig. 1.17A–C). Such ect-aquasperm have similar basic ultrastructural features – a short head, comprising a conical acrosome (small and spherical in most chitons) and a compact nucleus, a midpiece formed of four or five (sometimes more) mitochondria usually arranged in a ring around two centrioles and a tail or flagellum. The latter consists of the axoneme sheathed by the cell membrane and continuous with the distal centriole (Fig. 1.17A). Modified euspermatozoa, associated with internal fertilisation or fertilisation within the mantle cavity, are found in some vetigastropods, all caenogastropods and heterobranch gastropods, neomenioid aplacophorans and cephalopods (Fig. 1.17A–I; Healy 1988, 1996; Buckland-Nicks 1995; Healy, Schaefer & Haszprunar 1995).

Studies of the ultrastructure of molluscan spermatozoa are providing useful data for taxonomic and phylogenetic analysis, even within groups with ect-aquasperm. For example, within the Gastropoda, euspermatozoa of patellogastropods (Fig. 1.17B) differ from those of vetigastropods (Fig. 1.17A) in acrosomal features and the lack of an indentation in the nuclear apex. A suite of autapomorphic features of neritopsine euspermatozoa (Fig. 1.17C) suggests that Neritopsina is an ancient lineage well separated from other gastropods. Within the Neotaenioglossa, the Cerithoidea, Ampullarioidea and Cyclophoroidea are distinguished by, amongst other features, the lack of an accessory membrane or apical bleb in the acrosome (Fig. 1.17D). The euspermatozoa of other neotaenioglossan orders have these features as do those of all neogastropods (Fig. 1.17E). The helical nucleus, or keels on the nucleus, together with other features, are characteristic of heterobranch euspermatozoa (Fig. 1.17F). The presence of multiple acrosomal vesicles in the palaeoheterodont bivalve orders Trigonoidea and Unionoidea (*cf.* Fig. 7.5) is strong evidence for a close relationship, and the posterior position of the acrosome in anomalodesmatan bivalves is unique (Fig. 1.17G). The euspermatozoa of nautiloid cephalopods are quite different from those of coleoid cephalopods, as are those of decapods and octopods (Fig. 1.17H, I) within the Coleoidea (Healy 1988, 1996; Healy *et al.* 1995).

In addition to the fertile euspermatozoa, many groups of 'prosobranchs' produce another type of spermatozoan within the testes. Like the euspermatozoa, these paraspermatozoa (dispyrene or so-called 'atypical' sperm) (Fig. 1.17J–R) are produced in considerable numbers. They differ from the latter in the amount of contained nuclear material, which may be less (oligopyrene) or more (hyperpyrene) than that of euspermatozoa, or lacking entirely (apyrene). Usually they have numerous dense vesicles and often several axonemes – the latter sometimes projecting posteriorly as multiple flagella – (Webber 1977; Healy & Jamieson 1981; Buckland-Nicks, Williams, Chia & Fontaine 1982; Giusti & Selmi 1982; Dohmen 1983; Healy 1986a, 1986b, 1988, 1996).

Although sperm dimorphism occurs in other groups of invertebrates, notably insects, chilopods, symphylans, rotifers and some tubificid oligochaetes (see Wirth 1984; Jamieson 1991), the phenomenon in molluscs is essentially limited to 'prosobranchs'. In certain aphallic groups of caenogastropods, paraspermatozoa may be very large – sometimes over 1 mm in length – and bear numerous euspermatozoa attached via their acrosomes or embedded deeply in the posterior region of the cell (Fig. 1.17Q, R; Ankel 1930; Bülnheim 1968). This motile combination of sperm types, termed a spermatozeugma, could be viewed as fulfilling both a spermatophoral and penial function, and ensuring that euspermatozoa are successfully deposited within the female reproductive system (for discussion see Healy & Jamieson 1981). Of the various functions that have been ascribed to paraspermatozoa, the most likely general purpose of these cells is some role in nourishment or stimulation of euspermatozoa prior to fertilisation (see Healy 1988). The value of paraspermatozoan structure in understanding systematic relationships within orders is becoming increasingly apparent (Healy 1988).

Hermaphroditism is widespread in Opisthobranchia. Sperm and ova develop in the ovotestis, and pass down functionally separate parts of the reproductive tract. Allosperm received during copulation are held in the bursa copulatrix and then transferred to the seminal receptacle. Ova are fertilised in a special chamber, from whence they move along the female gonoduct, receiving albumen and protective coating from the albumen and mucous glands respectively.

Autosperm are produced in the ovotestis and stored in the ampulla prior to copulation. In the primitive opisthobranchs, sperm are transported along an external ciliated groove to the penis, but in more advanced forms the groove is enclosed to form the vas deferens.

Pulmonate gastropods are also hermaphrodites. The Ellobiidae exhibit the most primitive reproductive tract morphology. Morton, J.E. (1955) believed this family to be close to the point of divergence of the three gastropod subclasses. The genus *Pythia* (Ellobiidae) stands out among the pulmonates in having an external ciliated seminal groove, similar to that of many opisthobranchs, along which sperm pass to the vas deferens and finally to the penis. In all other pulmonates the vas deferens is tubular (Morton, J.E. 1955).

The reproductive system of pulmonates differs from that of 'prosobranchs' in four major features: all forms are hermaphroditic, the albumen gland is separate from the reproductive tract, the bursa copulatrix has an elongate duct, and the penis is retractile (Morton, J.E. 1955).

Bivalves are generally dioecious, although many are hermaphrodites and some are protandrous. The paired gonads enclose the loops of the intestine and the gonoducts primitively open into the nephridia. In the more advanced forms they open directly to the mantle cavity, although the gonopore remains close to the nephridiopore.

The hermaphroditic bivalves include shipworms (Teredinidae), oysters (Ostreidae), scallops (Pectinidae) and freshwater pea-shell mussels (Sphaeriidae). Some oysters show rhythmic consecutive hermaphroditism.

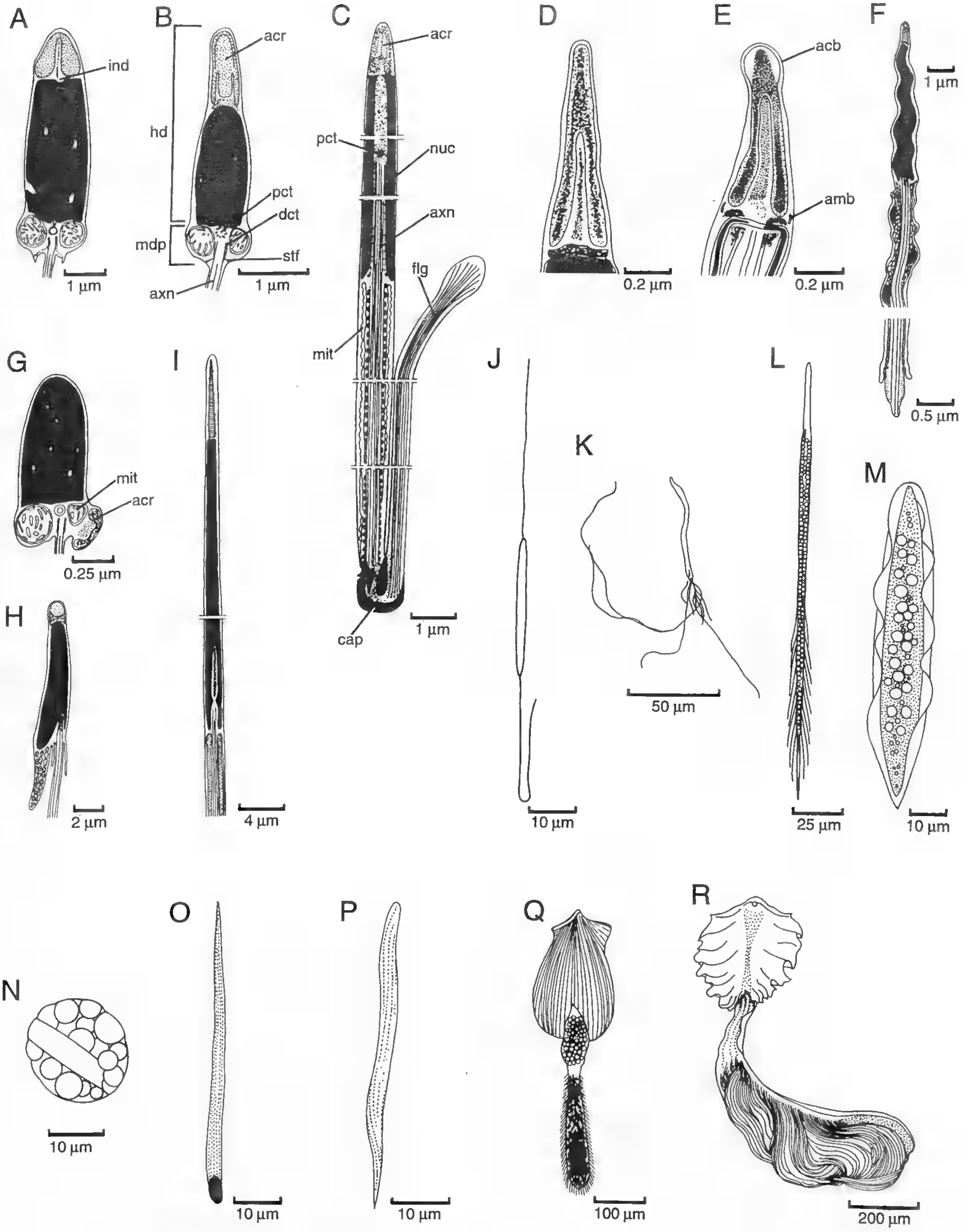


Figure 1.17 The structure of euspermatozoa and paraspermatozoa from a range of molluscan taxa. A–I, euspermatozoa. A, B, F–I, head and midpiece only. D, E, acrosomes. J–R, paraspermatozoa. A, *Perotrochus westralis* (Pleurotomariidae, Vetigastropoda). B, *Cellana tramoserica* (Nacellidae, Patellogastropoda). C, *Theodoxus fluviatilis* (Neritidae, Neritopsina). D, generalised acrosome of Cerithoidea, Neotaeniglossa. E, acrosome of *Eucithara arenivaga* (Turridae, Neogastropoda). F, *Chromodoris annae* (Nudibranchia, Heterobranchia). G, *Myochama australis* (Myochamidae, Anomalodesmata). H, *Loligo* sp. (Loliginidae, Coleoida). I, *Octopus* sp. (Octopodidae, Coleoida). J, *Nerita albicilla* (Neritidae, Neritopsina). K, Cochlostomatidae, Cyclophoroidea. L, *Diala varia* (Dialidae, Cerithoidea). M, *Strombus luhuanus* (Strombidae, Stromboidea). N, *Littoraria philippiana* (Littorinidae, Littorinoidea). O, generalised vermiform neotaenioglossan paraspermatozoa, as in *Cypraea moneta* (Cypraeidae, Cypraeoidea). P, generalised neogastropod paraspermatozoa, as in Terebridae (Conoidea). Q, spermatozeugma of *Janthina balteata* bearing numerous euspermatozoa on its tail (Janthinidae, Janthinoidea). R, spermatozeugma of *Cerithiopsis tubercularis* with longitudinal rows of euspermatozoa on the tail (Cerithiopsidae, Triphoroidea). **acb**, acrosomal bleb; **acr**, acrosome; **amb**, accessory membrane; **axn**, axoneme; **cap**, cap-like structure; **dct**, distal centriole; **flg**, flagellum; **hd**, head; **ind**, indentation; **mdp**, midpiece; **mit**, mitochondrion; **nuc**, nucleus; **pct**, proximal centriole; **stf**, satellite fibre. (A, B, F, G–I, after Healy 1996; C, after Selmi & Giusti 1983; D, E, K, P, after Healy 1988; J, M, O, Q, after Nishiwaki 1964; L, after Tochimoto 1967; N, after Reid 1986; R, after Fretter & Graham 1962) [R. Plant]

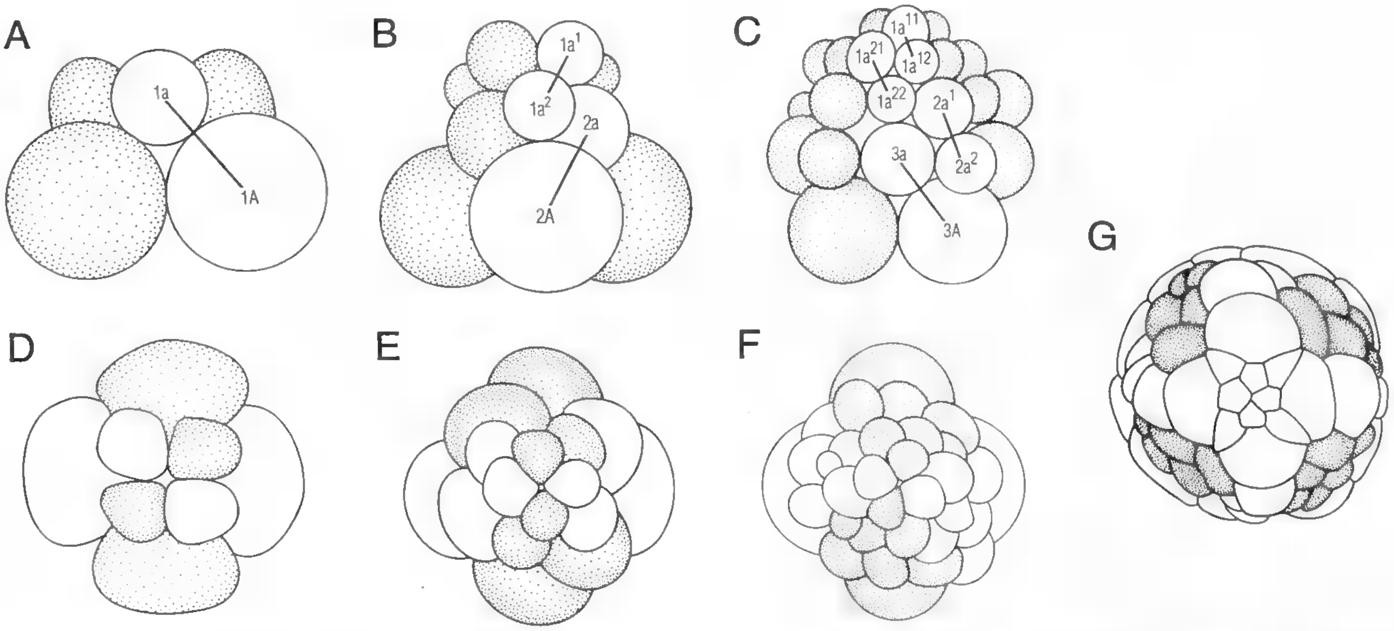


Figure 1.18 Spiral cleavage of the fertilised egg. Cells formed in successive divisions are coded for macromere 1A and micromere 1a only, according to E. Wilson's (1898) convention; cells derived from macromeres 1B and 1D and micromeres 1b and 1d are stippled; lines indicate the spiral orientation of the mitotic spindle during cleavage. A–C, lateral view. D–F, view of animal pole. A, D, unequal horizontal division of four-celled egg into four macromeres 1A–1D at the vegetal pole and four offset micromeres 1a–1d at the animal pole. B, E, division of macromeres 1A–1D to form second quartets of macromeres 2A–2D and micromeres 2a–2d, and division of micromeres 1a–1d to form daughters $1a^1$ and $1a^2$ through $1d^1$ and $1d^2$. C, F, division of macromeres 2A–2D to form quartets 3A–3D and 3a–3d, division of micromeres $1a^1$ through $1d^2$ to form $1a^{11}$ and $1a^{12}$ through $1d^{12}$ and $1d^{22}$, and division of 2a–2d to form $2a^1$ and $2a^2$ through $2d^1$ and $2d^2$. G, the cross characteristic of molluscan embryos is formed at the animal pole. (A–G, after Barnes 1963) [C. Eadie]

Cephalopods are almost exclusively dioecious. In both sexes, there is a single gonad, which lies at the posterior of the visceral mass, and in the male a spermatophore sac, termed Needham's sac, which opens into the left side of the mantle cavity. Copulation is generally complex and may follow ritualised combat between males. Many, such as the cuttlefish (Sepiidae), engage in displays of colour patterns, which serve to identify males to the females. Male cephalopods use a modified arm (hectocotylus) to place the spermatophore in the mantle cavity of the female. Fertilisation thus takes place in the mantle cavity.

Cephalopod eggs are laid in strings of gelatinous capsules, in clusters or on stalks. Some squid lay communal masses of eggs. Octopods frequently care for their eggs, clearing away sand and other debris that might settle on them. The shell of paper nautilus, *Argonauta* species, is a fragile calcareous brood chamber secreted by modified arms of the female.

Embryology

Following fertilisation the egg begins to divide synchronously in a process known as cleavage. With each division cells diminish in size, and the egg's cytoplasm is redistributed into two-dimensional morphogenetically active cell sheets. The pattern of cleavage is affected by the amount of stored yolk. In the eggs of molluscs, cleavage is regular (Fig. 1.18), as in most other animals, and takes place obliquely to form spiral cleavage planes at an angle of 60°. This pattern is characteristic of protostome phyla, such as the Annelida, Sipuncula, Echiura, Nemertea and Arthropoda.

The first division is perpendicular to the equator or slightly oblique, passing through the animal-vegetal poles. The second division is set at right angles to the first, and is also oblique. Two of the resulting four blastomeres are in contact at the animal pole, and the other two meet at the vegetal pole.

The third cleavage is also perpendicular and oblique, and separates the animal and vegetal hemispheres. The division is usually unequal; the small cells of the animal hemisphere are called micromeres, and the larger vegetal cells are called macromeres (Fig. 1.18). The micromeres are rotated with respect to the macromeres, either clockwise (dexiotropic cleavage) or counterclockwise (leiotropic cleavage).

The cleavage planes generally alternate at each division, until the hollow blastula stage is reached. Micromeres produce only further micromeres, and macromeres continue to divide unevenly, and generate both macromeres and micromeres.

The first larval stage of the most primitive molluscs is the trochophore, also found in annelids and sipunculids (Fig. 1.1). The characteristic band of locomotory cilia which encircles the larvae is called the prototroch and is derived from the apical micromeres. Direct development from the trochophore to adult is found in the Polyplacophora, Scaphopoda and protobranch bivalves. Among the Gastropoda, the trochophore larva is found only in the more primitive groups – the Patellogastropoda and Vetigastropoda. In Neritopsina, Caenogastropoda and Heterobranchia and the more advanced bivalves, larvae pass through another stage, the veliger, before metamorphosis. The veliger stage is often suppressed, and in cephalopods and the terrestrial and freshwater molluscs, the larval stage is usually modified or absent.

Characteristic of the free-swimming veliger is the ciliated velum, which is used in feeding and movement. Veliger larvae are usually planktotrophic, although many are lecithotrophic; they are the distributive phase of many molluscan life cycles.

Prior to metamorphosis, the gastropod veliger body undergoes torsion through 180°. The mouth and anus are brought close together, and the digestive tract and nervous system are looped. Subsequent growth is asymmetrical, usually dextral.

The larval shell or protoconch forms the apical whorl(s) of the adult shell. Molluscs with a lecithotrophic veliger larva usually have a paucispiral, inflated protoconch, and those which spend a long time as planktotrophic larvae usually have a tightly coiled multispiral protoconch.

Bivalves produce larvae which settle on suitable substrata as miniature versions of the adult. The freshwater mussels (Unionidae) have a parasitic larval stage.

Polyplacophorans lack a veliger stage. The trochophore larva develops a shell gland which secretes a dorsal shell, while the foot develops beneath it. The lower part of the trochophore, the post-trochal region, elongates to form the larger part of the body. Larval eyes, which develop near the prototroch persist for some time after the ciliated girdle has degenerated and the larva has settled on the substratum.

Scaphopods release planktonic eggs which develop into trochophore larvae. The subsequent veliger develops a bilobed mantle and shell, similar to that of a bivalve. However, fusion along the mantle and shell edges results in a cylindrical mantle and shell which communicate with the water at each end. Gradual metamorphosis involves an elongation of the body.

MOLLUSCAN LIFE HISTORIES

Molluscs exhibit an enormous range of reproductive strategies. Most are dioecious, but occasional marine species and many terrestrial species are hermaphrodites. In some species, eggs and sperm are liberated into the sea, so that fertilisation occurs at random. In others, particularly freshwater and terrestrial species, as well as many marine ones, copulation takes place and internal fertilisation occurs. Most marine species produce a pelagic larval stage, which serves to effect dispersal, but in some marine forms and most freshwater and terrestrial forms this pelagic stage is omitted, and small replicas of the adults emerge from egg capsules. Planktotrophic larval forms have little or no yolk, and obtain their food by feeding on plankton before they metamorphose into juveniles. Lecithotrophic larvae are provided with substantial food supplies, and some are nurtured by the adults until they have passed the larval stage (Fig. 1.19). These ovoviviparous adults give birth directly to juveniles.

This diversity of reproductive mechanisms makes it difficult to generalise about molluscan life cycles. Instead of attempting to do so, this section briefly reviews the variety of processes found at each stage in the life cycle. Adult reproductive morphology is discussed in the previous section.

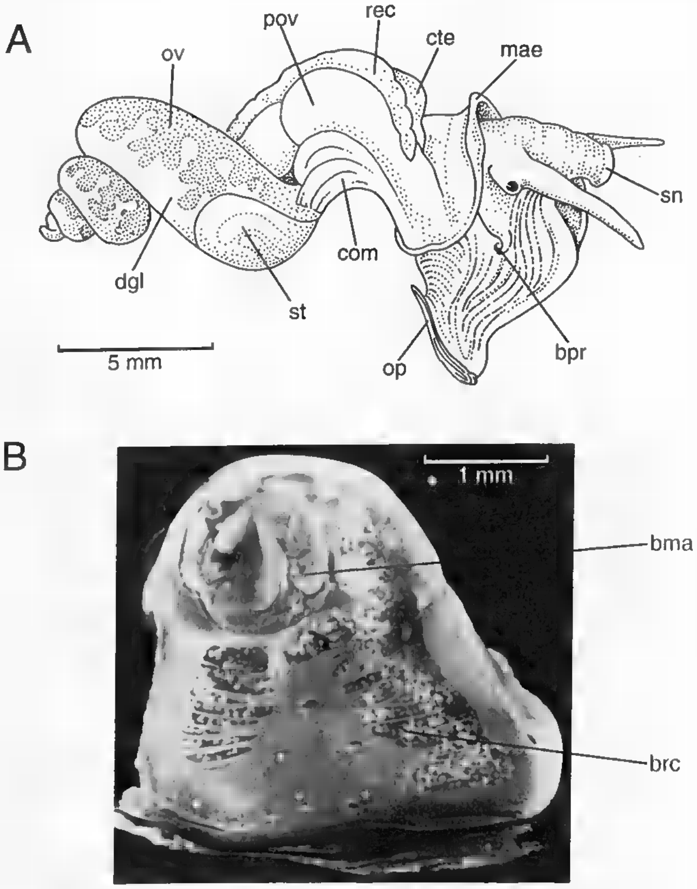


Figure 1.19 The female of the ovoviviparous gastropod *Planaxis sulcatus* (Planaxidae) protects and nurtures its young to the veliger stage in a brood pouch. A, body structure of adult without the shell, indicating the external opening of the brood pouch within the head-foot. **B**, transverse section of head-foot, showing developing larvae within horizontal chambers of the brood pouch. **bma**, buccal mass; **bpr**, brood pore; **brc**, brood chambers; **com**, collumellar muscle; **cte**, ctenidium; **dgl**, digestive gland; **mae**, mantle edge; **op**, operculum; **ov**, ovary; **pov**, pallial oviduct; **rec**, rectum; **sn**, snout; **st**, stomach. (A, after Houbrick 1987; B, from Houbrick 1987) [A, R. Plant]

Adult Reproductive Characteristics

Although the majority of molluscan species are dioecious, they show little external sexual dimorphism. Many gastropod males develop a penis when sexually mature, and male cephalopods have a specially modified, 'hectocotylised' arm, but in general the differences between the sexes are restricted to internal structures and often small differences in body size.

Males typically have a testis, or testes, opening through sperm ducts. Primitively, these led to the pericardium, and sperm reached the external environment through the kidney, but in many derived molluscs sperm ducts lead directly to the outside. A similar situation is found with the ovaries and oviducts of the females.

Most hermaphroditic molluscs are members of the classes Bivalvia and Gastropoda. For instance, species of the bivalved shipworm, *Teredo*, are simultaneous hermaphrodites, whereby individuals produce sperm and eggs simultaneously, and self-fertilisation may occur. Likewise in the opisthobranch and pulmonate gastropods, there are many examples of simultaneous hermaphrodites, such as the sea hares, genus *Aplysia*, and the garden snail *Helix aspersa*.

Among the 'prosobranch' gastropods, hermaphrodites are rare. Some species in several marine genera are protandrous hermaphrodites; they begin life as males, but later the same individuals become females. This process may occur in the Australian *Hipponix conicus* (Laws 1970), but this is not yet certain. Some limpets, such as species of *Acmaea* and *Patella*, are also protandrous hermaphrodites, but the phenomenon has been investigated in most detail in the American slipper limpet, *Crepidula fornicata*. Individuals of this species form chains, each attached to the shell of the one below. The lowest in the chain – the first individual to settle – begins as a male, but then the male sex cells regress, and eggs develop in the gonad so that the individual becomes a functional female. When a young individual settles on the shell of this female, it too begins as a functional male, producing ripe sperm when it matures, and therefore able to fertilise the female below. Further individuals may settle, creating a long chain. As the chain grows the lower individuals all become females while the apical individuals are males. In this species, the sex of the individuals is at least partly controlled by interactions between the various members of the chain. The females liberate a substance into the water which ensures that males at the top of the chain remain male, and do not change into females (see Fretter & Graham 1964; Webber 1977).

Very few molluscs have been shown to be parthenogenetic. The best known example is one of the 'prosobranch' gastropods *Potamopyrgus antipodarum*. This species, which is common in fresh and brackish waters in Europe, reached Australia via New Zealand (Ponder 1988). Most populations are parthenogenetic, and nearly all the individuals so far examined have been females; numbers of males are low. In Australia, parthenogenesis is also known to occur in the freshwater 'prosobranch' *Thiara balonnensis* (Stoddart 1983).

Production of Gametes

In the humid tropics, many molluscs breed all the year round (Berry 1975). Elsewhere, species adhere more or less strictly to an annual reproductive cycle, probably governed or triggered by environmental factors such as temperature. The timing of the spawning period varies radically between species, and ranges from spring to summer or winter. It is not often possible to establish the variables controlling the breeding cycles, and comparatively little information is available about Australian species, except in general terms (see Anderson 1960).

In south-western Western Australia, the trochid *Cantharidus pulcherrimus* spawns in March and April and juveniles recruit into intertidal populations during the southern winter, where they mature and spawn at one year of age. Removal of macroalgae and associated snails by winter storms is the largest identifiable source of mortality (Wells, F.E. & Keesing 1987). In the same region, the chiton *Acanthopleura hirtosa* spawns during April through June, and individuals probably survive for two years, whereas *Haliotis roei* spawns over several months from June onwards, predominantly in July and August, and individuals live for several years (Wells, F.E. & Sellers 1987; Wells, F.E. & Keesing 1990).

Underwood (1974) investigated the breeding cycles of ten common species of intertidal 'prosobranch' gastropods in eastern Australia. The spawning between August and March of several species with planktotrophic larvae correlated with the abundance of phytoplankton for the larvae to feed on. Such species include the littorinids *Nodilittorina pyramidalis*, *N. unifasciata* and *Bembicium nanum*, and the whelk *Morula marginalba*.

In contrast, the spawning periods of several vetigastropods and patellogastropods with lecithotrophic larvae are not related to phytoplankton abundance. The nacellid *Cellana tramoserica* breeds from March to October and *Patella peroni* breeds from June to September or February to May. The turbinid *Turbo undulatus* and the fissurellid *Montfortula rugosa* both breed from October to May. These larvae contain their own food supply in the form of yolk, and would not utilise the phytoplankton as food even if it were abundant. This is far from being the whole story, however, as several species of southern and Western Australian cowries with direct development, and therefore with no dependence upon the plankton, have been shown to be strictly summer breeders (Wilson, B.R. 1985), though for reasons presently not understood.

The timing of reproduction in bivalves has attracted much attention, because whole populations often spawn in phase (see Fretter & Graham 1964). A lunar periodicity has been shown for some marine bivalves, such as the European *Ostrea edulis*, and for chitons (Pearse 1979), but the exact cues involved and the biological advantages of specific breeding times have yet to be explained in detail. Reproductive cycles of five marine bivalve species in Western Australia have been described by B.R. Wilson & Hodgkin (1967). The breeding cycles of estuarine species may be governed by changes in salinity. For example, spatfall in *Xenostrobus securis* occurs later at stations upstream than those near the mouth of the estuary, probably because saline water does not penetrate up the estuary until later in the summer (Wilson, B.R. 1969).

Gametogenesis occurs throughout the year in the freshwater hyriid bivalve *Cucumerunio novaehollandiae*, with a peak in abundance of mature gametes from January through August. Like other freshwater bivalves, hyriids produce glochidia, larvae which parasitise fish. After brooding for nine weeks, glochidia were released from mid-May through July upstream and from June to August in the lower reaches of Macleay River; such differences in timing may be in response to environmental cues such as water temperature or water runoff (Jones, H.A., Simpson & Humphrey 1986). The brooding period for various species of *Hyridella* in the same river varied from 8–11 weeks depending upon water temperature (Jones, H.A. *et al.* 1986). Glochidia of *H. drapeta* parasitise fish in coastal Victorian streams most frequently in spring (Atkins 1979). Peaks in reproductive activity occur in *Velesunio ambiguus* in spring and late summer (Walker, K.F. 1981a).

During the annual reproductive cycle, the gonads of most species enlarge with the progress of gametogenesis, reach a peak size just at spawning time, and then regress until the following year. Such size changes are often associated with changes of colour, as the oocytes and spermatocytes develop.

As described in the preceding section, some vetigastropods and many caenogastropods produce paraspermatozoa in the testes in addition to euspermatozoa (see Webber 1977; Dohmen 1983; Healy 1988). These paraspermatozoa are thought to provide nutriment or stimulation to euspermatozoa prior to fertilisation (see Healy 1988). The more complex forms of these paraspermatozoa, termed spermatozeugmata, appear to function as mobile spermatophores capable of depositing euspermatozoa within the female reproductive system (Healy & Jamieson 1981).

In some molluscs the spermatozoa are enclosed in spermatophores, a feature particularly common in stylommatophoran pulmonates and in cephalopods. In the thecosome *Limacina inflata*, the spermatophores are produced by the prostate gland (Lalli & Wells 1978). Cephalopod spermatophores are complex structures. They contain a tightly wound sperm tube and an ejaculatory apparatus which, when everted, pulls the sperm tube to the front of the spermatophore so that the sperm can escape (Arnold & Williams-Arnold 1977; Wells, M.J. & Wells 1977).

In the ovaries, the oocytes develop into eggs, which are surrounded by a vitelline membrane, and sometimes other protective membranes. The eggs contain varying amounts of yolk, in relation to the type of nutrition of the larval forms. Those with planktotrophic larvae have little yolk; lecithotrophic forms lack a long pelagic stage and have large yolk supplies. Details of oogenesis in the littorinid *Bembicium nanum*, which has planktotrophic larvae, have been given by Bedford (1966), and in two *Turbo* species by Joll (1980).

The presence of two kinds of sperm in males is analogous with the occasional presence of two kinds of eggs in females. Most eggs are capable of development, but in some species 'food eggs' or 'nurse cells' which do not develop are eaten by developing embryos. The origin of these food eggs is uncertain. Some may be derived from normal eggs that were fertilised by dispyrene sperm, and therefore cannot undergo normal development, but others seem to be unfertilised.

Fertilisation and Egg Laying

Apart from those examples of simultaneous hermaphroditism mentioned above, fertilisation must be effected by the meeting of sperm and egg cells from separate individuals. The most primitive method of fertilisation occurs in many marine molluscs, whereby the eggs and sperm are liberated into the sea; fertilisation is fully external and not under the control of the parents. The chance nature of this process of fertilisation is often improved to some degree by synchronous spawning. In some gastropods, for instance, gametes are not shed from one individual unless there is another individual of the opposite sex nearby. In other species, the liberation of sperm may trigger subsequent liberation of eggs, particularly in bivalves, and whole populations may spawn in synchrony, greatly improving the probability of fertilisation.

Much greater efficiency of fertilisation is achieved, however, by the various forms of sperm transfer found in higher gastropods and in cephalopods. Most male gastropods have an extensible penis which is used to transfer sperm to the female genital aperture. Sperm transfer is often preceded by a period of courtship, although this may be brief in aquatic forms. Courtship is most highly developed in terrestrial pulmonates such as species of *Helix*. It involves stroking of the partner's body and the stimulation of the partner by discharge of darts into the partner's epidermis. These terrestrial pulmonates are hermaphrodites, and copulation is usually reciprocal, whereby the penis of each deposits a spermatophore in the female orifice of the other (Berry 1977). The spermatophores are dissolved, partly by the bursa copulatrix, and fertilisation occurs when the liberated sperm move up to the fertilisation pockets at the junction of the albumen gland and the hermaphrodite duct. It should be noted, however, that the details of the fertilisation process, and the exact functions of the bursa copulatrix in pulmonates are unclear. These are discussed by Duncan (1975) and Tompa (1984).

Fertilisation in cephalopods may be preceded by a prolonged process of mate selection, and may involve aggressive behaviour between males and courtship between male and female (Wells, M.J. & Wells 1977). In the solitary forms, such as *Octopus* species, the males become more mobile in the breeding season and search for mates, whereas shoaling species such as the squids already have potential mates close at hand. In both, visual displays involving changes of colour patterns are important in identifying the sex of the individuals, and copulation occurs after rival males have been defeated in aggressive encounters (Arnold 1984). Male cephalopods use the hectocotylus, a modified arm, to achieve internal fertilisation. This structure transfers spermatophores to the mantle cavity of the female and is then usually withdrawn. However, in some genera, such as *Argonauta*, in which sperm are not enclosed in spermatophores, the hectocotylus autotomises and remains inside the mantle cavity of the female. Sperm can be stored by the female for some months (Joll 1976), and egg laying may occur a considerable time after copulation.

Most polyplacophorans, vetigastropods, patellogastropods, bivalves and scaphopods liberate eggs directly to the surrounding water (see McFadien-Carter 1979; Pearse 1979; Sastry 1979), but more advanced gastropods and the Cephalopoda usually have specific egg laying procedures. Some marine 'prosobranch' gastropods produce gelatinous egg masses in a specific form, which are attached to rocks, hydroids or seaweeds (Fig. 1.20A; Fretter & Graham 1982). Some of the neogastropods such as European species of *Buccinum* and *Nucella* produce large egg capsules containing hundreds of eggs, from which only a few embryos will complete development. The other eggs act as nurse cells. Some egg masses may be formed of numerous capsules cemented together, for example, those of *Melo* species (Volutidae), in which each capsule may contain several eggs, but only one develops to hatch as a juvenile (Fig. 1.20B). Other caenogastropods lay capsules individually, each containing a few eggs (Fig. 1.20C, D). The Australian neogastropod *Bedeva paivae* lays capsules containing only about 10 eggs (Black 1976).

Several species of chitons in Australia have been shown to brood the young in the mantle cavity (Turner, E. 1978; Penprase 1981); the egg laying procedures that precede brooding have not been described.

Very few 'prosobranchs' exhibit any parental care for the eggs once laid, but a few species retain the eggs inside a brood pouch until a later stage of development. For instance, the European *Littorina saxatilis* broods its young until they have become miniature crawling snails, as does the Australian *Hipponix conicus* (Laws 1970). Many *Littoraria* species, including the Australian species related to *L. scabra*, retain the eggs until they have reached the veliger stage; the veligers are then shed directly into the water (Reid 1986). Planaxids, common on rocky intertidal shores in tropical and subtropical environments, protect their developing young in cephalic brood pouches finally releasing them as veligers (Fig. 1.19; Houbrick 1987). Members of the freshwater family Thiaridae are ovoviviparous, and some species release free swimming veligers (McMichael & Iredale 1959).

In the Opisthobranchia, which are almost entirely marine, oviparity is the rule (Beeman 1977). The egg masses often form ribbons containing thousands of eggs, and may be conspicuous on or near the shore because many species move inshore to breed (Fig. 1.20E, F). A few species brood the young (Lalli & Wells 1973; Hadfield & Switzer-Dunlap 1984).

Marine pulmonates, such as *Siphonaria* species, also produce gelatinous egg strings on rocky shores (for example, see Quinn 1983). On muddy shores, pulmonates, such as *Amphibola crenata* in New Zealand and species of *Salinator* in Australia, produce ring-shaped egg masses composed of a mixture of mud, eggs and mucus, which are shaped by the action of the foot (Fig. 1.20G). In other marine pulmonates, such as the American ellobiid *Melampus bidentatus*, eggs are laid on salt marshes in a pattern related to the tides, so that the veliger larvae which hatch can settle on the marsh on the next series of spring tides (see summary by Little 1983).

Freshwater pulmonates usually lay gelatinous egg masses like those of marine forms. Viviparity is recorded in the freshwater genus *Glacidorbis*. In *G. hedleyi*, the encapsulated eggs are brooded within the pallial cavity and display various stages of development from embryo to shelled juvenile (Ponder 1986a). B.J. Smith (1979b) reported developing embryos in the uterus of *G. paupela*.

Terrestrial pulmonates lay well-protected eggs. The parent selects sites in damp regions, usually in soil under logs or rotting timber, and the coatings of the eggs themselves are heavily calcified to provide mechanical strength (Fig. 1.20H). Many species of terrestrial pulmonates (the Stylommatophora) are ovoviviparous, retaining the eggs in the body during development so that the young are liberated as small snails (Tompa 1984).

Although most bivalves liberate their gametes directly into the water (Pl. 14.3), many also retain the eggs for some time, either in the mantle cavity, or in a special marsupium. This phenomenon has been recorded in the estuarine galeommatid *Arthritica semen* (Wells, F.E. & Threlfall 1982) and is relatively common in freshwater species (Mackie 1984). Fertilisation is internal in unionids and the young are brooded within a ctenidial marsupium, before release as larvae, termed glochidia, which are parasitic on the gills of fish. *Hyridella australis* releases its larvae in mucoid, worm-like strings, as do other North American unionids, presumably as a bait for potential hosts in the form of predatory fish (Kat 1984; Jones, H.A. *et al.* 1986; Heard 1992).

Decapod cephalopods enclose their eggs in layers of jelly, and lay them either singly (Pl. 18.2), or in groups (Pls 18.7, 18.8). There is no parental care. Eggs of octopods, on the other hand, have no protective jelly layer, but the eggs are deposited on the roof of the parent's lair, where the female keeps them clean, flushes water over them, and defends the surrounding territory (Pl. 20.10; Joll 1976; Arnold 1984). In *Hapalochlaena maculosa* the female retains the eggs on or under her tentacles until they hatch (Pl. 19.2; A.J. Butler personal communication). The process of brood protection is taken to an extreme by members of the pelagic genus *Argonauta*, in which the eggs develop in a complex egg case (termed the shell) secreted by the female's arms (Pls 21.3–21.5).

Larval Stages

Within the egg capsules, most molluscan eggs undergo spiral cleavage (Raven 1964; Verdonk & Biggelaar 1983). After gastrulation, an embryo forms, and development then proceeds along one of two lines. In a minority of forms, development is direct, and the embryo develops to form a juvenile mollusc, with no intermediate larval stages. This occurs in cephalopods (Joll 1978), but all other molluscs pass through larval stages, even if these are confined within the egg membranes. Metamorphosis from the larval form can therefore occur within the egg capsule, or at the time when the free-living larva settles out from the plankton. The stage at which this happens differs with habitat and latitude. In general, tropical 'prosobranch' species hatch as free-swimming larvae, whereas temperate species hatch as young snails, but there are many exceptions to this (Spight 1977a).

Two basic larval types are found among molluscs: the trochophore and the veliger. Some bivalves – the freshwater mussels – have a modified type, known as a glochidium. Trochophores occur in Patellogastropoda, Vetigastropoda, Polyplacophora, Bivalvia and Scaphopoda. This type of larva, characterised by an apical tuft of cilia and a band of cilia encircling the body, is relatively short lived (Fig. 1.1C).

In chitons, the trochophore may swim for several days before it settles and metamorphoses directly into the juvenile form (Pearse 1979). The patellogastropod trochophore lasts for only a few hours before being transformed into a veliger (Lindberg Chapter 15), and during its short existence it takes in little or no food. Most molluscan larvae hatch as veligers. These are characterised by the presence of a larval shell, and a large ciliated organ termed the velum which forms the larva's locomotory organ and food-catching system. Early gastropod veligers undergo the phenomenon of torsion, whereby the mantle cavity is brought to a forward-facing, rather than a backward-facing, direction (Morton, J.E. & Yonge 1964). As a result of this torsion, organs on the right side of the pre-torsional veliger come to lie on the left side in the post-torsional larva.

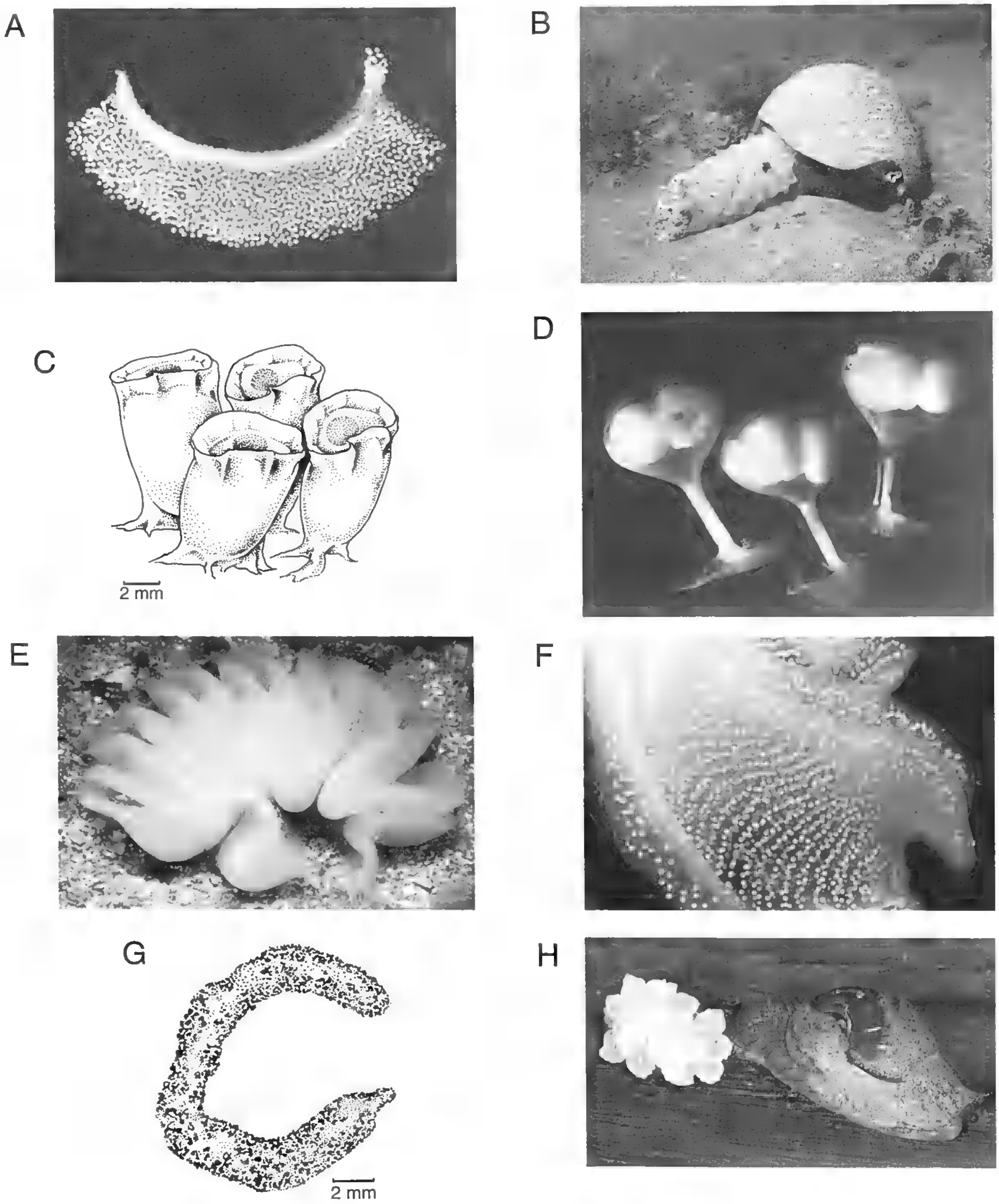


Figure 1.20 Gastropod egg masses and capsules. **A**, the gelatinous collar capsule of *Polinices incei* (Naticidae). **B**, the volutid *Melo amphora* laying an egg mass comprising numerous square capsules. **C**, the lens-shaped capsules of *Bedeva paivae* (Muricidae) contain as few as 10 eggs. **D**, one egg, nourished by nurse eggs, develops in each capsule of the ranellid *Sassia subdistorta* and hatches as a crawling juvenile. **E**, the folded ribbon of eggs produced by the anaspidean opisthobranch *Pleurobranchus hilli* (Pleurobranchidae). **F**, eggs of the nudibranch *Ceratosoma brevicaudatum* (Chromodorididae) within a gelatinous matrix. **G**, the sandy girdle of the marine pulmonate *Salinator fragilis* (Amphibolidae). **H**, the pulmonate 'semi-slug' *Helicarion virens* (Helicarionidae) with a clutch of calcareous-shelled eggs.
[A, D, F.V. Murray, from Smith, B.J., Black & Shepherd (1989); B, Australian Institute of Marine Science; C, G, R. Plant; E, F, N. Holmes; H, Queensland Museum]

Among the molluscan classes, the veliger larvae show a wide diversity of adaptive forms, and it is appropriate to consider several of the major molluscan classes in turn.

'Prosobranch' Gastropoda. The larval stages of most patellogastropods and vetigastropods are passed in the egg capsule, at least in those well-studied forms of Europe and North America. One well-documented example is the European limpet, *Patella vulgata* (Fretter & Graham 1962), in which a free-living veliger originates from a trochophore larva about two days after fertilisation. The veliger has a bilobed velum, a dextrally coiled larval shell and a foot bearing an operculum. After torsion has occurred, the velum and foot can be retracted into the shell, and the aperture closed by the operculum. At this stage, when about four days old, the larvae settle out of the plankton.

The veligers of neotaenioglossans and neogastropods differ little in basic structure from those of *Patella* species, exemplified by those of *Bembicium nanum* (Fig. 1.21A; Bedford 1966). In veligers that have a long pelagic life, the velum is often complex. For example, the velum of the European neogastropod *Nassarius incrassatus*, which is planktonic for two months, has four velar lobes instead of the normal two. In embryos that are never free living, however, such as those of the European neogastropod *Nucella lapillus*, the velum is small and has relatively little locomotory power.

'Prosobranch' veligers have a number of strictly larval adaptations which are lost when they metamorphose into juvenile snails. Some have organs known as larval kidneys, although their function is not clear. Most of these veligers have larval hearts, which are contractile portions of the presumptive anterior aorta, supplying blood to the most active and important organ, the velum. Other structures are retained by the adult, including the statocysts, necessary for orientation, the deep mantle cavity, and the digestive system including paired digestive glands.

The 'prosobranch' larvae grow in size in the plankton, from an average initial diameter of the order of 0.2 mm, to a final diameter of about 0.4 mm to more than 1.0 mm. During this time the shell continues to grow in a spiral, usually dextrally, and may become ornamented with sculpture which is usually unlike that of the adult. In some species with a long planktonic stage, the shell develops into an elaborate structure in which the two shell layers are separated by a fluid-filled space. The larvae of these species are called echinospira larvae. The outer layer of shell in these is made up of conchiolin, secreted by that part of the mantle that normally secretes the periostracum. The inner layer of shell is calcified, and is secreted by the mantle region that normally secretes the calcareous shell layers. The two shell layers therefore correspond to the periostracal and calcareous parts of the normal gastropod shell, but are separated by more than the usual extent. The function of this large and complex structure is not really understood, but it may reduce the sinking rate of the larvae.

The larval development of the neogastropod *Bedeva hanleyi* (Muricidae) takes place within the egg capsule (Anderson 1966). In the first four days the early veliger develops an inconspicuous velum, a simple transparent shell, the beginnings of the foot and a large yolky visceral mass. On the 15th day (Fig. 1.21B) the velum, foot and oral hood are well developed, as is the stomodeum, for the purpose of ingesting nurse cells. Eye spots are present and the shell has begun to coil. Over the next 10 days, the velar lobes diminish as the head, foot, shell and visceral mass grow (Fig. 1.21C). The juvenile escapes from the capsule, fully developed, some 30 days after hatching (Fig. 1.21D).

Heterobranch Gastropoda. The veligers of opisthobranchs vary from fully lecithotrophic forms, which may never spend time in the plankton, to fully planktotrophic forms, which may be planktonic for over a month. Although little information is available except from culture conditions, it is probable therefore that opisthobranch veligers generally spend less time in the plankton than those of the 'prosobranchs' (see Hadfield & Switzer-Dunlap 1984). A good example is the lecithotrophic veliger of the nudibranch *Hoplodoris nodulosa* which begins metamorphosis immediately or goes through a brief swimming-crawling phase before settling (Rose 1983). Opisthobranch veligers have many basic structural similarities with those of 'prosobranchs' (Bonar 1978), such as a prominent velum, an operculum on the foot, and a coiled shell. There are also essential differences. The velum in opisthobranchs is never complex, and it may be reduced in size and in degree of ciliation in lecithotrophic larvae. The shell shows the greatest external difference. In opisthobranch larvae the shell coils sinistrally and not dextrally. Internally, the mantle cavity of early opisthobranch larvae is small and enlarges during development, in contrast to that of the 'prosobranchs' which is large from hatching onwards. Opisthobranch larvae have a single larval kidney, in comparison with the paired structures of 'prosobranchs'.

The veligers in marine pulmonate genera such as *Siphonaria* and *Amphibola* are very similar to those of opisthobranchs (Fig. 1.21E). Indeed, the structure of the veliger in *Amphibola* has only one feature that distinguishes it from opisthobranchs – a unique larval pallial gland at the anterior end of the mantle cavity (Little, Stirling, Pilkington & Pilkington 1985). In the majority of

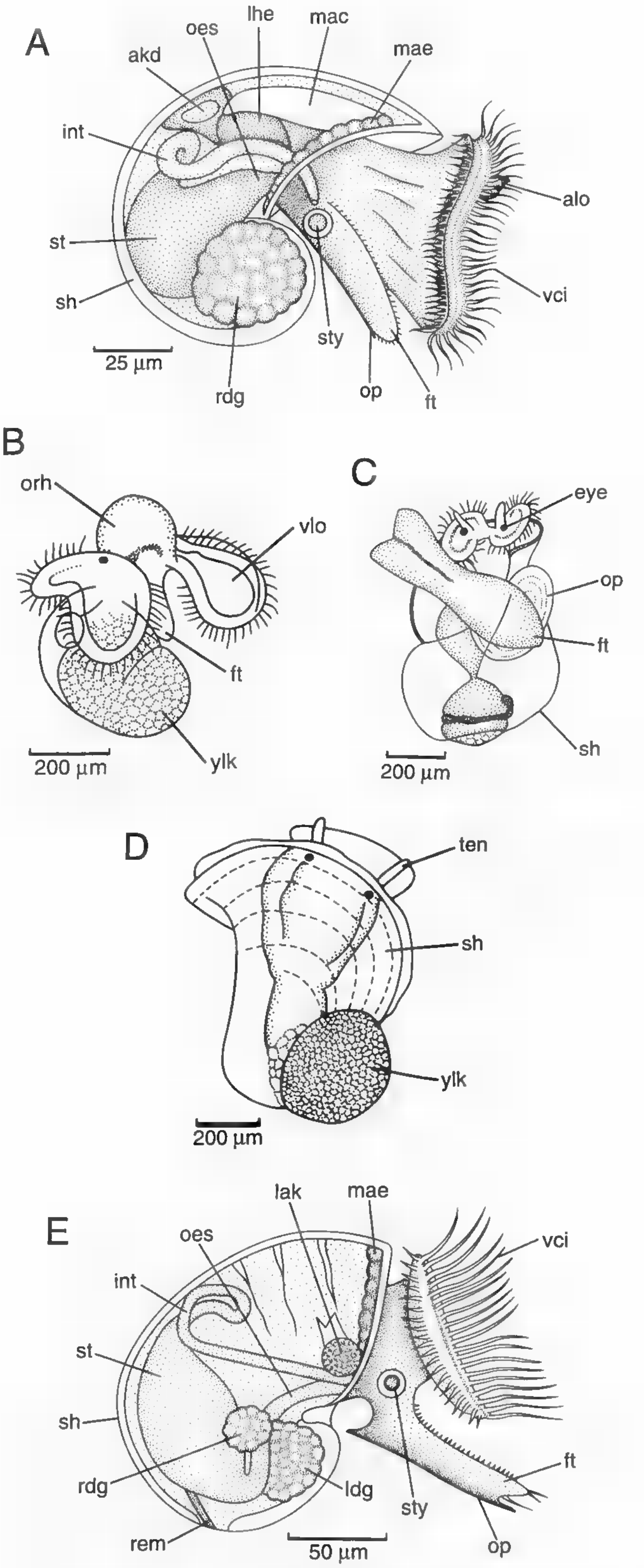


Figure 1.21 Gastropod veligers and juveniles. **A**, *Bembicium nanum* (Littorinidae), an Australian marine prosobranch just prior to hatching, showing an extensive mantle cavity, no larval kidney, only an adult kidney, a larval heart, and a large right lobe of the digestive gland. **B–D**, *Bedeva hanleyi* (Muricidae): **B**, 15 day old veliger; **C**, 25 day old veliger; **D**, newly hatched juvenile. **E**, *Amphibola crenata* (Amphibolidae), a marine pulmonate from New Zealand, newly hatched, showing a prominent larval kidney and unequal lobes of the digestive gland; the mantle cavity is not shown. **akd**, adult kidney; **alo**, apical organ; **eye**, eyespot; **ft**, foot; **int**, intestine; **lak**, larval kidney; **ldg**, left lobe of digestive gland; **lhe**, larval heart; **mac**, mantle cavity; **mae**, mantle edge; **oes**, oesophagus; **op**, operculum; **orh**, oral hood; **rdg**, right lobe of digestive gland; **rem**, retractor muscle; **sh**, shell; **st**, stomach; **sty**, statocyst; **ten**, tentacle; **vci**, velar cilia; **vlo**, velar lobe; **ylk**, ingested yolk. (A, after Bedford 1966; B–D, after Anderson 1966; E, after Little *et al.* 1985) [A–E, C. Eadie]

pulmonates, including the terrestrial forms, larval stages are confined to the egg capsules; in these the features associated with a free-living existence, such as the velum, the larval heart and the osphradium, are reduced.

Bivalves. Most marine bivalves produce planktotrophic larvae, which remain in the plankton for up to a month or longer (Sastry 1979). The lecithotrophic larvae characteristic of deep-sea species have a very short pelagic life (Mackie 1984). The European *Cardium edule* provides a good example of the development of planktotrophic larvae (Creek 1960), a pattern shown also by the Australian scallop *Pecten fumatus* (Dix & Sjardin 1975; Dix 1976). The trochophores of *C. edule* develop inside the egg membranes, and then are transformed into veligers which are planktonic for about two weeks.

These veligers differ from those of gastropods in that they have paired shell valves, connected by two adductor muscles, and a much simpler structure, at least on hatching. Some, including *Cardium edule*, bear an apical tuft of cilia on the velum. Bivalve veligers also develop gills during the last few days of their pelagic life, unlike many gastropod veligers, and in many ways have a less dramatic change to the adult form at metamorphosis.

Freshwater bivalves have glochidia larvae (Fig. 1.22A), which develop from fertilised eggs brooded in the gills of the parent. The edges of the larval shell valves bear hooks, and a long sticky thread protrudes from between the valves. When the larva is expelled by the adult, it sinks to the bottom, and then attaches to the gills or skin of passing fish. It extracts nourishment from the tissues of the fish, and develops further towards the juvenile stage before dropping off the host to settle permanently on the bottom.

Metamorphosis

When veliger or trochophore larvae settle out of the plankton, they metamorphose into juveniles. These are essentially similar in form to the adults, but are not yet able to breed. In most species the veliger larva terminates in a swimming-crawling phase, during which it is competent to metamorphose. This phase is still able to swim, using the velar cilia, but is also able to crawl on the substratum using the foot. This new ability is linked to the development of the propodium, a lobe of the foot not present in earlier stages. To some degree, the swimming-crawling veliger is able to select the substratum on which it settles, and can swim off and settle elsewhere if the initial substratum is not suitable.

At metamorphosis, the foot is modified for feeding and movement and the velum is lost or resorbed, as the larva, termed a pediveliger, settles on the substratum (Fig. 1.22B). The growth of the several stages in development of a bivalve larva from embryo to juvenile is illustrated by the doughboy scallop, *Mimachlamys asperrima* (Pectinidae) (Fig. 1.22C).

After settlement, the velar lobes disappear, either by resorption or by shedding. Other larval organs such as the larval heart and kidneys are also lost while the adult organs grow in size and, by differential growth, move to their adult positions. The change in shell structure is perhaps the most obvious external feature. In 'prosobranch' gastropods the shell continues to coil dextrally, but in a slightly different plane. In some 'prosobranchs', such as the patellid limpets, the larval shell is lost subsequently, and only the adult shell remains. In many opisthobranchs, both the larval shell and the operculum are lost at metamorphosis, and the adults lack shells. In other heterobranchs, the pitch of shell coiling alters greatly, and the larval sinistral shell is covered over by the dextrally coiled adult shell (Little *et al.* 1985). In bivalves, the paired shell valves continue to grow, and adopt the adult sculpture.

Growth of Juveniles to Maturity

Juveniles recruited to the benthos at settlement, or at direct hatching from benthic egg masses, may simply join the adult population immediately or they may settle in regions not previously inhabited by adults (Branch 1975). Growth to

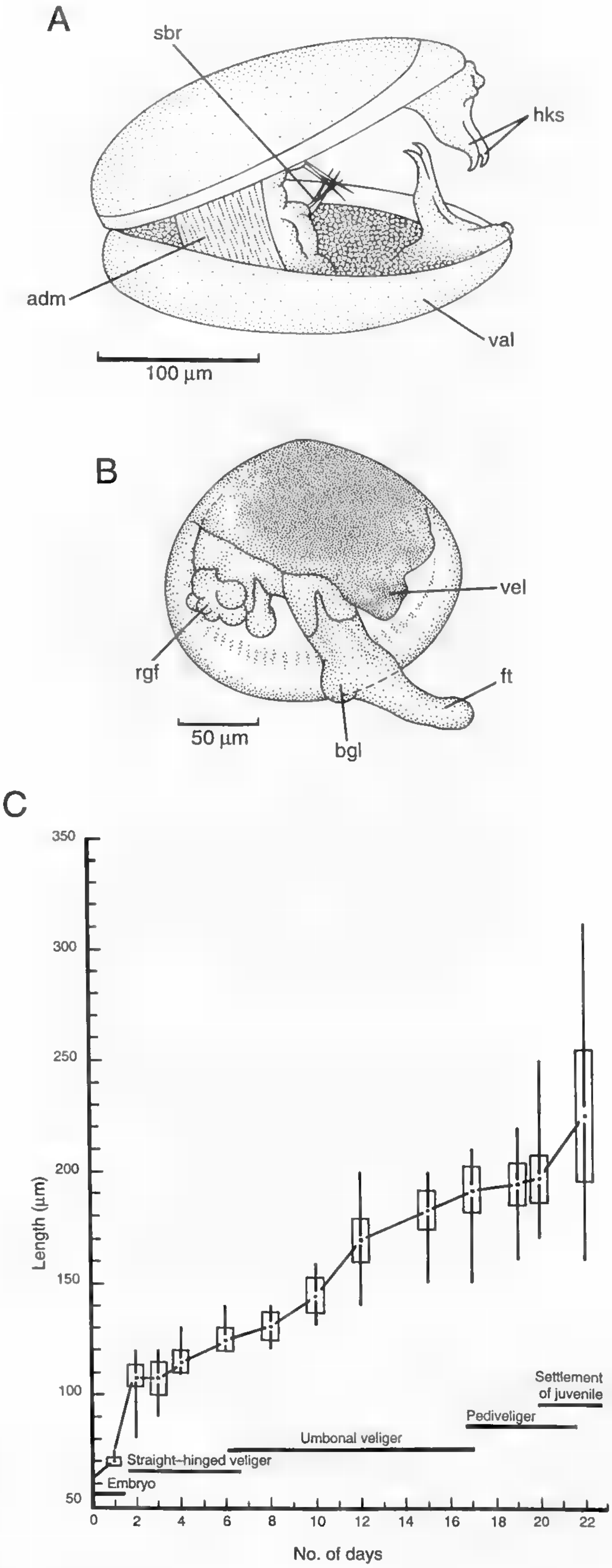


Figure 1.22 Bivalve larvae. **A**, glochidium of *Hyridella depressa* (Hyriidae) in lateral view. **B**, metamorphosing pediveliger of the doughboy scallop, *Mimachlamys asperrima* (Pectinidae), showing a well-developed foot, a prominent byssal gland, rudimentary gills and a partially resorbed velum. **C**, growth rate of larval stages from fertilisation to settlement, at 17°–18°C, showing mean, standard deviation and range for each stage. **adm**, adductor muscles; **bgl**, byssal gland; **ft**, foot; **hks**, hooks; **rgf**, rudimentary gill filaments; **sbr**, sensory bristles **val**, shell valve; **vel**, velum. (A, after Jones, H.A., Simpson & Humphrey 1986; B, C, after Rose & Dix 1984) [C. Eadie]

breeding size, involving development of reproductive organs, occurs at varying rates. In some European and Australian marine 'prosobranchs', spawning occurs within one to two years after settlement (Webber 1977). In *Nerita atramentosa*, for instance, spawning occurred at the earliest 20 months after settling, while in *Bembicium nanum* the first spawning took place within 10 months (Underwood 1975). In some cephalopods and opisthobranchs, however, life cycles are usually completed within a year, and maturity is reached in considerably less than a year (Thompson 1976; Wells, M.J. & Wells 1977; Todd 1983). The time to sexual maturity in marine bivalves varies from a few weeks to a year, depending upon ambient temperature; in deep-sea (cold water) forms, maturation takes even longer (Sastry 1979; Allen, J.A. 1983).

In fresh water and on land, the length of the juvenile phase is even more variable, because of the greater variability in environmental conditions. Most freshwater 'prosobranchs', for instance, reach maturity within a year (Calow 1983), but the time to maturity for one species of freshwater bivalve may vary from less than six months to two years (Burky 1983). Small species of terrestrial pulmonates may mature in much less than one year if they experience favourable conditions, but larger forms may take more than a year if they live in regions of poor water supply (Cain 1983; Calow 1983).

Life Cycles and Reproductive Strategies

The great variation in the time taken to reach maturity in various types of molluscs reflects a diversity of breeding strategies in relation to the life cycle. For instance, some molluscs, especially those that reach maturity within one year, die after mating. Such species, which include opisthobranchs, cephalopods, and many freshwater and terrestrial pulmonates, are termed semelparous. Other molluscs – often, but not exclusively, those that do not reach maturity within a year – continue to live after mating, and may reproduce many times. These species are called iteroparous, and include chitons, most 'prosobranchs', many bivalves and the larger terrestrial pulmonates. In extreme cases, some of these species may live for up to 100 years (Allen, J.A. 1983).

To some extent, these two different reproductive strategies can be linked with various other reproductive characteristics (Calow 1983). For example, many semelparous species invest a large amount of energy in reproductive activity because their production is concentrated in one burst rather than being spread over a number of years. With their rapid growth to maturity, these species are often opportunists, and tend to be common in unpredictable and rigorous conditions, where they can rapidly take advantage of environmental changes. Where the habitat persists for longer, and there is no need for dispersal in response to rapid environmental change, iteroparous species are more likely to predominate. Populations of such species may persist despite large variations in reproductive success from year to year.

These alternatives, however, are the simplest in a wide range of reproductive strategies requiring further investigation. In addition to semelparity and iteroparity, many other variable facets of molluscan reproduction are found in different combinations in different species. Brood size, for example, may vary from a few eggs to thousands, the individual size of eggs varies enormously, often in relation to brood size, and the amount of parental care may range from none to extensive brooding. In each species the total reproductive 'strategy' comprises a unique combination of these variables. Attempts to place breeding strategies into strict categories may not, therefore, be the most profitable approach (Grahame & Branch 1985). As yet little has been done to determine why various species allocate different amounts of resources to particular reproductive functions, and this remains a useful and exciting research area.

MOLLUSCS ON ROCKY SHORES

Intertidal habitats are subject to alternate periods of fully marine conditions and desiccatory, aerial conditions at high and low tides, respectively. Consequently, there are very striking gradients in the physical environments from the bottom to the top of the shore which tend to be correlated with decreasing sizes and diversity of the organisms.

The highest levels of rocky shores are occupied by grazing snails, mostly littorinids (Fig. 1.23A; Pl. 23.1) and small acmaeid limpets, and in more tropical areas, planaxids. In mid-shore regions the dominant molluscs comprise a variety of grazing snails such as trochids, neritids, patellid limpets and the pulmonate siphonariid limpets (Pl. 31.5). On Australian shores, several predatory neogastropods, particularly muricids, are abundant at these levels. Beds of mussels, such as occur along the Victorian coastline (Bennett & Pope 1953) are also conspicuous, as are oysters. At low levels on the shore, slit-limpets (Fig. 1.23B) may be common and chitons are important grazers of macroalgae (Fig. 1.23C; Pls 7–9; Otway 1989). The general patterns of vertical distribution have been reviewed extensively elsewhere (for example, Dakin, Bennett & Pope 1948; Bennett 1992; Underwood 1994).

Most early syntheses described patterns of distribution on the shore as 'zones' of co-occurring species at specified levels between low and high tides. There is no quantitative evidence to support this zonation (Underwood 1978a, 1978b; Chaloupka & Hall 1995). Zones simply represent the distributions of large or conspicuous species. Zonation is neither a useful, nor a realistic concept for understanding the ecology of intertidal organisms, including molluscs.

The initial studies also described the distributions and natural histories of molluscs on rocky shores in terms of the effects of, and responses to the physical factors of the environment, particularly the tidal cycle, as described in the reviews of Lewis (1964) and Stephenson & Stephenson (1972). More recently, however, these approaches have been superseded by an experimental appraisal of the influences of physical factors on the ecological interactions among intertidal organisms. These interactions form the focus of the present, abbreviated review.

Because the offspring of most molluscs disperse widely as planktonic propagules, their numbers are very variable in time and space. With few exceptions, they share this type of life history with most of the other organisms on rocky shores and thus live in a complex, dynamic and variable world (see also Fletcher, W.J. 1984). As a result, molluscs are involved in numerous important interactions with other animals and plants and play a key role in determining the structure and dynamics of intertidal life on rocky shores.

Molluscs on rocky shores have proved to be a very productive focus for the development of experimental procedures to investigate the ecology of populations and the structure and dynamics of complex assemblages of species. Many animals on rocky shores are numerous, sessile or relatively slow-moving and have lifespans in the order of several years, rather than weeks or decades. They are easily observed during low tide, readily manipulated and can be removed or relocated, so that hypotheses about processes influencing their ecology and life histories can be tested.

As a result, there have been great advances in our understanding of how these organisms live, and the importance of their interactions in determining the patterns of occupancy by other species in intertidal habitats (Underwood & Chapman 1993, 1995; Underwood 1994). The present review provides a brief account of some of the major interactions. The only results discussed are those supported by critical experimental tests conducted under field conditions. Only by properly conceived experiments can the intricacies of complex life histories and interactions be unravelled (see also Connell 1972; Underwood 1990). Inevitably, therefore, most attention is on temperate rather than tropical shores and on New South Wales and south-eastern regions, reflecting the published accounts of experimental studies of molluscs on Australian rocky shores. Most examples concern gastropods because so little experimental work has been published on chitons, bivalves or octopuses, despite their widespread occurrence (Underwood 1994).

Molluscan Grazers and Intertidal Macroalgae

A very widespread pattern on rocky coasts in south-eastern Australia is the presence of dense beds of foliose, fleshy algae at low levels on the shore. These algal beds often have an abrupt upper limit. Above this limit on sheltered shores, gastropods are abundant and the only algae are leathery, crustose species (Underwood 1981a).

Various competing mechanisms have been proposed to explain this upper limit of foliose plants (Underwood 1985). Grazing by intertidal gastropods is the only explanation that has been supported by rigorous experimentation (Underwood 1980; Underwood & Jernakoff 1981, 1984; Jernakoff 1983; reviewed by Underwood 1985).

In New South Wales, all species were prevented from entering areas of the shore. In such experimental areas foliose algae grew rapidly within a few days and occupied virtually all of the substratum for the ensuing two years (Underwood 1980). The plants could survive at levels much higher than they are normally found, provided that grazers were absent.

These experimental results have several important consequences for the life history of gastropods. Such intensive grazing removes virtually all early, microscopic stages of macroalgae; successional processes are confined to microscopic plants (MacLulich 1986). Secondly, as discussed later, grazers probably suffer from a shortage of food where they are sufficiently numerous or active. Finally, there remains the problem of why the grazers do not descend ever lower on the shore and eliminate the low-shore algal beds completely.

Macroalgae also influence the molluscs. Abundant mid-shore grazing gastropods do not venture to lower levels on the shore, but instead are found above the macroalgae, separated by a distinct boundary.

Underwood & Jernakoff (1981) demonstrated experimentally that *Cellana tramoserica* (Fig. 1.24; Pls 22.1, 22.2), limpets which feed on microalgae and do not eat macroalgae, tended to migrate away from areas with well-established algal beds more than from areas with little macroalgae. Limpets which remained amongst foliose plants lost more weight than those that moved away to bare areas. Microalgal grazers introduced into experimentally cleared areas within low-shore algal beds were unable to keep the substratum free of plants unless limpets were continually added to maintain unnaturally large densities. Algae grew rapidly at these low levels, ‘swamping’ the limpets and restricting the amount of space available to them for feeding. *Cellana tramoserica* eventually died, allowing increased rates of algal growth. Such positive feedback resulted in the rapid development of a continuous cover of foliose algae and the elimination of all the limpets.

Interactions between Sessile and Grazing Animals

Large grazing molluscs deleteriously affect the minute early life history stages of other animals such as barnacles and tube-worms, which settle from the plankton at very small sizes and are known to be very vulnerable to grazing by limpets (Dayton 1971). On sheltered shores, large grazing gastropods are abundant; where wave-exposure is greater, barnacles are abundant (Underwood, Denley & Moran 1983).

At all levels on the shore, the occupation of substrata is patchy. This patchiness of sessile species at several spatial scales is the outcome of variable patterns of recruitment of juvenile animals and the subsequent influences of interactions with grazing and predatory molluscs.

Grazing by limpets kills juvenile barnacles, *Tesseropora rosea*, by accidental ‘predation’, ‘bulldozing’ or crushing (Dayton 1971; Denley & Underwood 1979; Underwood *et al.* 1983). The interaction is complex. Where algae grow rapidly over the rock, they pre-empt occupation of the substrata, preventing settlement of barnacle cyprids, or grow over and smother the small barnacles. In such places, a few limpets can consume the algae thus enhancing the settlement and subsequent survival of

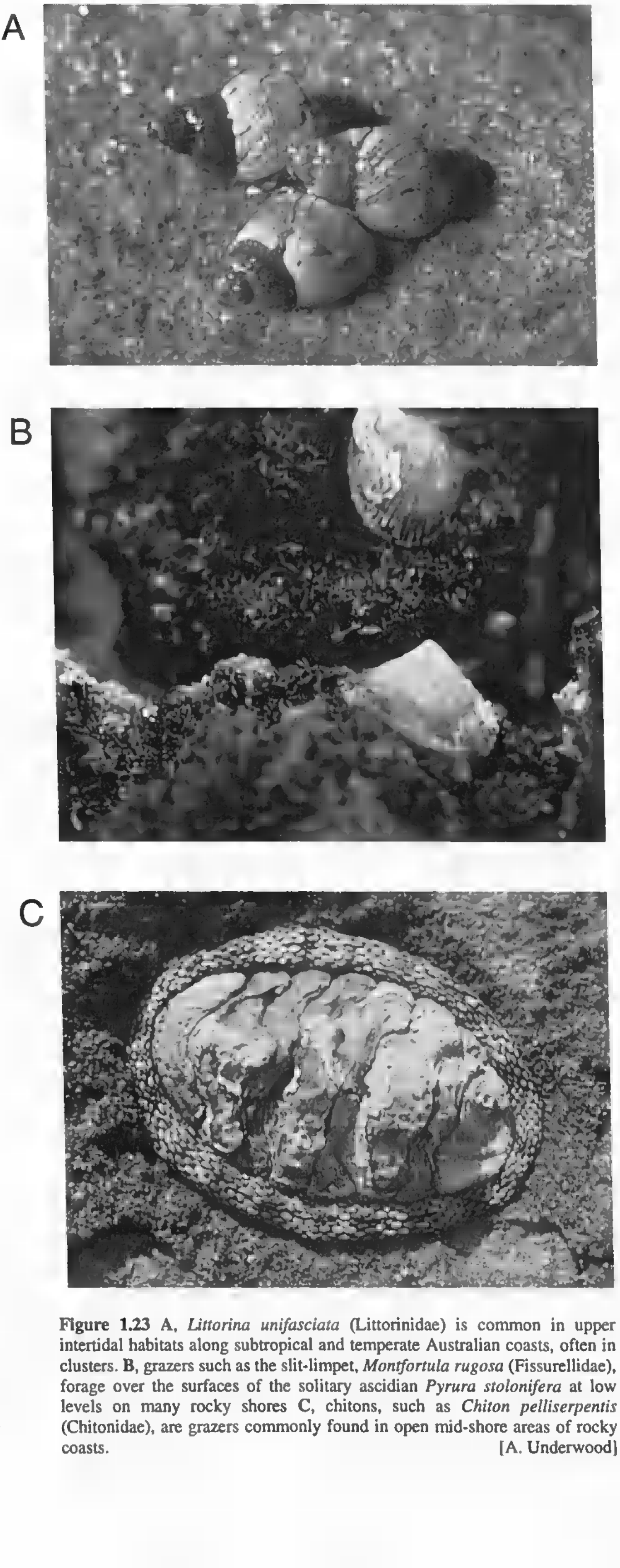


Figure 1.23 A, *Littorina unifasciata* (Littorinidae) is common in upper intertidal habitats along subtropical and temperate Australian coasts, often in clusters. **B**, grazers such as the slit-limpet, *Montfortula rugosa* (Fissurellidae), forage over the surfaces of the solitary ascidian *Pyrura stolonifera* at low levels on many rocky shores **C**, chitons, such as *Chiton pelliserpentis* (Chitonidae), are grazers commonly found in open mid-shore areas of rocky coasts. [A. Underwood]

Figure 1.24 *Cellana tramoserica* (Nacellidae), a conspicuous large grazer on rocky coasts from southern Queensland to South Australia. [A. Underwood]

barnacles (Underwood *et al.* 1983; Underwood 1985). Finally, adult limpets migrate away from areas where barnacles, either *Tesseropora rosea* or *Chamaesipho tasmanica*, are dense, because they require large areas of clear substratum on which to feed (Underwood *et al.* 1983). Clearly, pre-emption of space by barnacles prevents invasion by adult or juvenile *C. tramoserica.* This explains why some areas of the shore continue to be dominated by barnacles and also why occupation of other patches changes from limpets to barnacles or *vice versa.*

Examples are also available of 'facilitation' by barnacles. In New South Wales, the small acmaeid limpet, *Patelloida latistrigata*, is found almost exclusively on the tests of barnacles. In Creese's (1982) experiments, more juvenile *Patelloida latistrigata* recruited to areas where barnacles were present than to plots from which barnacles had been removed. Creese (1982) also investigated the absence of *Patelloida latistrigata* from mid-shore areas; where there were no barnacles to provide irregular substrata, larger limpets were more effective competitors for food. Competition among grazers is discussed later, but Creese demonstrated that mortality of adult *Patelloida latistrigata* was greater where large limpets, *Cellana tramoserica*, were present as a result of competition from the larger species.

Competition for Food

Grazing molluscs are capable of eating all microalgal spores in some areas. They also settle from the plankton in variable numbers. Therefore snails and limpets are often at, or exceed, carrying capacity because they exceed their food resources. Where adults are in high densities, intraspecific competition has been demonstrated between adult and juvenile *Nerita atramentosa*, such that juveniles cease to grow, but they can maintain their body weights and manage to stay alive (Underwood 1976a). The adults are, however, unable to maintain their body weight and are subject to increased density-dependent mortality. These results are attributable directly to insufficient availability of microalgal food. Such intraspecific competition can lead to rapid regulation of densities on a shore. When new juveniles recruit onto a crowded shore, the densities of snails increase, but are subsequently restored to lower numbers by excessive mortality of adults. When the number of adults is reduced, more food is available to juveniles and they can begin to grow. Similar processes were detected by Black (1977) for the limpet *Patelloida alticostata* in Western Australia.

Interspecific competition among intertidal snails is also widespread (see reviews by Underwood 1979, 1986; Branch 1981, 1984). Underwood (1978c, 1984) demonstrated that the snail *Nerita atramentosa* (Fig. 1.25A; Pl. 23.3) clearly out-competes the limpet *Cellana tramoserica* when the two are together in areas with inadequate food. Limpets lost weight and died much faster when *N. atramentosa* was present than when on their own. The effects of *N. atramentosa* were, however, not very different from those of *C. tramoserica* on themselves, that is, there was increased mortality and loss of tissue weight at increased density of the limpets alone. Increased densities of *C. tramoserica* did not affect *N. atramentosa*, so the competitive interaction was non-reciprocal (Connell 1983; Schoener 1983; Underwood 1986). Rates of mortality at different seasons and heights on the shore conformed to those predicted from the amounts of food available at different levels and seasons (Underwood 1984). Further, rates of mortality were entirely consistent with amounts of food in experimental enclosures with different densities of limpets and snails (Underwood 1984, 1985). Thus there is good evidence that interspecific competition was for food and not a result of other interference by the snails and limpets.

Carefully designed experiments are required to unravel the complex patterns in the densities of molluscs caused by interspecific and intraspecific competitive interactions (Underwood 1986). Competition for food due to feeding by the microalgal grazing limpet *Cellana tramoserica* was detrimental to tissue weights, growth and survival of the macroalgal grazing limpets *Siphonaria denticulata* and *S. virgulata* (Creese & Underwood 1982). The *Siphonaria* species were, however, not eliminated from areas of the shore where *C. tramoserica* was grazing. Siphonarians persisted even though they were inferior competitors and had no effect on *C. tramoserica.* They persisted because individual *C. tramoserica* were also competing with each other for food, causing decreased tissue weight and increased mortality. Thus, the numbers of *C. tramoserica* could not be maintained naturally, because of intraspecific competition, at densities large enough to continue the process of competition until all individuals of the *Siphonaria* species were dead. It is unlikely therefore that grazers compete sufficiently to eliminate any species from areas of seashore. Several subsequent studies have confirmed these conclusions (Fletcher, W.J. & Creese 1985; Ortega 1985).

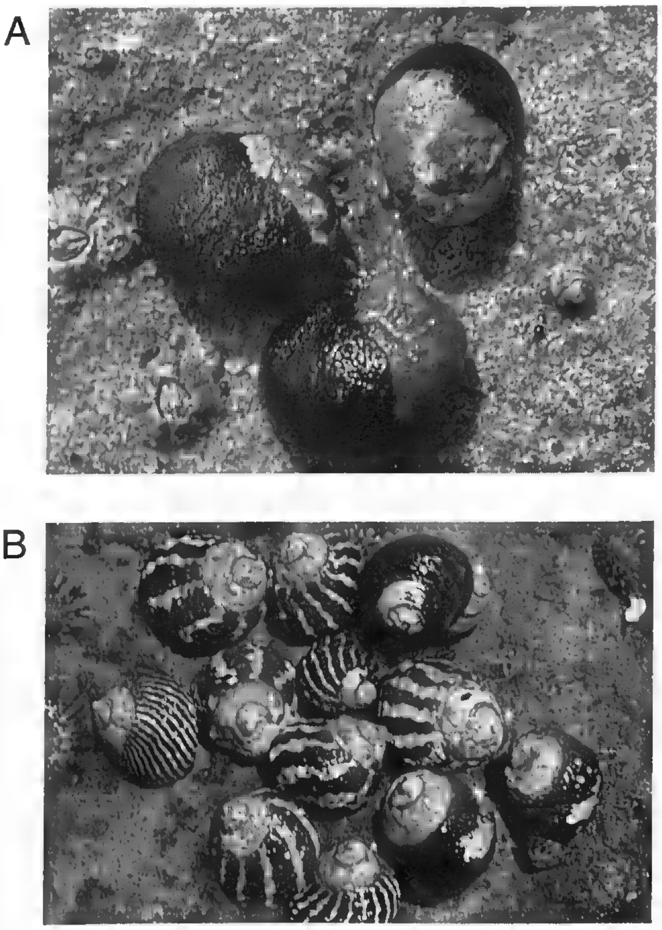


Figure 1.25 Common grazing snails. **A**, black snails, *Nerita atramentosa* (Neritidae) consume microscopic algae on rocky shores around subtropical and temperate Australia. **B**, *Austrocochlea porcata*, an abundant trochid on sheltered and some exposed coast-lines, exhibits great variation in its banding pattern along the southern Australian coast. [A. Underwood]

Predatory Molluscs on Rocky Shores

Predatory molluscs play an important role in structuring assemblages of species on seashores. In eastern Australia, the whelk *Morula marginalba* (Fig. 1.26; Pls 22.1, 27.11) drills and consumes virtually all shelled sessile species and many of the gastropods, although some of these do not have to be drilled to be eaten (Fairweather & Underwood 1983; Fairweather, Underwood & Moran 1984). Whelks are often present in very large numbers, but are patchy in their distribution. They are not found on very exposed coasts because they are swept away by waves (Moran 1985a). Studies on tagged populations demonstrated that *M. marginalba* grow at different rates on different prey (Moran, Fairweather & Underwood 1984). Whelks eating the tube-worm *Galeolaria caespitosa* grow very quickly to their asymptotic size, but relatively few survive and the population is dominated by juvenile snails. In contrast, whelks feeding on oysters, *Saccostrea commercialis*, grow very slowly but many more survive. Populations are therefore dominated by large numbers of adults. Whelks respond selectively to different types of prey in their environments; their choices are influenced by the densities, sizes and varieties of prey available (Hughes 1980; Hughes & Drewett 1985; Moran 1985b). *Morula marginalba* also have a hierarchy of preference for different types of prey (Fairweather & Underwood 1983; Fairweather *et al.* 1984).

Morula marginalba are commonly found in dense aggregations in cracks and crevices (Fig. 1.26) or pools at low levels on the shore (Moran 1985c). Moran suggested that the whelks aggregated when seeking shelter from inclement periods of weather, such as excessive heat, and from desiccation during low tides on hot sunny days. During favourable weather, *M. marginata* emerge from cracks and crevices and stay out to feed on prey during several successive periods of high and low tide. When the weather turns unfavourable – because of storms or during periods of low tide in calm sunny weather – the whelks must retreat to shelter. Where they are in large numbers and shelters are scattered or sparse, the whelks form dense aggregations.

As a result of its complex behaviour, *Morula marginata* has complicated effects on a variety of prey. Prey near crevices are susceptible to considerably greater rates of predation than those further away (see Fairweather *et al.* 1984). The distribution and behaviour of predatory whelks and their dependence on availability of suitable crevices are vital components of much of the faunal patchiness on mid-shore regions of the coast of New South Wales, because such patches reflect, in part, the patchiness of the distribution of the whelks themselves (Underwood & Denley 1984).

Further influences by whelks on their prey were demonstrated by Fairweather (1985) who found that the impact of whelks on a given species of prey was a function not only of the numbers of whelks and prey, but also of the availability of other, less or more preferred prey. Fairweather (1985) described this as the 'differential' effect of predation, that is the interaction between the preferences shown by the predator and the density of alternative prey of different preference ranking. These combine to influence the intensity of predation on a given species of prey.

Commensal Relationships

On shores in New South Wales, the small limpet, *Patelloida mufria*, can often be found on the shells of other gastropods, notably *Austrocochlea porcata*, *Turbo undulatus* and *Cellana tramoserica*, and rarely on the surface of the rock. The limpets are most common on snails that spend low tide in rock-pools and are usually found on the undersurfaces of the shells when host snails are outside pools. This choice of habitat and the various behaviours of the limpets when seeking or changing hosts result in the greatest probability of *P. mufria* being in a pool or damp place during low tide (Mapstone, Underwood & Creese 1984). When experimentally deprived of hosts, *P. mufria* rapidly succumb to desiccation if kept out of pools during low tide, or are rapidly eaten by predatory whelks. Such predation is rare when limpets are on other gastropods, because their hosts can evade predators (Fairweather & Underwood 1983). *Patelloida mufria* also choose to climb onto hosts that have not previously been grazed by another *P. mufria* and are less likely to climb onto *Austrocochlea porcata* that have been treated to remove microalgae (Mapstone *et al.* 1984). Thus, the hosts provide habitat and food for *P. mufria*; the behaviour of the hosts enhances survival of the limpets, which show very complex patterns of behaviour in response to their hosts.

The fascinating array of interactive processes involving molluscs on rocky shores is still being investigated to shed light on fundamental processes affecting natural assemblages of species and is a major testing ground for ecological theory. Molluscs are important in intertidal systems because of their abundance, size and the variety of different trophic groups they represent, including grazers and predators. The major features of life history and ecology of molluscs on rocky shores – growth, size at reproductive maturity, reproductive success, local abundance, spatial patchiness, temporal fluctuations – are clearly influenced by complex interactions with other organisms and with each other. This brief introduction to the results of experimental tests of ideas about life histories, patterns of distribution and general natural history of molluscs demonstrates the need for much more experimental work. Undoubtedly, similar influences of competition for food and space and of predation and commensalism will turn out to be important in understanding the life histories of bivalves, chitons and octopuses and of gastropods in other areas of Australia.

Given so little current knowledge, it is unfortunate that molluscs are under such threat in much of temperate Australia, where the rocky coastlines of most states have no protection from human vandalism, especially the widespread practice of removing tonnes of molluscs for food and bait (Kingsford, Underwood & Kennelly 1991). The above review indicates that such wanton destruction of the molluscan fauna of rocky shores will have a cascade of effects on other organisms and on the assemblages as a whole (Underwood 1993; Underwood & Chapman 1995).

It is a pity that such important components of the marine fauna in most of the parts of Australia where there is urban development should be ignored by, or fall between the cracks of, the indifference of governments and their management agencies.

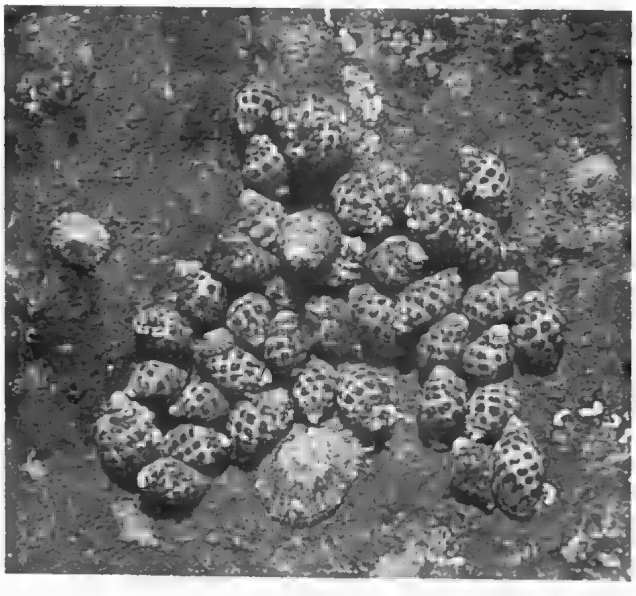


Figure 1.26 Predatory whelks, *Morula marginalba* (Muricidae), often live in cracks and crevices and come out to feed when weather, tides and waves are favourable. They eat prey near the crevices, creating a 'halo' of empty space around their shelters. Beyond this halo, barnacles and other prey are safe because whelks cannot find and eat them before the weather changes force the predators to retreat (Moran 1985c; Fairweather 1988). [A. Underwood]

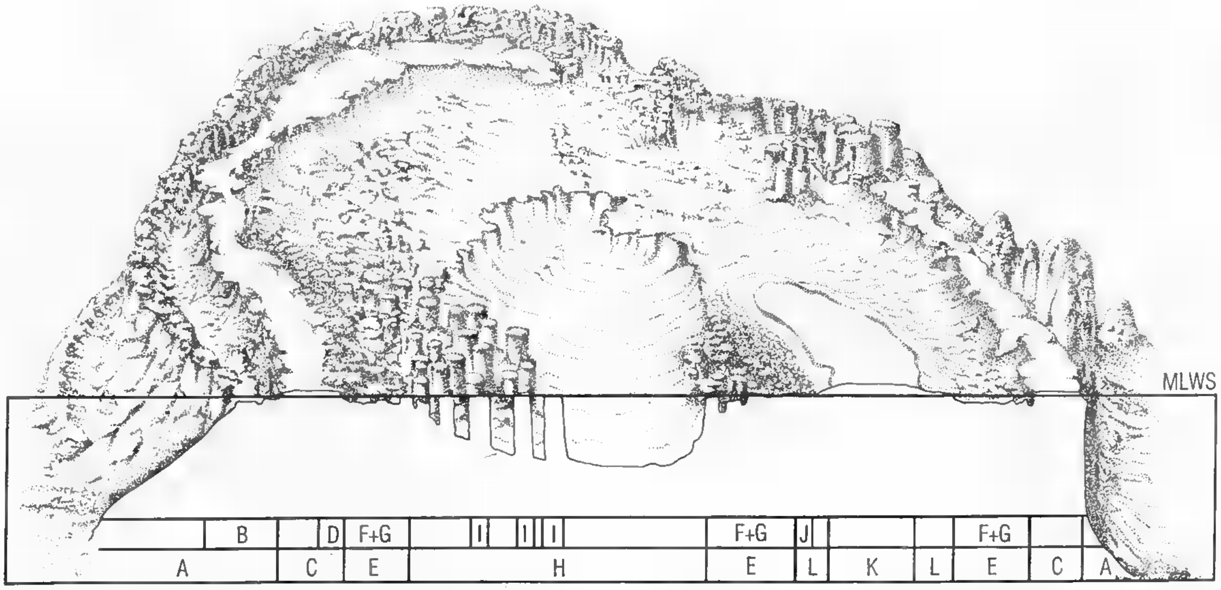


Figure 1.27 Distribution of topographical features and habitat zones within a coral reef, as indicated at the base of the vertical section. The ratio of the horizontal and vertical scales is 1 : 10. **A**, the reef slope, from adjacent sea bed at about 10–20 m to mean low water level of spring tides (MLWS), is characterised by a high cover of living corals and coral rock, interspersed with rubble and sand areas. **B**, the spur and groove zone of slope, in which buttresses alternate with surge channels. **C**, the flat-topped reef crest, or algal rim, extends above MLWS. It comprises calcareous rock cemented with encrusting coralline algae, with areas of fleshy algae or coral boulders. Reef crests are well developed mainly in areas exposed to wave action, and may be up to several hundred metres wide. **D**, rubble banks may form part of the reef crest. **E**, the reef flat (platform) is a broad, flat area of sand, rubble and limestone rock in varying proportions. Pools of water, up to 1 m deep at low tide, are interspersed with flat-topped conglomerates of living coral, coral rock and algae which may project slightly above the MLWS. In northern reefs, the flats may support seagrass beds. **F**, coral flats may be present within the reef flat, dominated by coral-algal conglomerates. **G**, the reef flat may also include sand or rubble flats interspersed with limestone rock and smaller coral/algae conglomerates. **H**, the lagoon is usually 5–15 m deep, and seagrasses may be present. **I**, patch reefs occur up to MLWS and support scattered colonies of coral and associated organisms. **J**, calcareous beachrock may be present in the lower intertidal zone. **K**, an island. **L**, the intertidal shore, formed of high sand or rubble deposits, including islands. (After Jones, O.A. & Endean 1973a, 1973b, 1976; Mather & Bennett 1984; Talbot, F. 1984) [I. Hallam]

MOLLUSCS ON CORAL REEFS

Coral Reef Environments

In Australia, coral reefs occur off the eastern, northern and western coastlines. As elsewhere in the world, these areas are preferred by reef-building corals for their shallow clear water, and water temperatures of 20°–30°C. The most extensive and best known system is the Great Barrier Reef, which stretches for more than 2000 km along the east coast. It includes more than 24 000 individual reefs which collectively occupy about 9% of the continental shelf waters in this area (Talbot, F. 1984).

Australian coral reefs are part of a large complex of reefs distributed throughout the Indo-West Pacific region – the northern Indian and western Pacific oceans – which in turn constitutes the world's largest set of coral reefs (Veron 1986). This region is a geographical centre of high diversity for many marine organisms, including molluscs (Kohn & Nybakken 1975; Wells, F.E. 1986a, 1990). However, studies of the geographic pattern of molluscan diversity are frustrated by a lack of good taxonomic knowledge of many families (Wells, F.E. 1990). Furthermore, there has been little scientific research into the ecology and natural history of the rich Australian coral reef mollusc fauna, although its diversity is illustrated in a variety of books, such as those of Coleman (1975), Hinton (1978, 1980), B.R. Wilson & Gillett (1979) and Short & Potter (1987).

Nevertheless, the taxonomic composition, ecology and natural history of Indo-West Pacific coral reef molluscs are broadly similar over a wide geographic area (Taylor, J.D. 1971; Kohn 1983a; Kay, E.A. 1984; Wells, F.E. 1986a, 1990), although particular species may vary in abundance among locations. This makes it possible to identify general features shared by coral reef areas throughout the Indo-West Pacific, and therefore this account is based on information from both Australia and the rest of the region. Most published work deals with 'prosobranch' gastropods of the intertidal and shallow subtidal areas, a bias reflected in the present text.

A high diversity of mollusc species is a characteristic feature of coral reefs (Coleman 1975; Kohn & Leviten 1976; Taylor, J.D. 1976), for which several explanations have been proposed. They include the great variety and diversity of environments within coral reefs generally (Taylor, J.D. 1971; Kohn 1983a), the high microtopographic complexity within some coral reef habitats (Kohn & Leviten 1976), and general within-habitat trends of increasing species richness at lower latitudes (Taylor, J.D. 1976; Spight 1977b).

Most of the species in several mollusc families occur in coral reefs of the Indo-West Pacific region and also contribute to the characteristic nature of Australian coral reefs. These include the gastropod families Strombidae (Pl. 25.3), Cypraeidae and Conidae (Pls 29.4, 29.5) and the bivalve family Tridacnidae (Pl. 24). Many other molluscan families encountered frequently on Australian coral reefs also share a significant number of species with other environments. For example, the gastropod families Cerithiidae, Volutidae (Pls 28.4, 28.5) and Terebridae and the bivalve families

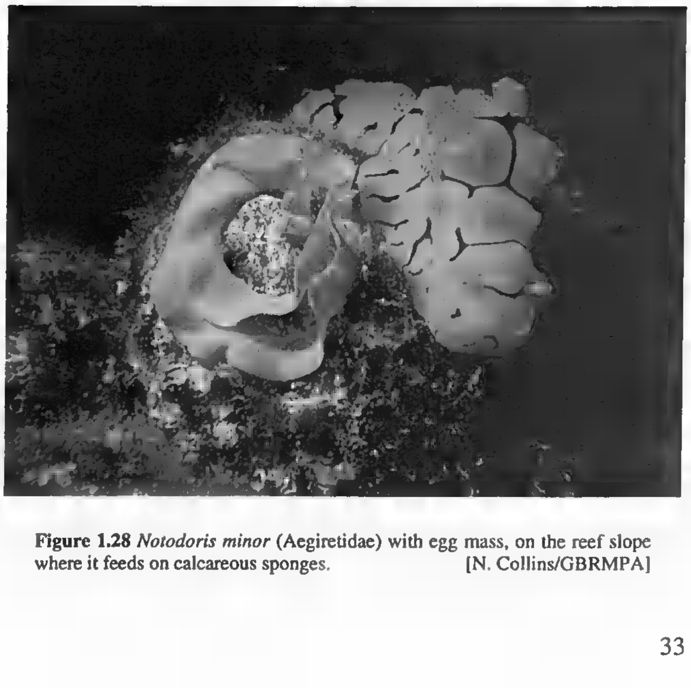


Figure 1.28 *Notodoris minor* (Aegiretidae) with egg mass, on the reef slope where it feeds on calcareous sponges. [N. Collins/GBRMPA]

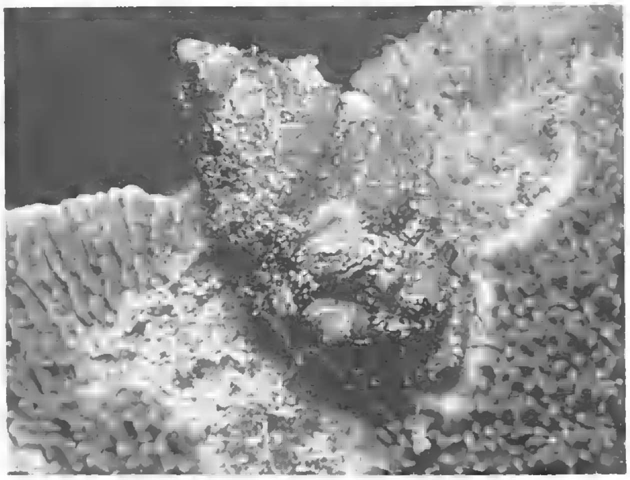


Figure 1.29 Species of the muricid genus *Drupella* consume living coral, leaving characteristic feeding scars, as shown by *Drupella cornus* at Heron Island, Great Barrier Reef. [L. Newman/A. Flowers]

Cardiidae, Veneridae and Tellinidae (Pls 15.2, 15.3) all include some species which are common in coral reefs as well as others common in sandy environments outside of coral reefs. This is not surprising since molluscan habitats within coral reefs display much of the range of habitat types present elsewhere. For example, Coleman (1975) described the habits of many sand and rubble dwelling molluscs which occur both within coral reefs and in other areas.

Diversity of Reef Habitats and Mollusc Communities

Coral reefs vary enormously in their pattern of growth and mode of formation, and a number of schemes have been devised to classify this variation (for example, Maxwell 1968; Stoddart 1978). Reefs are classified largely on the basis of their topography and position. Widely used categories within the Great Barrier Reef complex include: Fringing Reefs, which lie immediately adjacent to volcanic islands or continents; the generally elongate, narrow Linear, Ribbon, or Wall Reefs which are aligned along the edge of the continental shelf; and oval Platform Reefs, scattered on the continental shelf. Coral atolls are scattered throughout the Indo-West Pacific region, and are formed as a result of the growth of reef-building corals upon submerged volcanic peaks.

Within each reef there is a variety of different 'zones' or topographically-based habitat types, the spatial arrangement of which varies both within and between reef types. The number of recognised zones and the names applied to them also vary among published descriptions. The range of possible topographical features and the zones within a platform reef are shown in Figure 1.27. Five major habitat zones are commonly present: the reef slope, reef crest and reef flat, a lagoon which is often absent from small reefs, and an intertidal shore if an island is present. Within each zone a wide variety of microhabitats is available to molluscs. These comprise many different combinations and arrangements of sand, coral rock, algae or live coral substrata (Kohn 1983a; Taylor, J.D. 1971). Some microhabitats are shared between zones. For example, submerged sand, rock, dead coral and live coral are all available to settling larvae in parts of the reef flat, reef slope and lagoon zones, and each microhabitat may support similar sets of mollusc species across zones (Taylor, J.D. 1971).

Figure 1.30 *Conus omaria* (Conidae), upper right, feeding on the common fasciolariid *Pleuroploca filamentosa*. [Clay Bryce/WA Museum]

The number of mollusc species typically present in an area varies among the zones within a reef. All microhabitats within the intertidal shore zone support distinctly fewer species than the other zones, although the total mollusc density within this zone may be very high (Taylor, J.D. 1971; Grassle 1973; Kohn 1983a). Variation in species numbers in the other zones is poorly documented. Large numbers of species are often present where microtopographical complexity occurs together with high algal abundance, such as in parts of the reef crest (Taylor, J.D. 1971; Grassle 1973; Reichelt 1982; Reichelt & Kohn 1985), or seagrass beds within the reef flat (Taylor, J.D. 1971). Microhabitats of this type probably favour high mollusc diversity because they provide both a high density of food and refuges from predation and disturbance (Kohn 1983a; Reichelt & Kohn 1985).

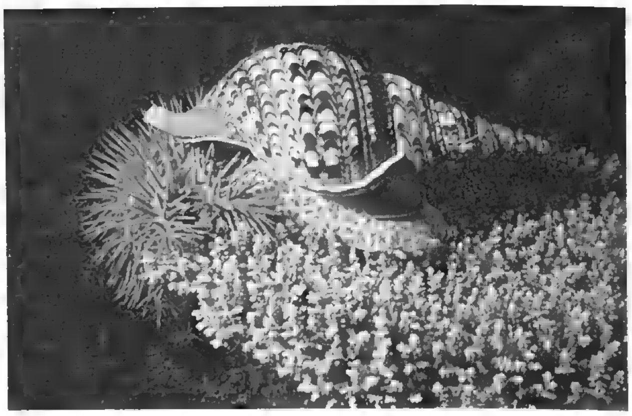


Figure 1.31 *Charonia tritonis* (Ranellidae), here eating a crown-of-thorns starfish, *Acanthaster planci*, is one of the largest gastropods and may attain lengths of 450 mm. [Great Barrier Reef Marine Park Authority]

Live corals support relatively few mollusc species (Robertson, R. 1970) with the result that areas with an extensive cover of live coral generally do not have high molluscan diversity, whereas areas of dead coral within or adjacent to live coral colonies may support a larger number of bivalve and gastropod species (Taylor, J.D. 1971). Coral polyps have tentacles with stinging nematocysts, which enable them to feed on mollusc larvae and also to repel potential predators. However, a number of mollusc species have evolved the ability to cope with these defences, and live in close association with live corals in a variety of interesting and specialised relationships. Species that feed on live hard and soft corals, such as nudibranchs and some members of the gastropod families Ovulidae, Epitoniidae and Muricidae (including coralliophilines), often use only a few coral host species from the wide range available (Robertson, R. 1970).

Many of these coral-feeding molluscs are strikingly coloured, for example, the *Epitonium* species found on dendrophylliid corals of the reef slope – both mollusc and coral equally bright orange – and many nudibranchs, such as *Notodoris minor* (Fig. 1.28), which is bright yellow (Page & Willan 1988). Other species with plain shells may be encrusted with various marine organisms such as pink or purple coralline algae.

Figure 1.32 The giant clam, *Tridacna gigas* (Tridacnidae), on a sandy area of the reef slope. [Great Barrier Reef Marine Park Authority]

Among these molluscs are many coral-feeding muricids, such as *Drupella* species, which hide at the bases of coral colonies during the day and emerge at night to feed (Fig. 1.29). Population outbreaks of a *Drupella* species in north-western Australia in the late 1980s led to widespread loss of live coral cover, creating management dilemmas similar to that of the crown-of-thorns starfish on the Great Barrier Reef. Whether this is a new phenomenon or a long-term natural cycle is unknown.

Coral colonies often contain numerous molluscs which bore into the coral matrix. These include vermetid and coralliophiline gastropods and lithophagid bivalves (Robertson, R. 1970; Hutchings & Peyrot-Clausade 1988; Massin 1988), which can only be extracted by dissolving the coral. Specialisation for symbiotic life is also a feature of the gastropod family Eulimidae, many members of which live as parasites on or in echinoderms, particularly sea cucumbers and seastars (Pl. 24.5; Warén 1983).

The huge diversity of coral reef habitats and molluscs frustrates general statements about the families, genera or species which are typically found in any area. The following paragraphs broadly describe some characteristic patterns, though exceptions to almost every statement can be found. Coleman (1975) described in some detail the natural history of many mollusc species of Australian coral reefs.

The reef slope, the zone with the highest coral cover, is the home for many of the specialist coral-feeders. It often includes large coral heads, such as species of *Porites*, which grow to several metres in diameter on the reef slope and contain many coral-boring molluscs, for example, some members of the bivalve families Gastrochaenidae, Pholadidae and Teredinidae. Bivalves may be cemented to these corals, sometimes in large clusters, among them tridacnids, chamids, gryphaeids and spondylids (Pl. 12.5).

More mobile and less specialised predatory caenogastropods in a wide range of families also occur in the reef slope zone, including ranellids, muricids (Pl. 27.4), fasciolariids, volutids, terebrids, conids, columbellids, buccinids, harpids, mitrids and others. These predators vary greatly in size and habits, and feed on a wide range of marine organisms, including other molluscs (Fig. 1.30), polychaete worms, ascidians, and other small invertebrates. A notable ranellid of the reef slope is the giant triton, *Charonia tritonis*, which has achieved fame as a predator of the crown-of-thorns starfish, *Acanthaster planci* (Fig. 1.31). Many species are small and easily overlooked since they hide in crevices or among pieces of rubble. Others bury in the sand at the base of the slope, probably to escape being eaten by diurnal predators such as rays and tuskfish (Labridae), and many emerge to feed at night. The brightly coloured giant clam, *Tridacna gigas*, sits unattached on the sand surface in these areas (Fig. 1.32). Like other tridacnids, this species obtains both its colourful mantle and part of its nourishment from zooxanthellae that grow within its tissues.

The reef crest and coral platform areas may also support a variety of different predatory neogastropods (Reichelt & Kohn 1985). Herbivorous trochids and turbinids are often common. During the day they retreat into crevices and at night they emerge to graze on the thin film of algae which coats most surfaces. The sheltered undersides of dead coral boulders which are thrown up onto the reef crest by storm waves provide habitat for a further suite of species, including cypraeids (Fig. 1.33), which graze on encrusting algae and/or colonies of sponges and ascideans. Such generalist grazers also feed on the leaf epibiota of seagrasses and fleshy algae. A variety of bivalves may also be found cemented to the coral boulders, as on the reef flat (see below).

In sandy parts of the reef flat, large numbers of herbivorous gastropods of the families Strombidae and Cerithiidae often aggregate on the surface of the sand. Even larger numbers of molluscs spend most of their lives buried beneath the surface of the sand. These include various predatory caenogastropods, especially mitrids, volutids, conids and naticids (Pl. 10.1), as well as a wide range of bivalves, members of the families Veneridae, Cardiidae, Lucinidae, Tellinidae and Arcidae. Many of these species are suspension-feeders, sifting organic detritus from the sand within which they live. Most of these molluscs can only be seen by lifting off the top few centimetres of sand, although some betray their presence to careful observers by the siphon which protrudes just above the sand surface for intake of oxygen-rich water. Octopus lairs can be located by the concentrations of empty shells around their entrances. The grain size of sediment, ranging from large rubble particles to fine silt, and the presence or absence of seagrass cover have a major influence on exactly which species occur in an area of reef flat habitat.

Figure 1.33 Like most cowries, *Cypraea cribraria* (Cypraeidae) is an Indo-Pacific species, but also occurs subtropically from south-western Western Australia to southern Queensland. Australian populations are markedly variable in form and colour, a feature common to many cowry species. [L. Newman/A. Flowers]

Figure 1.34 *Limaria fragilis*, a free-swimming member of the Limidae, shelters under coral boulders in pools and lagoons. [L. Newman/A. Flowers]

The coral/rock/algal conglomerates found within parts of the reef flat support a different range of molluscs, including abalones (family Haliotidae; Pl. 22.4) and sea hares, which hide during the day but emerge at night to graze on the surface. The many holes and crevices also contain cowries, nudibranchs and a range of neogastropods. Bivalves, such as tridacnids, ostreids, spondylids, chamids, pteriids, mytilids and limids (Fig. 1.34), become cemented into the conglomerates or attached by byssal threads to the underside of coral slabs and clumps, and obtain food by filtering small planktonic organisms from the surrounding water.

The lagoon habitat comprises mainly the sandy lagoon floor, which supports a molluscan community dominated by a similar group of families to that of the sandy parts of the reef flat and reef slope, although the species composition is different. Large helmet shells (Cassidae), which feed on echinoderms, are sometimes a feature of lagoon floors. Large coral heads and coral/rock/algal conglomerates found in lagoons have a molluscan fauna that broadly resembles those of similar areas in the reef flat and reef slope.

The intertidal shore has areas of sand, in which buried bivalves may be found, and beach rock. The latter typically supports chitons and gastropods that can tolerate exposure, such as cerithiids, neritids and planaxids (Fig. 1.35), and which graze on algal films. The intertidal rocky shores of coral reefs support a group of molluscs broadly similar to that found on other rocky shores in the same general region (Endean, Stephenson & Kenny 1956).

Ecology of Coral Reef Mollusc Populations

The persistence of any species within a particular coral reef area depends on the life cycle processes of reproduction, dispersal, settlement, growth and survival. Intraspecific variation in shell size, shape, and colour of particular molluscan species collected from different reefs provides information useful in understanding the dispersal and replenishment of populations. For example, many cowrie species display striking examples of divergence in shell shape and size among widely separated populations within their geographical range (Tissot 1984). Since the veliger larvae of many cowries are pelagic for a only few days or less (Wilson, B.R. & Gillett 1979; Kay, E.A. 1985), their ability to disperse is restricted, which may result in the accumulation or maintenance of genetic differences between the populations of different areas.

The opportunity for the development of regional variation is even greater in taxa in which a shelled juvenile hatches directly from the egg, as do volutes. A good example is variation in the colour of the volute *Cymbiola pulchra* on the Great Barrier Reef (Wilson, B.R. & Gillett 1979). Life histories involving direct development have also favoured the evolution of many of the Australian endemic species (Wells, F.E. 1990). In contrast, many other reef molluscs have a life cycle which includes a pelagic larval phase lasting several weeks (for example, see Perron 1981). The probability of these larvae dispersing to suitable reef habitat hundreds of kilometres from their natal reefs depends on both the pattern of ocean currents in the area and the behaviour of larvae. Present knowledge of both currents and larval behaviour is still sketchy (Williams, W.D., Wolanski & Andrews 1983; Leis 1986), so that the area over which the offspring from any Australian coral reef mollusc population disperse is unknown.

Population densities of many mollusc species within a particular reef may fluctuate greatly between years if the number of larvae recruited to the reef varies. Other irregular variations in population density are created by the effects of tropical cyclones on both the molluscs and their microhabitats (Frank 1969; Kohn 1980). Both these processes will cause fluctuations in numbers over a time scale of decades.

An understanding of the ecology of mollusc populations is needed for planning for the conservation of exploited species. In pre-European times, many coral reef mollusc species were gathered by the indigenous people, mainly for food (Fig. 1.36). Species within the Strombidae and Tridacnidae were often important in this respect (Catterall 1986).

Exploitation patterns changed dramatically after European settlement, and the current use of Australian coral reef molluscs is discussed in the section on Economic Significance. In the past, burying behaviour and the presence of deeper subtidal populations provided many mollusc species with refuges from traditional styles of human predation. However, the use of new fishing technology, including SCUBA equipment, dredging, and fast boats, will increase the risk of local population decline (Wells, S.M. 1981; Catterall & Poiner 1987). The rate of replenishment of depleted areas depends largely on the availability of settling larvae, which should vary according to a species' life history in the manner described above. Taxa, such as volutes, which lack a pelagic larval stage, would be less likely to broadcast propagules to depleted reefs, and are especially vulnerable to modern exploitation.

Clearly, many challenging questions concerning the ecology and natural history of coral reef molluscs remain to be answered.

MOLLUSCS IN MARINE AND ESTUARINE SEDIMENTS

The diversity of marine sedimentary habitats, each with its own suite of physical and biotic conditions, is such that the ecology of the molluscs of marine sediments is best understood by separate reviews of each major habitat. The habitats considered here are intertidal sandy beaches, shallow subtidal sand plains, coastal seagrass beds, the continental shelves and deep-sea sediments, estuarine sandy and seagrass environments, and mangroves.

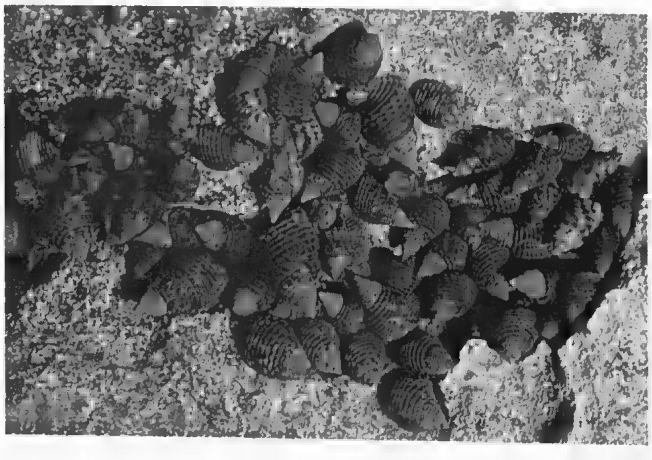


Figure 1.35 A cluster of *Planaxis sulcatus* (Planaxidae) on intertidal beach rock, Heron Island, Great Barrier Reef.
[L. Zell/Great Barrier Reef Marine Park Authority]

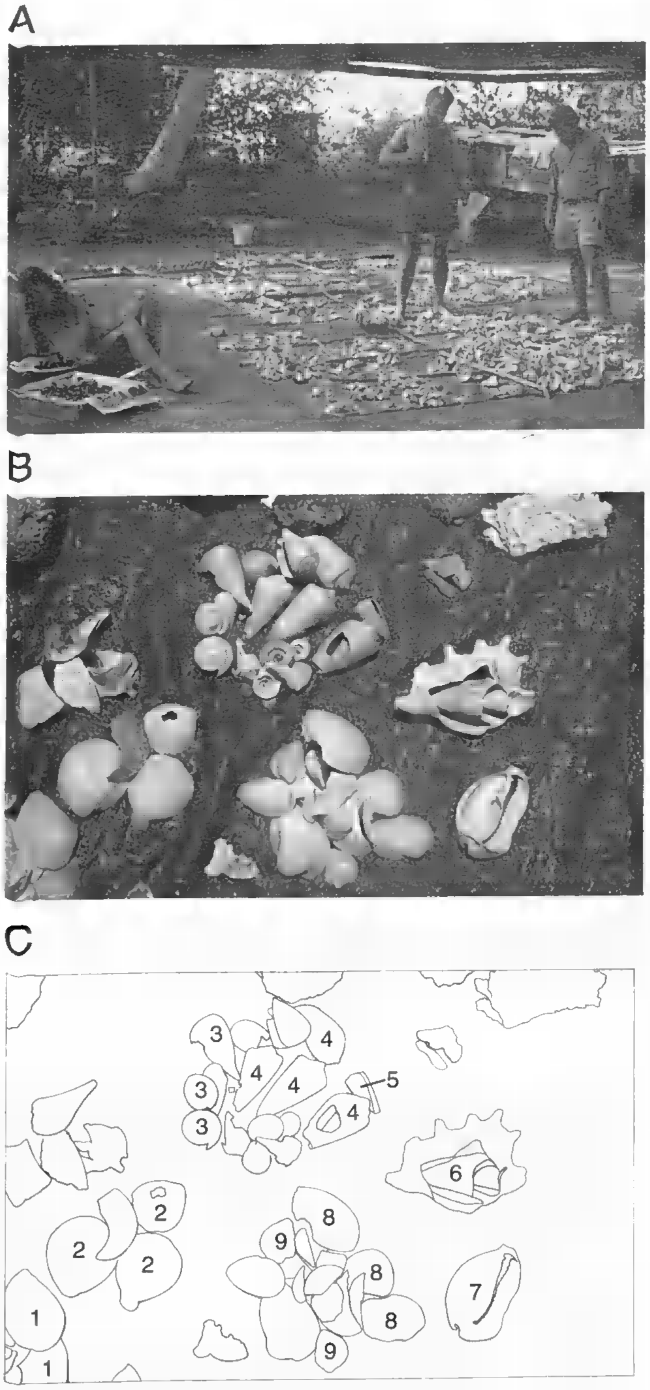


Figure 1.36 Shell middens provide a record of the pattern of human exploitation of coral reef molluscs stretching thousands of years into the past. Holes were made in the shells for meat extraction. A, archaeologists in the process of sorting shells from a midden on a coral cay off the coast of New Guinea. **B**, a selection of these shells, mapped in **C**. **1**, *Acrosterigma reeveanum* (Cardiidae); **2**, *Asaphis violascens* (Psammobiidae); **3**, *Strombus luhuanus* (Strombidae); **4**, *Conus planorbis*; **5**, *Conus vitulinus* (Conidae); **6**, *Lambis lambis* (Strombidae); **7**, *Cypraea* cf. *tigris* (Cypraeidae); **8**, *Anadara antiquata* (Arcidae); **9**, *Fragum fragum* (Cardiidae).
[A, B, C. Catterall; C, I. Hallam]

Intertidal Sand Beaches

The intertidal sandy beach is a physically rigorous environment which experiences to varying extents the impact of waves, substantial water currents, and widespread sediment transport, in addition to the periods of aerial exposure that characterise any intertidal habitat. Sediment transport occurs on short time scales with resuspension during each wave. Storms can erode more than 1 m of beach sands within hours and most beaches experience a seasonal cycle of inshore and offshore movement of sediment, as a consequence of seasonal variation in wave action (Komar 1976). Intense wave action produces erosion from intertidal beaches and wide gentle slopes to the subtidal contours, whereas calm seas return the sand to the intertidal zone and build back a more steeply sloping intertidal beach.

Presumably because of this physically rigorous environment, few molluscan species have adapted to life in the sediments of the intertidal beach (for example, Dahl 1953). Those that do live in this environment are typically mobile, to respond to the constraints imposed by the extensive mobility of the sediments, and thick-shelled, perhaps in part to tolerate the forces of breaking waves (Dahl 1953; Leber 1982). Three potential food sources make the intertidal beach a food-rich environment, and as a result, those few molluscs that inhabit ocean beaches can be extremely abundant because of limited competition from other species and because of the rich food supply. The substantial flow of water along the beach continually renews planktonic food supplies. The intertidal beach also provides well-illuminated substrata for growth of various microalgae, such as benthic diatoms. In addition, waves bring ashore and deposit large quantities of detritus on beaches, especially seagrasses, kelps and other algal debris (Lenanton, Robertson & Hansen 1982).

Worldwide, most high-energy intertidal beaches, particularly in temperate zones, are inhabited by a single, abundant species of suspension-feeding bivalve mollusc. Species in genera such as *Spisula*, *Paphies* and *Mactra* can be quite common on many sand beaches. These bivalves are rapid burrowers, capable of reburial when sediments erode away. Because they are frequently large and occur locally in high densities, living bivalves are often economically valuable resources for human consumption. In cold temperate climates, razor shells in the genera *Ensis* and *Siliqua* can also be found on intertidal sand beaches. These bivalves are such rapid and deep burrowers that one often cannot dig fast enough or deeply enough to capture them. On warm temperate beaches, smaller suspension-feeding bivalves in the family Donacidae, known as pipis in Australia (Fig. 1.37), are extremely widespread geographically. *Donax* species tend to exhibit large spatial and temporal fluctuations in abundance. When and where they are common, they are so dense that they may compete for space with mole crabs (*Emerita* species), which often co-occur at high density. Worldwide on warm temperate and subtropical high-energy beaches, species of *Donax* and *Emerita* form important prey for surf fishes as well as for shorebirds and crabs such as ghost crabs, *Ocypode* species (Jones, A.R. & Short 1995).

On the Australian continent, the ecology of molluscs on intertidal beaches is little understood. As on other continents, suspension-feeding bivalves are the dominant group of molluscs represented on high-energy beaches (for example, Kershaw 1958; Ponder, Colman, Yonge & Colman 1981; Dexter 1984). Pipis in the genera *Donax* (*Plebidonax*) and *Paphies* (*Donacilla*) occur, but rarely in the same high densities as *Donax* on other continents. The wedge shape of these bivalves suggests a functional significance for this common morphology of the small shallow-burrowing bivalves in the surf zone (Stanley 1970). *Paphies* species also occur subtidally in Australia, for example, *P. elongata* in South Australia, where it is preyed upon by the gastropod *Polinices conicus* (Laws & Laws 1972, as *Donacilla angusta*).

Shallow Subtidal Sand Plains

Shallow sand plains extend from the surf zone out to about 20 m depth. This habitat is sufficiently shallow and close to the coast that the energies of ocean waves and longshore and offshore water currents seriously impinge upon the bottom. These physical forces maintain a sandy substratum by preventing much deposition of fine particles. Sediment transport is substantial, even outside the surf zone, because these sand plains participate in both longshore sediment transport and seasonal inshore and offshore sand transport. Simple storm events can erode or deposit up to 1 m of sediment in this environment (Morin, Kastendiek, Harrington & Davis 1985).

Figure 1.37 *Donax columbella* (Donacidae), from the intertidal zone at Fremantle, Western Australia, showing the extended foot and siphons during reburial. [C. Bryce/Western Australian Museum]

The rigorous physical environment interacts with biological factors to determine patterns of distribution and abundance of the benthic fauna of the subtidal sand plains. Wave action and water currents increase in intensity towards the shallow (beach) end of this habitat. The substantial currents create an excellent environment for growth of those suspension-feeders that can withstand the physical forces.

Strong zonation of species is produced in these subtidal sand plains by the combination of the gradient in wave intensity and intense competition for space among individuals of the largely suspension-feeding macrofauna of this habitat (Kastendiek 1982; Morin *et al.* 1985). Predation is typically more intense at greater depths, in part because the predators are larger, surface-active and more susceptible to wave dislodgement in shallow water than the partially anchored prey (Kastendiek 1982). Sand dollars (echinoids) are often prominent, along with sea pansies – colonial cnidarians of the pennatulacean genus *Renilla.* The molluscs of this habitat include suspension- feeding bivalves, such as large cardiid cockles and others, such as tellinids and venerids. The filter-feeding trochid *Bankivia fasciata* is a very important component in temperate Australia, and other trochids such as *Umbonium* species are important in the tropics. Because light penetrates readily to the bottom in this environment, benthic algae grow sufficiently well to support numerous gastropods.

This environment is also characterised by the presence and activity of predatory gastropod species, such as naticids of the genera *Polinices* and *Natica,* which drill countersunk holes in the shells of their molluscan prey, and olivids, terebrids (Fig. 1.38A), marginellids, buccinids and volutes. Scavenging gastropods such as *Nassarius* species (Fig. 1.38B) are prominent members of this system (Morton, B. & Britton 1991). Wherever any hard-bottom relief is found in the sand plains, octopuses can be important predators that include many bivalve and gastropod molluscs in their diets. Two groups of molluscs common worldwide in this environment are the poorly understood ectoparasitic gastropod families Pyramidellidae and Eulimidae. Eulimids live on the exterior of many echinoderm species whereas pyramidellids live on some molluscs and other invertebrates in this habitat (Crossland, Alford & Collins 1991).

In Australia, the shallow sand plain has received very little attention from molluscan ecologists. *Glycymeris* species (Glycymerididae) can be abundant in temperate Australia (Kershaw 1958) and some cardiids prominent on Australian shores (Wilson, B.R. & Stevenson 1977) are evident in warm-temperate sand plains on other continents. The ecology of Australian sand plain molluscs is likely to resemble that of molluscs in this habitat elsewhere.

Coastal Seagrass Beds

Seagrass beds occur around the entire coast of Australia in shallow, protected marine lagoons and mouths of some true estuaries. Seagrass beds are most prominent and widespread along coastlines of minimal riverine runoff and relatively oligotrophic waters, because high turbidity can exclude seagrasses from certain areas (Thayer, Kenworthy & Fonseca 1984). These beds are most extensive along the southern half of the Australian continent, where they are a major feature of lagoonal systems (Keough & Jenkins 1995).

Seagrasses fix substantial quantities of carbon during growth (Kirkman & Reid 1979). However, very little of this production is utilised directly by herbivores (Fenchel 1977; Robertson, A.I. & Mann 1980; Zieman 1982). In Australia, dugongs and black swans, like green turtles and black brant geese elsewhere, consume some seagrasses directly (and probably ingest some attached molluscs, as well). Most carbon fixed by seagrasses enters into detrital food chains of the lagoonal and nearshore seafloor, through shedding of leaves which occurs quite frequently. In addition to the direct importance of seagrass to detrital food chains, the presence of abundant seagrass plants has a significant impact on the marine faunal assemblages (for example, Thayer, Wolfe & Williams 1975; Poiner 1980; Summerson & Peterson 1984).

Seagrass habitats are important for molluscs both directly and indirectly (Heck & Wetstone 1977; Heck & Orth 1980). Seagrass provides a firm surface in an environment where mobile sediments otherwise dominate (Heck & Wetstone 1977). Such emergent features offer a surface for colonisation by numerous microalgae (Kitting, Fry & Morgan 1984). This epiflora is grazed by abundant small gastropods, particularly trochids (Nielsen & Lethbridge 1989), amphipod crustaceans and other micrograzers (Kitting *et al.* 1984). Even some chitons graze the leaf surfaces of

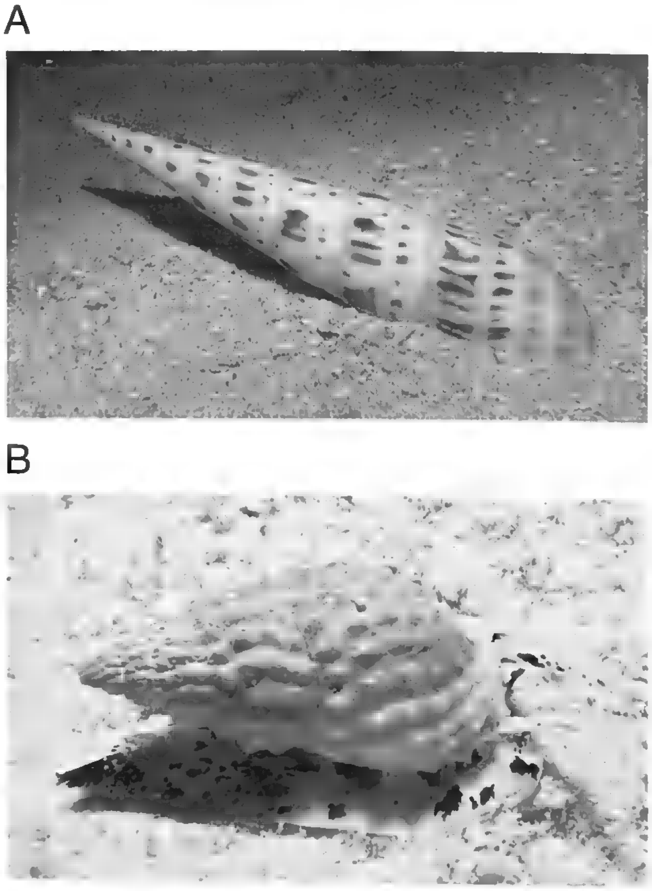


Figure 1.38 Carnivorous and omnivorous gastropods are important components of the subtidal sand plain fauna. **A**, *Terebra maculata*, largest of the Terebridae, preys on surface or near-surface worms and other invertebrates in littoral and sublittoral sandy areas. **B**, a scavenger, *Nassarius papillosus* (Nassariidae). [C. Bryce/Western Australian Museum]

Australian seagrasses (Roberts & Wells 1980; Pl. 7.2). These grazers in turn serve as prey for abundant mobile consumers, especially fishes, crabs, rock lobsters, and octopuses, and contribute to the value of seagrass beds as important nurseries for young fishes and crustaceans (Young, P.C. 1978). Such young predators commonly enter the seagrass beds in spring and grow and develop there through the summer before departing for adult habitats in autumn.

The seasonally variable predation on grazers commonly leads to tremendous seasonal fluctuations in the abundance of the prey species, including many gastropods (Hutchings & Recher 1974; Wadley 1981). This nursery function of estuarine and lagoonal seagrass beds makes them extremely valuable habitat for the maintenance of coastal fisheries. The production of benthic invertebrates, especially the numerous small epifaunal gastropods, in coastal seagrass beds of the southern portion of Western Australia leads directly to high production of the commercially important top carnivore, the rock lobster (Joll & Phillips 1984). Populations of epifaunal molluscs may decline or disappear altogether after loss of seagrass through pollution (for example, as discussed by Larkum 1976; Wells, F.E. & Threlfall 1980a).

Seagrass blades are also colonised by hydroids, sponges, and bryozoans, which themselves harbour and feed many predatory nudibranchs. Short-lived colonial animals like hydroids are prey for eolid nudibranchs, while dorids are associated with more permanent colonial prey such as sponges (Todd 1981). Seagrass ecosystems are highly productive at all trophic levels and turnover of populations is generally great because of high consumption rates (Keough & Jenkins 1995).

Seagrass plants also provide a stable subsurface structure, and form attachment surfaces for byssate bivalves, such as mussels, *Brachidontes*, *Mytilus* and *Modiolus* species, and some juvenile scallops and date mussels. These bivalves require a firm, stable subsurface attachment of the byssal anchoring threads and consequently their patterns of distribution and abundance closely mirror the distribution of seagrass.

The subsurface roots and rhizomes of the grasses and algae greatly affect the penetrability of the sea floor by digging and burrowing predators, such as benthic fishes and crustaceans (Peterson 1982b; Summerson & Peterson 1984), and thus provide a partial refuge for infaunal invertebrates, including many bivalve molluscs. Seagrasses also enhance the abundances of many other soft-bottom species (Reise 1977).

Abundance of benthic molluscs may also be enhanced by the indirect effects of seagrass blades, which project into the water column and moderate currents (Peterson, Summerson & Duncan 1984). Emergent seagrass blades slow water currents near the bottom by deflecting the flow around and above the seagrass canopy. The local slowing and deceleration of tidal currents enhances deposition of organic-rich fine particles, detritus, and even larvae (Peterson 1986). This process adds organic material to the sediments which can support an abundance of deposit-feeding species, such as tellinid bivalves. Suspension-feeders also benefit from the presence of seagrasses (Jackson 1972; Summerson & Peterson 1984). Some portion of the enhanced invertebrate density inside seagrass beds may be explained by hydrodynamic entrapment of larvae by the projecting seagrass blades (Peterson 1986). Because the zone of active current deceleration and particle deposition is the upstream margin of the seagrass bed, it is possible that food particles and larvae are filtered out at the edges and become depleted further towards the interior of the bed. If so, the scale of patchiness of seagrass beds and the location within a bed will be major factors contributing to the pattern of response of benthic molluscs. Seagrasses are often found in distinct zones relative to both tidal elevation and distance from the open sea, as are the molluscs associated with them.

In Australia, coastal seagrass beds seem to play the same role that they do elsewhere in the world (Bell, Burchmore & Pollard 1978; Conacher, Lanzing & Larkrus 1979; Scott, J.K. 1981; Hutchings 1982). They appear to be more abundant, however, along the open coast of Australia than along the margins of other continents. Beds of *Posidonia* or *Amphibolis* species are especially prominent. The genus *Heterozostera* is commonly found at low intertidal levels (for example, Hutchings 1982; Peterson & Black 1986) whereas *Posidonia* commonly forms extensive meadows below the low tide mark (for example, Hutchings 1982; Wells, F.E. *et al.* 1985). The lower boundary of *Posidonia* beds is probably set by light availability, because deeper unvegetated basins often occur further from shore. The distribution of seagrasses in tropical Australian waters was discussed recently by Mukai (1993).

Continental Shelf

The continental shelf is not a habitat readily accessible to scientists and consequently has been little studied by molluscan ecologists. Molluscan densities in continental shelf sediments are usually not very high. However, the diversity of shelf molluscs is reasonably high, with all trophic groups represented: suspension-feeders in areas where currents are sufficient; deposit-feeders ingesting detritus from terrestrial, coastal and oceanic sources; grazers consuming benthic microalgae directly in zones of sufficient water clarity and light penetration; scavengers; ectoparasites; and predators. Bivalves are either deposit-feeders or suspension-feeders, whereas gastropods occur in all of the trophic groups. Some shelf gastropod species have broad geographic ranges because their larvae are long-lived, teleplanic forms (Scheltema, R.S. 1971).

On the continental shelf various crustaceans, such as tanaids and phoxocephalid amphipods, prey on small molluscan recruits. Prawns, crabs and stomatopods consume larger molluscs, as do demersal fishes and asteroids. Seastars typical of soft substrata, such as species of *Astropecten* and *Luidia*, are prominent predators on small molluscs of continental shelves worldwide.

Figure 1.39 Scallops, *Pecten fumatus* (Pectinidae), attempting to leap clear of a scallop dredge off Goose Island, Bass Strait. [CSIRO Fisheries]

Commercially harvestable populations of scallops are found on many continental shelves, where adults are susceptible to capture in dredges as they lie on the sea floor (Fig. 1.39). Such scallop populations are typically quite variable in time and space, which complicates their efficient utilisation (for example, Dredge 1981). Seastars of soft-bottom habitats can be significant predators on juveniles of these scallops.

Molluscan faunas of Australian continental shelves are probably similar to those elsewhere. They are little studied, although there are commercially important scallop populations in Western Australia around Shark Bay, in Tasmania, and off the Queensland coast (for example, Dredge 1981).

Deep-sea Sediments

Molluscs, especially bivalves and gastropods, extend even to the deepest parts of the soft sea floor. Because of the costs in sampling time and ship support, the collection of just a single sample from the floor of the deep sea is expensive and therefore rare. Use of a device like the epibenthic sled (Sanders, H.L. 1968), which is towed some distance along the bottom and, therefore, collects animals from a wide area, revolutionised benthic sampling from the deep sea. Sampling with the epibenthic sled has demonstrated (Sanders, H.L. 1968) that the total density and biomass of the soft-sediment benthos declines with increasing water depth. This situation might be expected from the greater separation between the energy source at the surface and the benthic fauna and from the generally greater distances from coastal zones with their higher productivity.

Species diversity, including that of bivalves, increases with depth. Three factors have been proposed to explain the high diversity of benthos in the deep sea: the greater physical stability of the environment has allowed greater diversification by evolution of more narrowly specialised forms (Sanders, H.L. 1968); greater disturbance by predators prevents competitive exclusion and thus maintains high species diversity (Dayton & Hessler 1972); and the great area of deep-sea habitat worldwide has led to evolution of many species by chance alone (Abele & Walters 1979). Despite the general pattern of increasing species diversity in the benthos with depth, gastropod diversity appears lowest at abyssal depths, perhaps because of extremely low productivity at these depths (Rex 1973).

With increasing water depth, molluscs of marine sediments become progressively smaller in body size. A reduced incidence of planktotrophic larvae accompanies this trend in body size (Thorson 1950; Ockelmann 1965). In explanation, Thorson (1950) proposed that food may not be sufficiently concentrated in the open ocean gyres for planktotrophic larvae released by deep-sea organisms to feed and grow successfully. Furthermore, the added risk of mortality and increased energetic cost of movement may outweigh the potential benefits gained by planktotrophic larvae of deep-sea benthic molluscs and other invertebrates if they were to ascend to feed in the photic zone, and subsequently descend to settle and metamorphose to adult form (Vance 1973).

Alternatively, because body sizes of benthic invertebrates are so small in the deep sea, it is possible that constraints on body size may be involved in determining reproductive mode. For example, from an allometric viewpoint, the greater difficulties faced by larger animals in providing adequate brood care may limit brooding of young to smaller-bodied species (Strathmann & Strathmann 1982).

In the deeper waters off Australia, the soft-bottom molluscan assemblages are likely to exhibit patterns similar to those shown worldwide and may even include some of the same widely distributed species. This suggestion receives support from the recent discovery off the North-West Shelf, in depths of 300–500 m, of over 100 mollusc species with close affinities to the deep-sea fauna long known from the Philippines-Japan vicinity but not previously described for Australia (Kosuge 1985). However, so far as is known, deep-sea faunas of southern Australia appear to be mainly endemic.

Estuaries

Molluscs are especially important components of all estuarine and marine lagoon ecosystems (Wells, F.E. & Roberts 1980; Inglis 1995). The three most critical physical variables in these low-energy systems affecting the types and abundances of the constituent molluscs are salinity, substratum type and exposure. This review of the ecology of estuarine molluscs describes and explains the patterns generated by variation in these three major variables (Fig. 1.40).

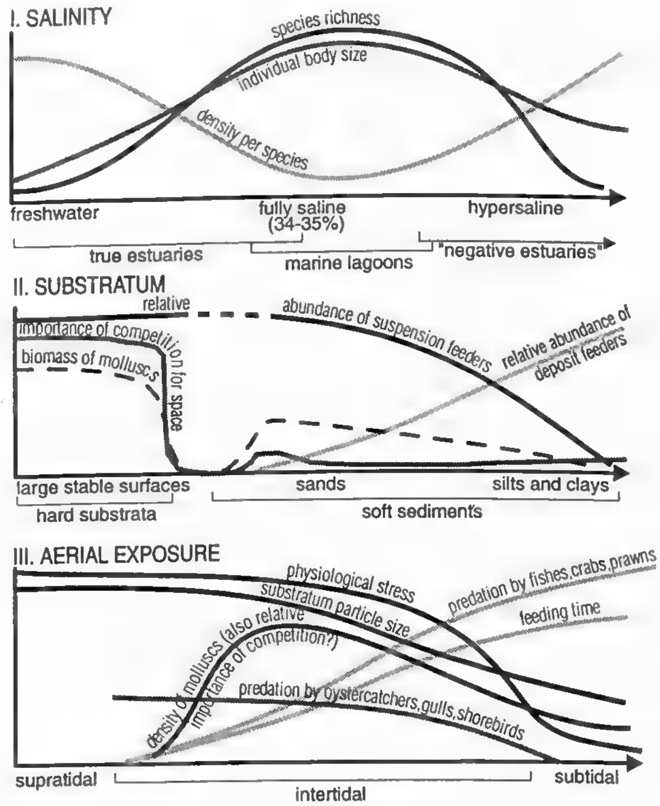


Figure 1.40 The three fundamental physical determinants of patterns of molluscan distribution in estuaries. [C. Peterson]

The salinity regime is a principal determinant of molluscan distribution and abundance. By definition it is the factor that separates a marine lagoon, with its high diversity of stenohaline molluscs, from a true estuary with reduced numbers of euryhaline molluscs. The type of bottom substratum available for molluscan occupation also explains many distributional patterns of this largely benthic phylum.

Mobile, soft sands and muds dominate the floors of estuaries and marine lagoons. Within the range of sedimentary substrata, sediment grade, or particle size, has a controlling influence on molluscan distributions and ecologies. Hard or firmer substrata, such as the leaves of seagrasses, emergent bivalves like *Pinna*, and mangrove forests, are rare in estuaries and marine lagoons, and are discussed separately; they provide radically different habitats from those offered by sediments. The third physical factor of importance to the ecology of estuarine and lagoon molluscs is the degree of aerial exposure, resulting from tidal movements.

Salinity. The salinity regime varies greatly among estuaries and marine lagoons, depending upon the input of freshwater and degree of interchange with the sea. Coastal marine lagoons have little or no freshwater inflow and maintain high salinities year-round (for example, Warme 1971). Certain large marine lagoons, best exemplified by Shark Bay, experience sufficient evaporation that, in the absence of freshwater input, a gradient is established of increasing salinity towards the distal end (Logan & Cebulski 1970). These systems are termed 'reverse estuaries' because the usual estuarine gradient is one of decreasing salinity with distance from the ocean inlet.

Australia has many typical estuaries with freshwater inflows. Some of these flow year-round (predominantly in the north), while others (in the east) flow only in summer and others (in the south-west) only in winter (Rochford 1951; Morrisey 1995). Some estuaries have too small a tidal prism – the difference in water volume in an estuary at mean high-water and mean low-water – to maintain continuous interchange with the sea. The closure of such estuaries greatly reduces their suitability as molluscan habitat because salinities drop, current flow declines and oxygen concentrations at the bottom occasionally become negligible. In parts of Australia, these largely freshwater embayments of intermittent estuaries are termed lagoons, which should not be confused with marine lagoons. Marine lagoons are fully saline and except for the negligible action of waves could often be considered part of the ocean beach system.

In general, the more fully saline an estuary or lagoon the more species of molluscs will be present (for example, Hodgkin 1977; Wells, F.E. & Threlfall 1980b, 1981). Few species can adapt to the physiological stress of high salinities of about 60 parts per thousand. However, those that can live in hypersaline zones, such as the small suspension-feeding bivalve *Fragum erugatum* at Shark Bay, can be extremely abundant (Fig. 1.41). This pattern of extremely high population densities of a few species in physiologically harsh environments is common, and is well expressed by several estuarine species. Molluscan diversity is also low in the least saline areas of typical estuaries, although densities of those few species present can be extremely high. Examples occur in the gastropod genus *Hydrococcus* and the bivalve genera *Arthritica* (Wells, F.E. & Threlfall 1981) and *Spisula* (Jones, A.R., Murray & Skilleter 1988).

Estuaries with intermittent freshwater influx usually also have intermittent connection to the sea. When terrestrial runoff produces water flow, these estuaries again break their sand plugs and re-connect to the sea. Many such systems can be found in south-western Australia. These intermittent estuaries are among the most demanding physiologically, because salinity, temperature, flow regime, oxygen content and other properties all vary greatly depending upon the degree of ocean connections. Even estuaries with permanent connection to the sea can exhibit large seasonal variation in salinity as a function of seasonal rainfall variation (Chalmer, Hodgkin & Kendrick 1976), and many rivers in northern Australia flow only during the monsoonal 'wet' season.

This environment selects for opportunistic species that can invade, grow and reproduce rapidly during favourable periods, because of the extreme temporal variability of physical conditions in true estuaries. Such molluscs tend to be small-bodied and their young develop directly. Some, such as species of the gastropod genus *Hydrococcus* and the bivalve genus *Arthritica*, provide good examples of life histories appropriate for exploiting the short opportunities offered by Australian estuaries with massive seasonal flows of freshwater or with only periodic connection to the sea (Wells, F.E. & Threlfall 1982). Curiously, widespread broadcasting of planktotrophic larvae, the opposite extreme from protection of young in capsules, is the other reproductive strategy utilised by truly estuarine molluscs, including many mussels (Wilson, B.R. 1969).

Substratum Grade. Sedimentary substrata are in dynamic equilibrium with the overlying flow regime (Sanders, H.L. 1956; Rhoads & Young 1970; Krumbein 1971). Given adequate sources of sediment particles of differing sizes, areas of higher prevailing currents will be characterised by coarser, sandier bottoms. In rapid current flows, fine particles like silts and clays are transported and not deposited. In areas of slower currents, fine particulate matter settles out of the water column to produce muddy bottom substrata. Although the hydrodynamic regimes of estuaries are exceedingly complex, many estuaries share common patterns in the distribution of fine and coarse sediments. Sediments are often coarse in channels near the ocean inlet, where faster tidal currents prevail, and grade to fine towards the top of the estuary away from strong tidal flows (for example, Warme 1971; Morrisey 1995). In addition, the action of wind-induced waves often creates sandier sediments on intertidal flats, while deeper areas less affected by surface wave energy accumulate fine sediments (for example, Tenore 1972).

The sedimentary dynamics and distributional patterns of the estuary are important to understanding the molluscan ecology because of the close interrelations between the animals and the sediments they occupy (for example, Sanders, H.L. 1958). The inlets between estuaries and the sea are often benthic deserts because of extreme currents and sediment transport that prevent establishment of molluscs and other benthic invertebrates (Stephenson, Williams & Lance 1970; Wildish & Kristmanson 1979). Somewhat less turbulent systems with clean sand bottoms and substantial water flow are ideal for suspension-feeding bivalves, which feed on particles suspended in the water column. Cockles and other bivalves in the family Veneridae are a prominent element of this habitat, where they often occur in high densities (for example, Wells, F.E. & Roberts 1980; Wells, F.E., Rose & Lang 1985; Peterson & Black 1987).

Estuarine, suspension-feeding bivalves are of greatest economic importance as human food and fish bait, because of their relatively large body sizes and tasty flesh. They grow best in relatively rapid currents, in part because these renew water masses rapidly and mix more surface waters into the benthic boundary layer, which might otherwise become depleted of food (Wildish & Kristmanson 1979). As substantial sediment transport occurs in sandy habitats, bivalves in such environments are mobile and can dig relatively rapidly through the sediments (Stanley 1970).

Muddy sediments of estuaries tend to be populated by deposit-feeding bivalves and gastropods rather than by suspension-feeding bivalves (Rhoads & Young 1970). Deposit-feeders ingest sediments, detritus, and associated microbes located on or in the substratum. Various species in the bivalve family Tellinidae are prominent members of this feeding group in estuaries.

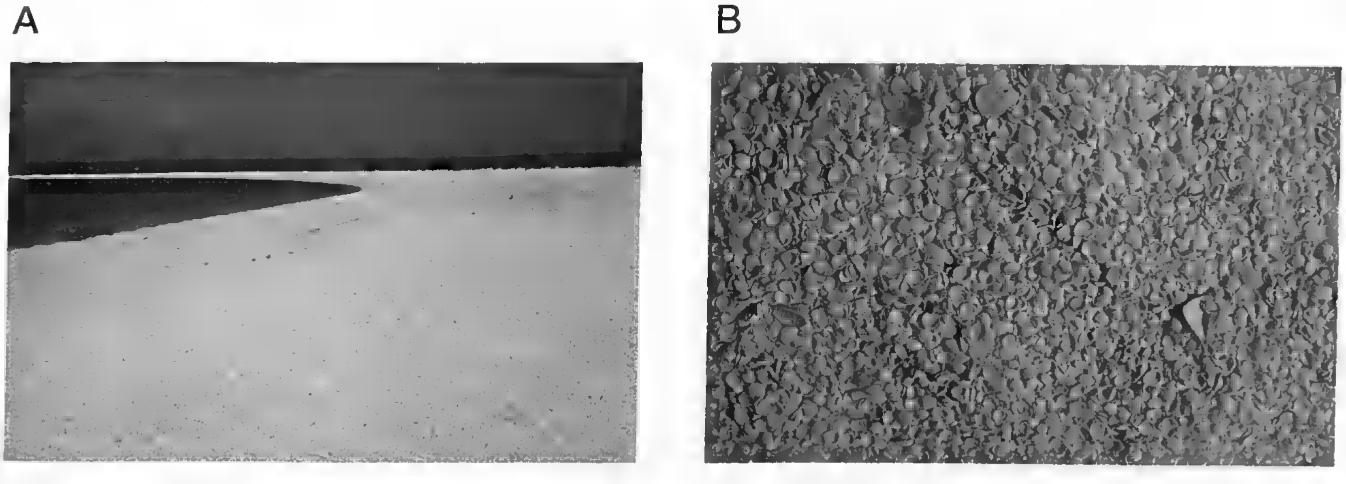


Figure 1.41 Under extreme conditions, some bivalves can become superabundant. **A**, a beach composed almost entirely of shells of *Fragum erugatum* (Cardiidae). **B**, a closer view shows the preponderance of this species. [C. Peterson]

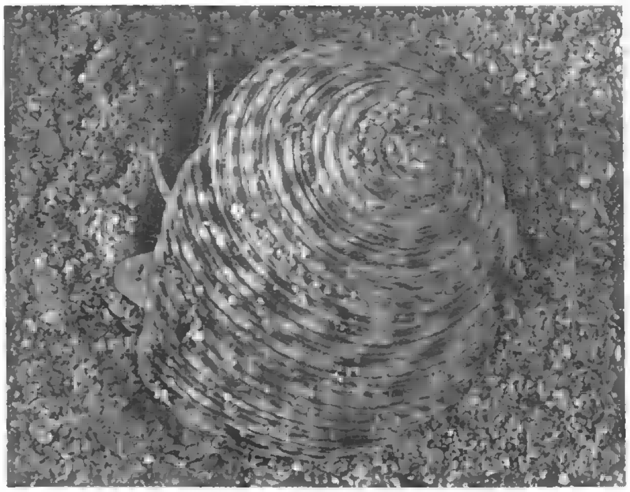


Figure 1.42 The trochid *Monilea callifera* is widespread on sublittoral, muddy sand substrata from south-western Western Australia to central Queensland. [C. Bryce/Western Australian Museum]

Deposit-feeders dominate in fine sediments because of the abundance of detritus and associated microbes. Suspension-feeders tend to be inhibited from occupying fine sediments by movement of deposit-feeders as they forage; movement increases the water content of the sediments and thereby enhances the level of resuspension of those sediments by tidal currents. Excessive resuspension of inorganic material clogs the gills of suspension-feeding bivalves. This process is termed 'trophic group amensalism' (Rhoads & Young 1970). This indirect negative interaction between trophic types appears to reduce the numbers of suspension-feeders in muds to levels far below those that might otherwise be set by the availability of suspended food particles. For example, in seagrass beds, where projecting blades baffle water movement and reduce sediment resuspension such that trophic group amensalism cannot occur, suspension-feeding bivalves are abundant despite the simultaneous presence of fine sediments and large numbers of deposit-feeders (Rhoads & Young 1970; Summerson & Peterson 1984).

Some bivalve molluscs exhibit an ability to switch feeding mode from suspension-feeding to deposit-feeding in response to changing energy gains from these different feeding behaviours. Several *Macoma* species and other tellinids are apparently able to extend their siphons up into the water column and feed on suspended material during periods of sufficient water flow, then switch to deposit-feeding by vacuuming surface deposits when currents diminish (Brafield & Newell 1961; Hughes 1969). Such facultative feeding may be widespread (for example, Taghon, Nowell & Jumars 1980) and tends to blur distinctions between feeding types in those groups capable of such switching.

Of all molluscs, bivalves are most readily categorised as either deposit-feeders or suspension-feeders (Stanley 1970) associated with muds or sands, respectively. In estuaries, many deposit-feeding gastropods are also associated with muds. Other gastropods and also members of rarer molluscan classes exhibit preferences for particular sedimentary habitats (Fig. 1.42). Sandy sediments of estuaries and lagoons are a preferred habitat for many gastropods and occasional scaphopods and cephalopods.

Predatory naticid snails, especially moon snails in the genus *Polinices*, are prevalent in sandy sediments (for example, Green 1968; Laws & Laws 1972). Moon snails often move in large aggregations such that their predation can be highly variable in time and space (Peterson 1982a). Naticids (Fig. 1.43) prey upon bivalve and some gastropod molluscs by drilling a countersunk hole through the shell of their prey with specialised radular teeth. Additional carnivorous gastropods in this environment include species of *Fusinus* and olives (*Oliva*). Other gastropods characteristic of sand bottoms in the estuary are scavengers, such as certain species of *Nassarius* and *Cominella* (Green 1968; Wells, F.E. & Roberts 1980). *Nassarius pauperatus*, which both scavenges carrion and grazes microalgae on sand flats of the southern coast of Australia, appears often to be food-limited (McKillup & Butler 1983). Ectoparasites in the family Pyramidellidae can be found on the exterior surface of some bivalve molluscs and other invertebrates (for example, Peterson & Black 1987; Crossland *et al.* 1991). These mysterious gastropods presumably derive some benefits from the tight associations with hosts, but the specific advantages and mechanisms of interaction are unknown.

Unusually high densities of infaunal sea anemones characterise some Australian estuarine and lagoonal sand flats (Peterson & Black 1986). Most are radianthids attached to molluscan shell fragments and seagrass detritus, rather than the burrowing cerianthids more typical of muddy soft bottoms elsewhere. These anemones prey upon molluscs that land on their outspread tentacles. In Cockburn Sound, Western Australia, such prey includes the opisthobranch *Akera soluta* (Fig. 1.44), which is capable of swimming, and other opisthobranchs abundant on sand flats, such as species of *Bulla* and *Haminoea*. Mussel tissue and shell fragments found in many anemones suggest that mussels already dislodged or damaged by the foraging of other mussel consumers, such as blue manna crabs or puffer fish, are probably scavenged (Peterson & Black 1986). The anemones in turn may fall prey to a wentletrap (*Epitonium* species) which inserts its proboscis into the column of buried sand-flat anemones (Peterson & Black 1986).

Other gastropods prefer muddy substrata in estuaries. Those few muricid gastropods not confined to rocky shores, tend to be found in finer sediments, where currents are reduced. Muricids drill characteristic cylindrical holes through shells of bivalve, gastropod and crustacean prey. Nevertheless, the majority of gastropods in muddy sediments can be classified as deposit-feeding and can be found in this sedimentary habitat because of abundant microbial and detrital food sources.

Tidal elevation. For marine organisms the degree of coverage by water versus exposure to air is potentially a factor of major importance. A vertical exposure gradient generates, both directly through physiological effects and indirectly through effects on predators and competitors, well-known zonation patterns on rocky intertidal shores (Connell 1972). Surprisingly little work has been done in the sedimentary shorelines of estuaries and lagoons to describe the vertical patterns of molluscan community organisation and to determine the causes of zonation. However, some observations that are available suggest a strong influence of exposure time in this system as well (for example, Wells, F.E. & Roberts 1980; Wells, F.E. & Threlfall 1980b; Peterson & Black 1987). Patterns are not generally evident without excavation because the fauna of sedimentary environments is largely buried (infaunal), as opposed to the epifauna dominant on hard substrata.

Figure 1.43 The moon shell, *Natica euzona* (Naticidae), preys on other sand-dwelling molluscs. [C. Bryce/Western Australian Museum]

The suspension-feeding bivalves of intertidal flats in Australia are low in density and diversity at and near the high tide mark, where water coverage is minimal (Wells, F.E. & Threlfall 1980b; Peterson & Black 1987). On a vertical transect down the flat, density increases rapidly to a maximum relatively high in the intertidal zone. Densities then tend to decline with decreasing elevation down into the subtidal zone (see Sutherland, W.J. 1982a), whereas species diversity of bivalves as well as gastropods increases with depth. In addition to these patterns in overall molluscan density, individual bivalves and gastropods often exhibit ecological segregation along the depth gradient. For instance, on the sand flats at Monkey Mia in Shark Bay, the bivalves *Placamen berryi* and *Anomalocardia squamosa* and the gastropod *Rhinoclavis vertagus* are virtually restricted in distribution to the high and mid-intertidal zones, whereas most other abundant species, including the bivalves *Placamen gravescens* and *Circe tumefacta* and the gastropod *Rhinoclavis fasciata* are subtidal inhabitants (Fig. 1.45). Of the six most common bivalve species (all suspension-feeders) at Monkey Mia, only *Callista impar* is abundant along the complete gradient from high intertidal (+1.0 m) to shallow subtidal (-0.1 m) (Fig. 1.45; Peterson & Black 1987). Similar zonation patterns occur on the tidal flats of other Australian lagoons and estuaries (Wells, F.E. & Roberts 1980; Wells, F.E. & Threlfall 1980b).

The causes of molluscan zonation pattens on tidal flats are largely unknown. Nevertheless, it is clear that many ecologically important factors vary with elevation in this system and doubtless contribute to zonation. Physiological stress clearly must increase with elevation on a tidal flat, but this factor probably acts more by its influence on predators than by its direct influence on the benthic molluscs (for example, Kneib 1984). The infaunal nature of molluscs on tidal flats buffers them against physical variation in temperature and moisture (Johnson 1965) and interspecific competition between molluscs of sedimentary environments does not seem to produce widespread mortality of the competitively inferior species (Peterson 1979, 1982a), as it often does on rocky shores. Thus desiccation and competition seem unlikely to play a major role in setting zonation patterns of soft-sediment molluscs on tidal flats.

On broad tidal flats incoming food-rich waters may first be depleted of food by suspension-feeders lower on the flat before the food even reaches higher elevations (Peterson & Black 1987); time available for feeding decreases with increasing elevation. Thus competition for suspended food may act in combination with decreased feeding time and increased physiological stress to set upper distribution limits for some suspension-feeding bivalves on tidal flats (for example, Kneib 1984).

This suggestion is supported by the observed patterns of substantially lower growth as a function of elevation for three suspension-feeding bivalves at Monkey Mia in Shark Bay (Peterson & Black 1987). Some of the effects of subtidal processing and clearance of incoming tidal flows by the lower suspension-feeders are probably countered by resuspension of benthic diatoms and other microalgae by wave action, which probably increases with elevation.

Figure 1.44 *Akera soluta* (Akeridae), an abundant anaspidean omnivore on sand and mudflats around mainland Australia.
[C. Bryce/Western Australian Museum]

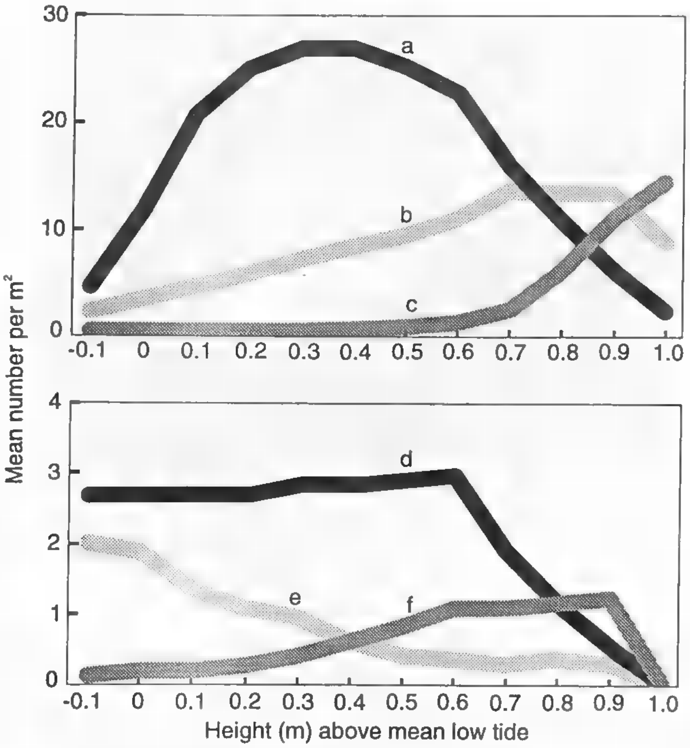


Figure 1.45 Zonation in relation to tidal height of venerid bivalves on sand flats at Monkey Mia, Shark Bay, Western Australia, shown by the upper and mid-intertidal species, *Anomalocardia squamosus* (b), *Placamen berryi* (c) and *Pitar citrinus* (f), and the mid- to sub-tidal species, *Callista impar* (a), *Placamen gravescens* (d) and *Circe tumefacta* (e). (After Peterson 1991)
[I. Hallam]

The physiological effects of alternating inundation and aerial exposure on predators of tidal flat molluscs are probably the major factors controlling elevation gradients in diversity, abundance and community composition on tidal flats in lagoons and estuaries. Predation rates are probably most intense at the subtidal end of the gradient, where crabs, prawns and predatory fishes, especially sharks and rays, have uninterrupted access to the benthos (Kneib 1984). Avian predators, among which gulls, oystercatchers, and probing shorebirds are generally the most important for molluscs (for example, Hancock 1971), may prey more intensely higher on the flat where exposure to air is greater; however, many of these predatory birds seem to follow the tide line and thus distribute their feeding fairly equally across tidal elevations (Sutherland, W.J. 1982b). Predatory gastropods are usually restricted to lower elevations; their influence resembles that of the other aquatic predators, and is likely to be strongest low on the flat, probably because of decreased feeding time higher on the flat. This pattern of enhanced predation lower on tidal flats probably accounts for the reduction in the density of bivalve molluscs toward the subtidal margin of many Australian tidal flats.

Patterns of variation in the intensity of predation with elevation on tidal flats and in estuarine sediments in general are difficult to predict because of the gamut of different predators faced by each mollusc through its life history. Benthic suspension-feeders, especially bivalves, consume settling larvae (Peterson 1982a), and even after settlement, consumption or inadvertent destruction by adult deposit-feeders can decimate new cohorts of soft-sediment molluscs (Woodin 1976). These new recruits are often consumed by predatory meiofauna, such as turbellarians and some nematodes (Watzin 1983), and if they survive, they are vulnerable subsequently to consumption by predatory fishes, prawns, crabs and shorebirds. Muricid gastropods appear to be most effective predators on small bivalves, whereas naticid gastropods and octopuses often consume larger molluscs (Green 1968; Kitchell, Boggs, Kitchell & Rice 1981; Peterson 1982a). The largest of tidal flat molluscs are still susceptible to consumption by predatory birds (Sutherland, W.J. 1982b).

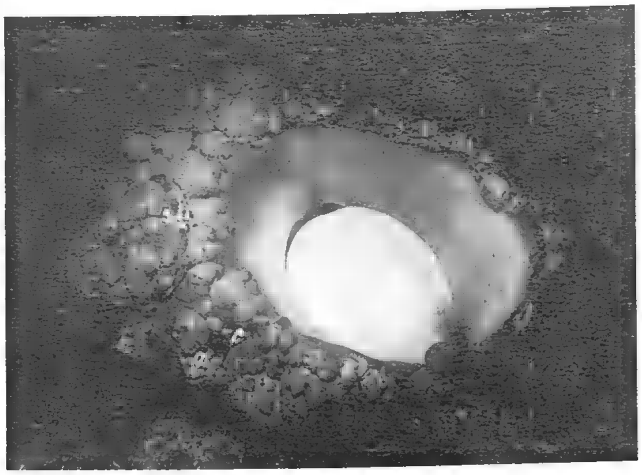


Figure 1.46 A large individual of the intertidal and sublittoral turbinid *Turbo jourdani*, bearing over 100 *Sabia australis* (Hipponicidae), on its ventral margin. [C. Bryce/Western Australian Museum]

Molluscs as a substratum. Many lagoonal molluscs have shells of sufficient size and longevity that they themselves serve as hard substrata for the attachment of various suites of epibiotic organisms. Dead shells are not usually heavily utilised because they are rapidly buried in sediments and thus are not long accessible for colonisation and growth of epibiota (Conover 1975, 1979; Stachowitsch 1977). However, the surfaces of gastropod shells carried by hermit crabs are often well colonised, possibly by organisms selected by the occupant (Conover 1979). Living shells that project up into the water column present the best habitat for epibiotic species, especially for algae, which require light for growth, or for suspension-feeding invertebrates, which require some contact with the water column for respiration and feeding (for example, Laws 1970). Surprisingly, however, even some totally buried molluscs often carry epibiotic species on their shells. Probably the most important molluscs providing hard-bottom habitat in Australian marine lagoons are oysters, pen shells (*Pinna*) and scallops. Oysters live projecting up from the sediment surface, often in large clumps. Pen shells are largely infaunal but their ventral margin projects up into the water column to a height of about 5 cm (Keough 1984; Butler 1987); they are especially good epibiotic habitat because of their large size and longevity. Scallops lie on the estuarine or lagoonal sea floor, resting on one valve such that the other is always elevated into the water column. Their short life and mobility may limit colonisation to a subset of the epibiota that occupies more permanent substrata.

Species colonising the shells of these exposed bivalve molluscs include members of virtually all invertebrate and algal groups known to occupy estuarine and marine hard bottoms (Kay, A.M. & Keough 1981; Keough 1984). Invertebrates, such as bryozoans, hydroids, sponges, tunicates, barnacles, anemones, serpulid polychaetes and other molluscs are prominent. Microalgae as well as red, green and brown macroalgae occur on bivalve shells.

Molluscs attached to these bivalve shells include slipper limpets (Calyptraeidae) and cap limpets (Hipponicidae), such as species of *Crepidula* and *Sabia* (Fig. 1.46), *Ischnochiton*, and the mussel genera *Brachidontes* and *Modiolus*. One group of shell occupiers comprises actual bio-eroders and can cause the death of the host. These include boring bivalves, such as pholadids and gastrochaenids, certain polychaete worms (*Polydora* species) and boring sponges. In Australian estuaries and lagoons (Peterson 1983), fully infaunal, shallow-burrowing bivalves, especially cockles, harbour many of the same suite of epibiotic species, including ectoparasitic gastropods of the family Pyramidellidae. The ecology of the epibiotic species and assemblages living on mollusc shells has only begun to be investigated. The patchy nature of the habitat offered by such shells implies that individual molluscs may hold quite different epibiotic species as a consequence of the history of colonisation events (Keough 1984).

Physical characteristics of mollusc species play an important role in dictating the epibiotic organisms that they will host. For example, at Princess Royal Harbour near Albany, the large brown macroalga *Hormosira banksii* is more frequently found attached to the mussel *Brachidontes erosus* than to the cockle *Katelysia rhytiphora*, and only rarely to the cockle *Katelysia scalarina* (Black & Peterson 1987). This habitat preference is likely to be a consequence of the differential force required to dislodge these bivalves from the substratum. Wave action during storms exerts a substantial drag force on large plants projecting into the water column and can dislodge, and perhaps carry to shore and kill, poorly anchored bivalves hosting *H. banksii* or other large macroalgae. *Brachidontes erosus* is best anchored because of its byssal interconnections among several mussels, whereas *Katelysia scalarina* is least securely anchored because of its small size (Black & Peterson 1987). These physical constraints may also act to limit macroalgal occupation of other estuarine bivalve shells and to increase mortality of those bivalves that are occupied (O'Gower & Nicol 1971). Much research is required to explore the ecological relationships between molluscs and their epibiota.

Mangroves

A large fraction of the Australian estuarine coastline, particularly along the northern half of the continent, is covered by mangroves from the mid to the high tide mark. Mangroves are intertidal communities dominated by trees (Adam 1995) and represent the tropical and subtropical equivalent of the salt marsh in colder latitudes (Hutchings & Saenger 1987; Clarke, P.J. & Jacoby 1994).

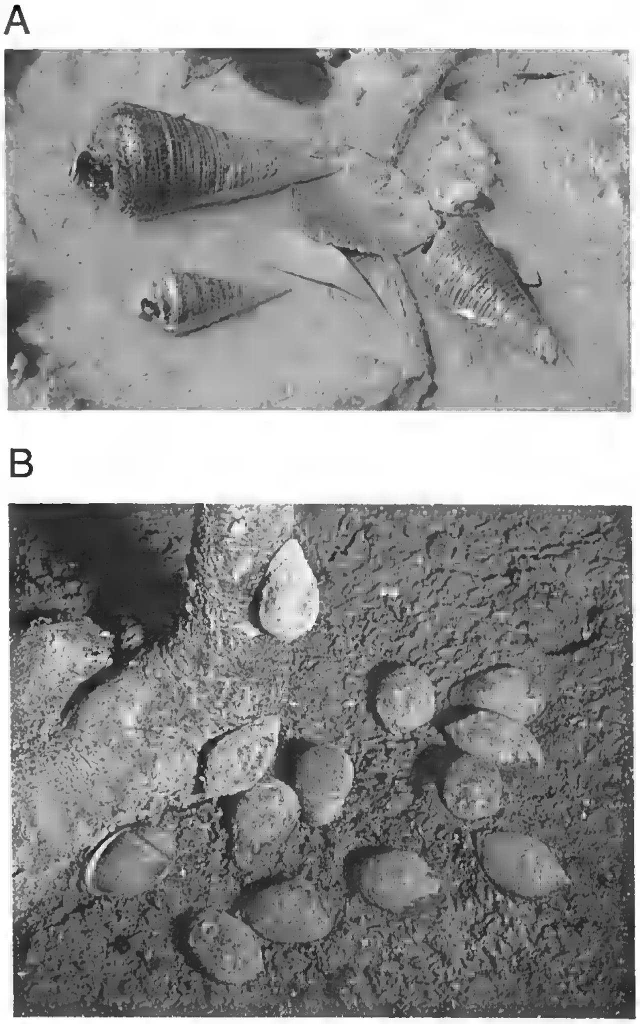


Figure 1.47 Deposit-feeding gastropods typical of mangrove mudflats. **A**, a mud creeper, *Telescopium telescopium* (Potamididae), at Darwin, Northern Territory. **B**, the pulmonate *Cassidula angulifera* (Ellobiidae), from Monte Bello Islands, Western Australia. [C. Bryce/Western Australian Museum]

Mangroves and salt marsh grasses (and succulents) live in the same zones high on protected estuarine shorelines. Within both systems, the individual plant species exhibit significant zonation along the elevation gradient (for example, Bunt & Williams 1980). Furthermore, mangroves and salt marsh plants are highly productive, yet characterised by relatively low rates of direct herbivory. These plants shed their leaves, which then contribute in substantial ways to the detrital food chains that make estuaries so productive (Odum & Heald 1975; Hutchings & Recher 1982).

Molluscs and crustaceans (especially crabs of the genera *Uca* and *Sesarma*) are significant consumers of mangrove detritus and microalgae, bacteria, and fungi growing on the detritus. These groups, therefore, may represent important trophic links between the highly productive mangroves and carnivores, such as many waterbirds. Much of the mangrove detritus, like that from salt marshes, is transported into the estuary and even the coastal sea, where it fuels important food chains leading to mollusc, fish, crab and especially prawn production (Hutchings & Recher 1982; Robertson, A.I. & Duke 1987, 1990).

Along the mangrove-dominated shorelines of estuaries, mudflats usually extend up to about the mid intertidal zone. The mudflat habitat contains the usual mixture of infaunal deposits and suspension-feeding bivalves together with epifaunal deposit-feeding gastropods (Fig. 1.47; Wells, F.E. 1984a). Deposit-feeders dominate because of the fine sediments and the potential for trophic group amensalism. Infauna is abundant (Wells, F.E. 1984a). Mangroves begin at about the mid intertidal zone and extend to around the high tide mark with different mangrove species exhibiting characteristic zonation patterns along the elevation gradient (for example, Bunt, Williams & Bunt 1985; Hutchings & Saenger 1987).

The molluscs of the mangrove respond with a zonation pattern that matches to a large degree that of the plants (Hutchings & Recher 1974, 1982; Wells, F.E. & Slack-Smith 1981; Wells, F.E. 1984a). The zonation of mollusc species in a mangrove in southern New South Wales is shown in Figure 1.48, after Kaly (1988). The conspicuous molluscs tended to form two groups. *Bembicium auratum*, *Batillaria australis* and *Salinator fragilis* were the most prominent gastropods on the lower shores, from the lower forest seawards, whereas *Assiminea buccinoides*;in mangroves, *S. fragilis* and *Ophicardelus* species formed an upper shore group, extending from the upper mangrove forest to the salt marsh.

Wells, F.E. & Slack-Smith (1981) reported zonation of molluscs in mangroves of the tropical Kimberley region, where diversity and densities of individual species were low. They recognised five zones, characterised by particular mangrove species, in which the distribution of molluscs varied with changes in species of tree.

The seaward margin of mangroves supports the highest density, diversity and biomass of molluscs (Reid 1985; Morgan & Hailstone 1986; Wells, F.E. 1986b; Roach, Hunt & Ward 1989; Robertson, A.I. & Alongi 1995). Even the wood-boring teredo seems to be restricted to the seaward margin (Rimmer, Battaglene & Dostine 1983). The molluscs of this zone tend to be surface deposit-feeding gastropods such as *Terebralia* and *Cerithidea* species. Occasionally, bivalves such as mangrove oysters (Sutherland, J.P. 1980) or mytilids can be common, especially on mangrove prop roots extending into permanently flooded drainage channels.

Higher on the shore, arboreal gastropods become more important, although total molluscan densities are lower. Species in genera such as *Littoraria* and *Nerita*, which feed by rasping microalgae (Branch & Branch 1980; Reid 1986) from the hard substrata provided by the mangrove trees, are the dominant elements of the molluscan fauna. Few mangrove molluscs are restricted to this habitat: most are typical of nearby rocky or muddy habitats (Wells, F.E. & Slack-Smith 1981). In drier climates, a bare zone of salt-saturated mud occurs at or above the high tide line. This zone is effectively devoid of all molluscs (Wells, F.E. 1984a).

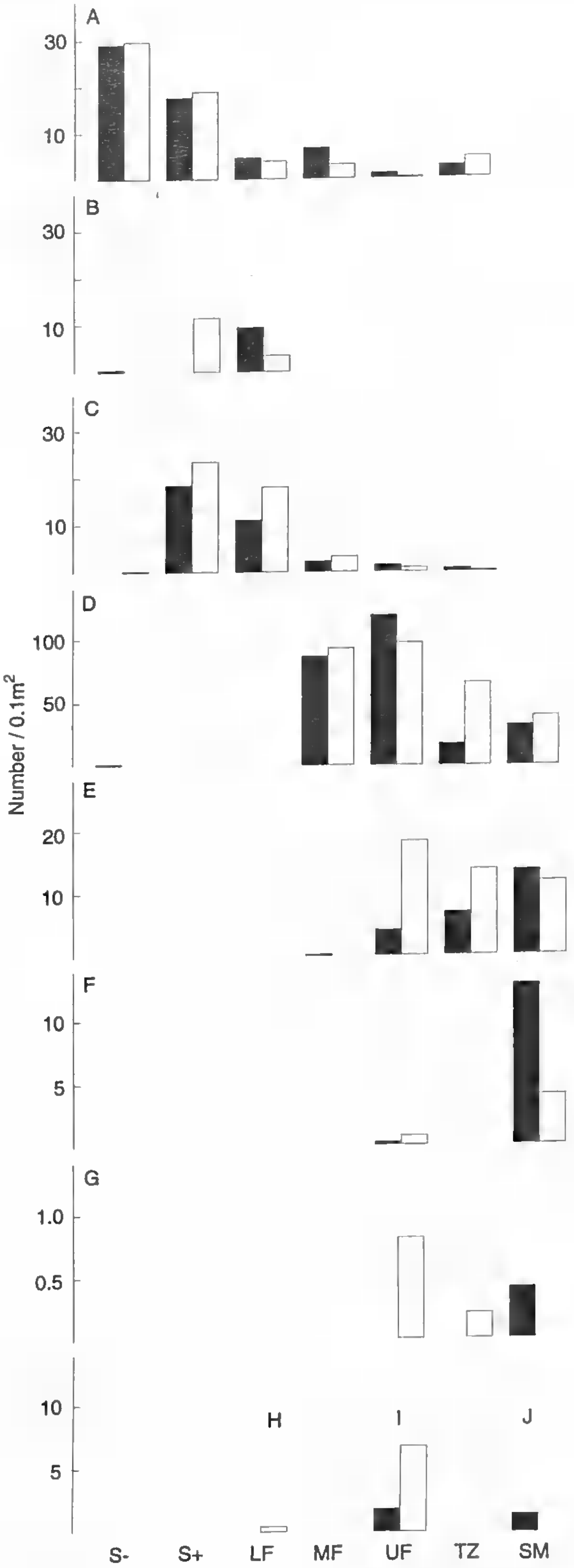


Figure 1.48 The distributions of eight common mollusc species across a mangrove in Woolooware Bay, Sydney, form two groups – a low-shore group seaward of mid-forest zone, and a high-shore group from mid-forest to the salt marsh; other species may occur only within a single zone. Series of counts were made at two sites. **A**, *Salinator fragilis* (Amphibolidae). **B**, *Batillaria australis* (Batillariidae). **C**, *Bembicium auratum* (Littorinidae). **D**, *Assiminea tasmanica* (Assimineidae). **E**, *Salinator solida* (Amphibolidae). **F**, *Ophicardelus* sp. (Ellobiidae). **G**, *Tatea rufilabris* (Hydrobiidae). **H**, *Pyrazus ebeninus* (Batillariidae). **I**, *Melosidula zonata* (Ellobiidae). **J**, *Littorina scabra* (Littorinidae). Zones of the mangrove, from low water to high water: **S-**, seaward edge, oysters absent, pneumatophores present; **S+**, seaward edge, oysters and pneumatophores present; **LF**, lower forest, oysters on mud, mangroves and pneumatophores; **MF**, mid-forest, pneumatophores present, oysters on tree trunks, below mid-point of upper LF–lower TS; **UF**, upper forest, pneumatophores present, oysters on tree trunks, above mid-point of upper LF–lower TS; **TZ**, transitionary zone, pneumatophores and few small trees present, sandy mud; **SM**, salt marsh. Solid bars, site 1; open bars, site 2. (After Kaly 1988)

One of the most surprising features of the molluscs of mangroves is the virtual absence of infaunal molluscs in all zones containing mangrove trees. Perhaps the dense roots and material just beneath the sediment surface in the mangrove make burrowing more difficult than in salt marshes or seagrass beds, which also have root mats but still support abundant infaunal molluscs. Alternatively, Vermeij (1973) has suggested that the high acidity of mangrove soils in the absence of oxygen makes difficult or impossible retention of calcium carbonate for shells. This could be a critical physiological limitation to molluscan exploitation of the infaunal habitat of mangroves.

The molluscs of most mangroves tend to be subjected to relatively intense predation. This may occur in part because they lack some of the protection from predators which infaunal benthic organisms have. Crabs prey heavily on many of the surface deposit-feeding gastropods, as do various egrets, herons, and other water birds. In some areas, mammals forage in mangroves and eat crabs and molluscs. Rays are important predators on many estuarine and mangrove molluscs in Australia; F.E. Wells (1986b) hypothesised that higher molluscan densities around emergent pneumatophores are a consequence of the physical protection they provide from foraging rays. Consumption of molluscs by higher level consumers is important to the total energetics of this ecosystem.

PELAGIC MOLLUSCS

Many molluscs live in the water column, either throughout their lives (holopelagic) or during part of their life cycle (meropelagic). Some of these comprise very important components of pelagic ecosystems, such as the Cephalopoda, and the opisthobranch groups Thecosomata and Gymnosomata, traditionally known as the 'pteropods'. Several holopelagic groups of caenogastropod and opisthobranch gastropods are also holoplanktonic, their movements being strongly influenced by water currents throughout their lives. Many of the smaller pelagic cephalopods are also holoplanktonic. However, squids longer than about 20–30 mm, especially the muscular forms, are quite capable of movement independent of the effects of water currents; the early stages of such forms are really meroplanktonic, and subsequently become part of the nekton as they grow. In many other gastropod groups, for example, Scaphopoda, most bivalve and a few cephalopod families, only the larval component of the life cycle is planktonic. Such meropelagic animals form part of the meroplankton. Accordingly, discussion of this diversity of life styles is treated under the three topics – holopelagic gastropods, cephalopods and meroplankton.

Holopelagic Gastropods

The holopelagic habit occurs in four neotaenioglossan families of caenogastropods and three opisthobranch nudibranch families, and two opisthobranch orders, the Thecosomata (five families) and Gymnosomata (six families). Most, if not all, of these species are cosmopolitan in distribution and are found in warm subtropical and tropical water masses, including those around Australia (van der Spoel, Newman & Estep 1997). For food, transport and protection, many rely on pleustonic animals floating passively at the surface such as cnidarian communities, particularly the siphonophore genera *Velella*, *Porpita* and *Physalia* (Fig. 1.49). In terms of biomass, the bulk of the holoplanktonic molluscs – shelled and shell-less pteropods – live in colder seas circumglobally, where they may occur in huge swarms. Some species may become so abundant that they are a food source for baleen whales.

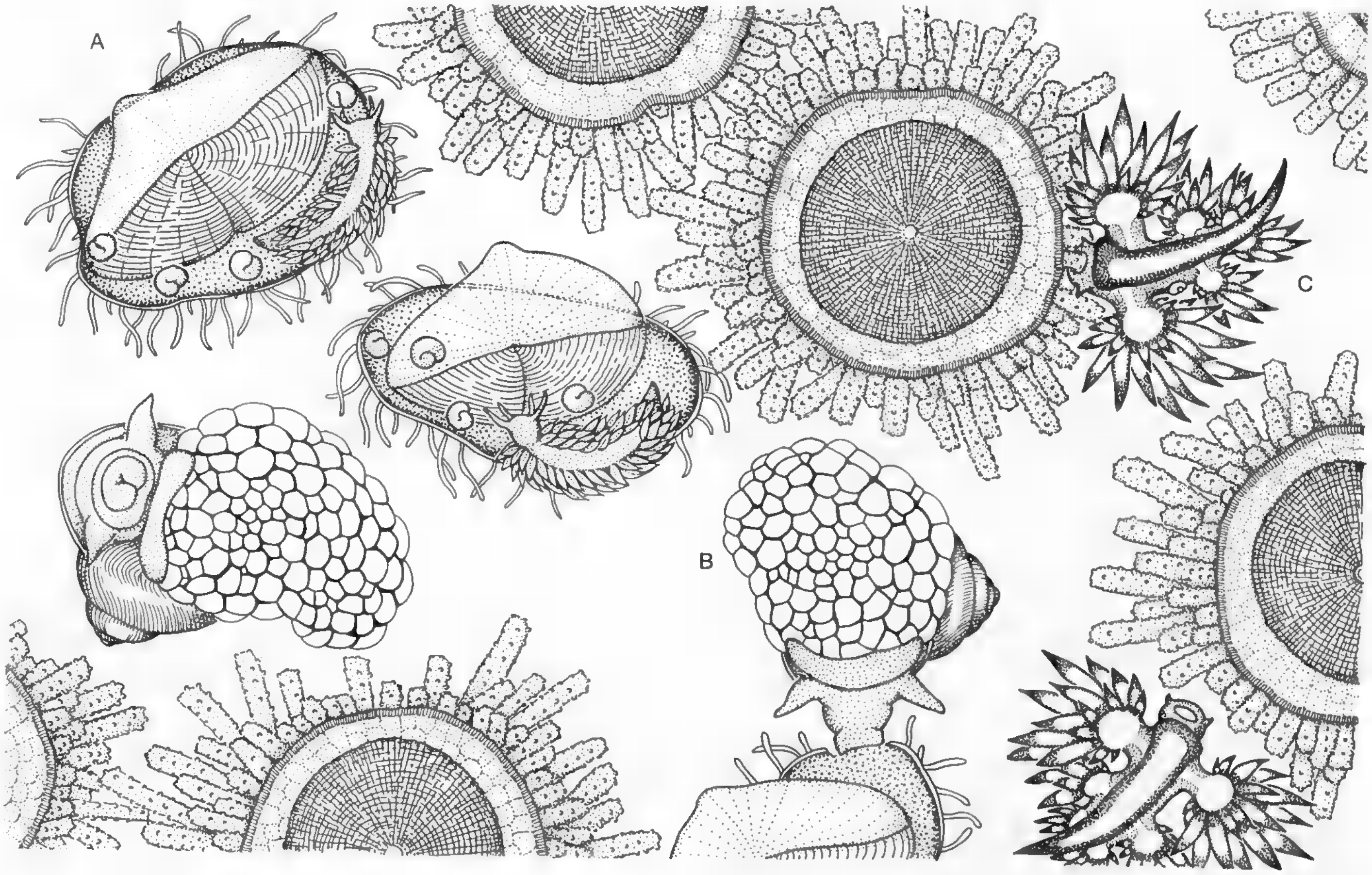


Figure 1.49 The holoplanktonic mollusc community associated with pleustonic cnidarians. **A**, *Fiona pinnata* (Fionidae) feeding on the chondrophoran *Velella velella* on which it has laid several circular egg masses. **B**, *Janthina exigua* (Janthinidae) feeding on *Velella velella* while supported by its air bubble raft. **C**, *Glaucilla* (Glaucidae) species feeding on a species of the chondrophoran genus *Porpita*. [L. Newman]

Least specialised of the caenogastropod holoplanktonic molluscs are the violet snails (Janthinidae) which float at the surface with the aid of air bubble rafts (Fig. 1.49B). Members of the three families in the second prosobranch group, the Heteropoda, are highly modified for a planktonic existence. The Atlantidae are relatively small and have a shell into which the animal can retract, whereas the shell in the Carinariidae covers only the visceral organs. Adult pterotracheids lack a shell altogether and the body is highly transparent and streamlined.

Nudibranchiate holoplanktonic gastropods are assigned to three specialised opisthobranch families. The least modified are the nudibranch-like Fionidae which crawl among floating objects such as siphonophores, and stalked barnacles upon which they prey (Fig. 1.49A). Because they require a floating substratum, their inclusion as holoplankters is somewhat debatable although they are found commonly with other pleustonic molluscs. The Glaucidae include a few species of pleustonic molluscs that are able to float within the surface film (Fig. 1.49C). The highly specialised Phylliroidae are as transparent and streamlined as the heteropods, and form part of the neuston, the community of organisms inhabiting the uppermost few centimetres of the sea surface.

The largest group of holoplanktonic molluscs, the pteropods, are commonly known as the sea butterflies because of their two wing-like projections. Two groups of thecosomes (shelled pteropods) are recognised. Euthecosomes have two 'wings' and an aragonite shell into which they can retract, whereas pseudothecosomes have a wing-plate and a transparent slipper or a pseudoconch composed of a firm gelatinous material, into which the viscera fit. Members of an aberrant group, Desmopteridae, lack a shell but their muscular swimming plate suggests affinities with the pseudothecosomes. Shell shapes of these molluscs are often bizarre but may be important in buoyancy.

The naked pteropods or gymnosomes have lost their shell and have two muscular wings attached laterally to the 'neck' for swimming. They are the only other group of molluscs besides the Cephalopoda in which some members have suckers on their complex buccal appendages. Gymnosomes and thecosomes have quite different lifestyles, suggesting that close affinities between them is questionable.

Holoplanktonic molluscs are notoriously difficult to study. Many species are oceanic and only encountered when brought into shore by storms. Others are deep-dwelling and rarely encountered. Traditionally these animals were collected in plankton nets which damaged fragile shells or stretched and tangled body parts beyond recognition; transparent structures such as pseudoconchs and mantle appendages were always lost. To make matters worse, samples were usually fixed with unbuffered formalin which cause animals to contract violently or dissolves their fragile shells. Mesopelagic species were also subject to rapid changes in pressure which contort their bodies. Most original descriptions were based on unrecognisable specimens.

Only recently have planktonic molluscs been studied *in situ*. Observations have been made on the larger species from submersibles at depth. However, many of these molluscs can be seen in quite shallow waters and useful observations have been made by SCUBA divers (see Hamner, Madin, Alldredge, Gilmer & Hamner 1975; Gilmer & Harbison 1986; Lalli & Gilmer 1989; Newman 1990a, 1990b; Harbison 1992).

The truly holopelagic species are renowned for being difficult to keep in captivity, and laboratory observations have been misleading (Davenport & Bebbington 1990) since, as a result of damage during collection, these animals do not behave as they would *in situ* (Harbison 1992). For example, shelled pteropods are known to sink when they encounter a solid object and become entangled with their own mucus (Harbison 1992; L. Newman personal observations).

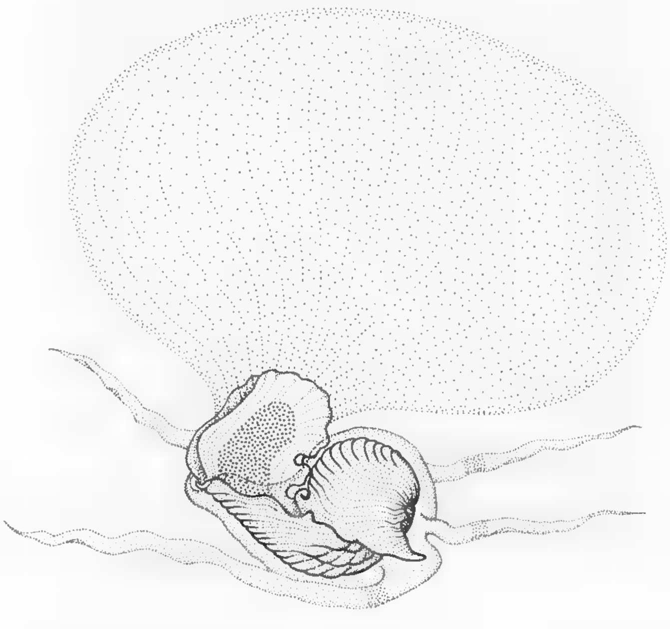


Figure 1.50 The euthecosome *Diacavolinia longirostris* (Cavoliniidae) suspended from its extended mucous feeding web. [L. Newman]

For a successful life in the plankton, holoplanktonic molluscs have some unique and unusual adaptations for buoyancy and locomotion not seen in any other molluscs. Maintenance of position in the water column is the most important, and most show adaptations for flotation or to remain neutrally buoyant.

Janthinids have a coiled shell which is sufficiently heavy to sink the animal were the buoyancy not maintained by producing rafts of air bubbles (Fig. 1.49B; Pl. 24.4). Air bubbles are produced by the pedal gland on the foot and the snail must remain attached to this float to avoid sinking. Sometimes they attach their float to the edge of their prey. They have no means of producing the lifesaving raft if they lose contact with the surface (Lalli & Gilmer 1989). Glaucids also float upside down at the surface using the surface film, and maintain their position by swallowing air which is stored in their digestive tract.

The most specialised of the holoplankters are the animals that live within the water column. As there is nowhere to hide in the open ocean, these molluscs have a tendency towards an increase in size and transparency, which counters the absence of protective cover.

The phylliroid nudibranchs are highly modified since the foot is considerably reduced and they swim by undulating the entire body. However, it is probable that these molluscs do not swim all the time as they are often found at or near the surface, attached to their cnidarian prey (Martin, R. & Brinckman 1963; Thompson & Brown 1984).

Although the thecosomatous pteropods have 'wings' they do not swim continuously. Instead many are neutrally buoyant and remain motionless, suspended from individual mucous feeding webs (Fig. 1.50). Transparent mantle appendages, observed when the animals are undisturbed, can also serve as buoyancy aids (Gilmer & Harbison 1986; Harbison 1992). Pseudothecomes are the most highly advanced of the shelled pteropods, having a large surface area on their wing-plate, a light weight pseudoconch and the ability to deploy a huge mucous web up to 2 m across. It is not yet known how some of these animals remain neutrally buoyant when they are detached from their web or not swimming (Harbison 1992).

In contrast, gymnosomatous pteropods swim actively by flapping their 'wings' although many animals remain motionless at the surface in wait for prey. It is thought that oil droplets in the skin increase buoyancy (Lalli & Gilmer 1989).

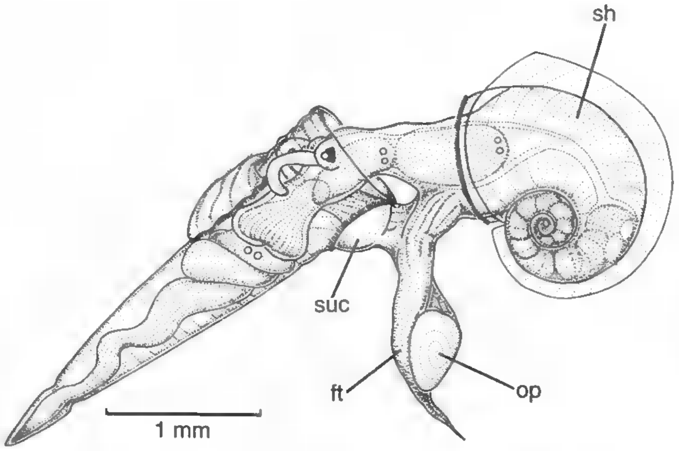


Figure 1.51 The heteropod *Atlanta gaudichaudi* (Atlantidae) (right) feeding on a euthecosomatous pteropod *Creseis chierchiae* (Cavoliniidae). The heteropod holds onto its prey with its fin sucker, seizes the body of the prey and pulls it out of the shell. **ft**, foot; **op**, operculum; **sh**, shell; **suc**, fin sucker. (After photograph by L. Newman/A. Flowers) [L. Newman]

The shelled and shell-less heteropods undulate their single large fin in a sculling motion to swim, which they generally do upside-down. The large carinariids and pterotracheids may spend most of their time motionless, as many species have been observed to grasp their tail with their radula, hanging suspended while digesting their last meal (Hamner *et al.* 1975). Atlantid heteropods have a large keel encircling their shell which increases drag and they can also use a mucous parachute to hang motionless in the water column (Lalli & Gilmer 1989; Newman 1990a).

Specialised feeding strategies have evolved in these holoplankters to enable them to feed either at the water surface or within the water column. Most are roving carnivores. Janthinids, phylliroids and fionids are all dependent on pleustonic cnidarians (siphonophores and medusae) as their only food source. Their prey is abundant and well protected by stinging tentacles from most other predators.

The heteropods and cephalopods have the most well-developed eyesight of the planktonic molluscs and are considered opportunistic carnivores as they will take a variety of prey, including salps, chaetognaths, other pelagic molluscs such as pteropods and smaller cephalopods and even small fish (Fig. 1.51; Seapy 1980; Lalli & Gilmer 1989; Newman 1990a, 1990b). They are truly visual predators that rely on their transparency, vision and speed to hunt prey within the water column.

Gymnosomes have reduced eyes and must rely on chemical or tactile means to detect their prey. They feed only on euthecosomes, using highly modified feeding appendages including hook sacs, adhesive tentacles or suckers and a protrusile proboscis (Lalli & Gilmer 1989; van der Spoel, Newman & Estep 1997).

Perhaps the most specialised of feeding strategies is seen in the shelled pteropods which deploy a mucous feeding web to catch phytoplankton, small zooplankton and detritus. According to Gilmer & Harbison (1986) it is debatable whether these molluscs are actually carnivorous trappers or suspension-feeders.

Holoplanktonic molluscs have developed sophisticated ways to avoid predation by using deception, defence or escape. This has lead to problems in studying these animals since many of the larger species are capable of rapid swimming and hence avoid plankton nets.

As with other pleustonic zooplankters, countershading helps to conceal molluscs from sharp-eyed predators above (birds) and below (nektonic fish) the surface. The janthinids are a deep purple/blue above and lighter below, a colour pattern typical of oceanic zooplankton. Glaucids are also deep blue on their upward-facing ventral surface and more strongly countershaded by their silvery dorsal colour below. Fionids are protected by colour incorporated from their prey and appear dark blue or yellow when feeding on species of *Velella* or *Lepas*, respectively (Bayer 1963; Bennett 1966). Some large heteropods can orientate the dark silvery colour of their visceral mass to reflect light and actually conceal themselves (Seapy & Young 1986). Phylliroids have been shown to emit flashes of light when disturbed, presumably to frighten predators (Martin, R. & Brinckman 1963).

Shelled pteropods do not appear to have much protection from predators since they can only detach from their feeding webs and either sink or swim away (Gilmer 1974; Gilmer & Harbison 1986; Newman 1990b; Harbison 1992). Pseudothecosomes minimise predation by being large, highly transparent and more common at greater depths.

The shell-less gymnosomes also appear to have little protection although they are known to be fast swimmers. Some may secrete defensive chemicals. Bryan, Yoshida, McClintock & Baker (1995) identified the antifeedant, pteroenone, in the Antarctic gymnosome *Clione limacina*, a product also known to occur in other opisthobranchs. Moreover, this antipredatory defence has been put to use by an amphipod: as a defence against predation by fish, the amphipod uses its pereopods to hold the gymnosome over its back (McClintock & Janssen 1990). Van der Spoel (1992) reported that gymnosomatous pteropods use small clouds of ink as an escape mechanism, in a similar manner to pelagic cephalopods.

Few holoplanktonic molluscs can defend themselves actively against predation. The glaucids are the only holoplanktonic molluscs which ingest and store nematocysts for defensive purposes in special sacs in the cerata. They are known to have caused irritation to bathers in southern Australian waters (Thompson & McFarlane 1967; Thompson & Bennett 1970).

It is especially difficult for planktonic animals to find a mate when they are widely dispersed. To overcome this problem the majority of planktonic molluscs are hermaphrodites – heteropods and cephalopods are not – and are able to store sperm. They are able to act as either male or female and thereby take full advantage of encounters to mate. Self fertilisation may also be possible. Pteropods, heteropods and many cephalopods also transfer sperm directly to their partner via spermatophores which greatly reduces the loss of reproductive products into the water column.

Pelagic molluscs may release their eggs directly into the plankton, lay them on other objects or brood them until they hatch. Most holoplanktonic molluscs lay transparent masses of spawn in the surface waters. Shelled veligers emerge from these eggs and develop directly into adults in a matter of days. In some, such as the atlantid heteropods, the development is extended and the larvae metamorphose into adults.

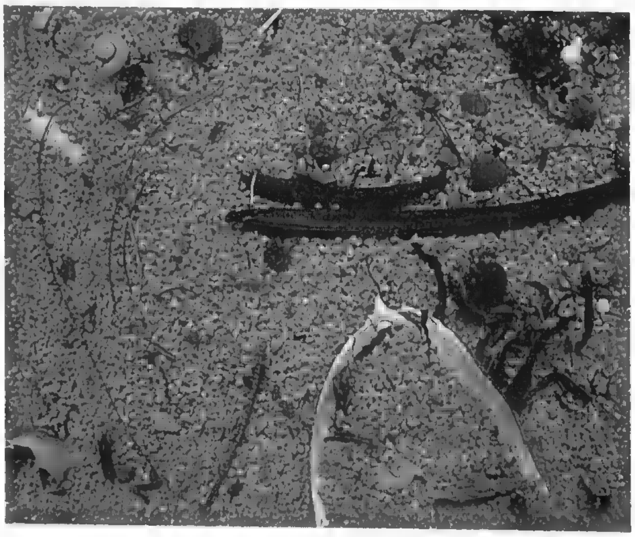


Figure 1.52 Innumerable shells of *Diacavolinia longirostris* (Cavioliniidae) washed onto the beach at Lizard Island, Great Barrier Reef. [L. Newman/A. Flowers]

Fionids lay spiral egg masses which they attach to the floats of *Velella* species and other floating objects such as cuttlebones, logs and *Spirula* shells (Bennett 1966; Thompson & Brown 1984). Females of the heteropod *Firoloida desmaresti* carry egg strings permanently attached to their tail and janthinids also carry around eggs capsules attached to the underside of their float (Laursen 1953; Lalli & Gilmer 1989).

In a few ovoviviparous forms, such as members of the deep-sea euthecosome genera *Limacina* and *Clio*, the females brood their eggs in their oviducts and a free-swimming larval stage is lacking (Tesch 1946, 1948; van der Spoel 1964).

Some holoplanktonic molluscs are known to occur in huge swarms although it is not certain if this behaviour is related to feeding and/or reproduction. Holoplanktonic molluscs associated with pleustonic cnidarian communities are often found in huge shoals some 200 nautical miles across (Laursen 1953; Bennett 1966). The euthecosome *Diacavolinia longirostris* occasionally forms dense swarms in Great Barrier Reef waters, and millions of empty shells have been reported washed up onto beaches (Fig. 1.52; Newman 1987, 1990b). According to Lalli & Gilmer (1989), limacinids are believed to be the most abundant marine gastropods in the world since they can occur in huge swarms. Shelled pteropods are so abundant at times that they may directly influence the ecology of epipelagic communities. These molluscs are an important food source for nektonic animals such as whales, birds and commercially important fish.

The relatively large heteropod *Firoloida desmaresti* has been found in such large swarms off southern Australian waters as to cause sonic scattering layers (Blackburn 1956). Seapy (1996) found that male atlantids swarming at the ocean surface are not unlike mating swarms of some insects. Females enter the swarm, are captured by a male and then drop down to mate. Seapy suggested that this swarming behaviour is necessary for bringing together mating adults in low density populations.

The hazards of planktonic existence also include being used as a substratum by other animals. A species of *Glaucus* has been reported to lay its eggs on janthinid shells and janthinid floats are used as a resting place by blue swimming crabs (Laursen 1953). Hydroids often attach to shelled species such as janthinids and euthecosomes (Wilson, D.P. & Wilson 1956; Lalli & Gilmer 1989). Janthinids have been found to be intermediate hosts for parasitic copepods and cestode larvae (Ho 1966; Reimer 1976), and heteropods have been reported as hosts for trematode cercariae (Lester & Newman 1986).

Atlantid heteropods have occasionally been found with yellow egg-like objects attached to their shells. Tesch (1949) surmised that these were large spermatophores, but copulation has never been observed in atlantids (Lalli & Gilmer 1989; Newman 1990b). Seapy (1996) recently determined that these objects are egg cases of the ocean strider or sea skater, *Halobates sericeus* (Halobatidae), which is known to deposit its eggs on floating objects (Fig. 1.53).

Ecologically, holoplanktonic molluscs are very important regulators in carbonate recycling since the dissolution of shells is a major contribution to the carbonate cycle in the world's oceans (Betzer *et al.* 1984; Byrne, Acker, Betzer, Feely & Cates 1984). Shells of most holoplanktonic molluscs contain aragonite, a form of calcium carbonate, which is 50% more soluble than calcite (Mucci, in Fabry 1990) and 98% of pteropod and heteropod shells dissolve while sinking (Berner 1977; Byrne *et al.* 1984).

Deep-sea aragonite sediments or 'pteropod oozes' are formed from limacinids, creseids and the shelled atlantids (Chen 1964). The shell mass in these sediments may even exceed that of the foraminiferans (Thiede 1975). Empty shells also provide habitats for amphipods, sipunculiids and isopods (Just 1977) and abandoned mucous food webs are a major source of the highly proteinaceous marine snow (Alldredge 1972; Gilmer 1974). The more abundant shelled pteropods are known to be associated with certain water masses and can act as hydrological indicators (Furnestin 1979; van der Spoel & Heyman 1983; Schalk 1990).

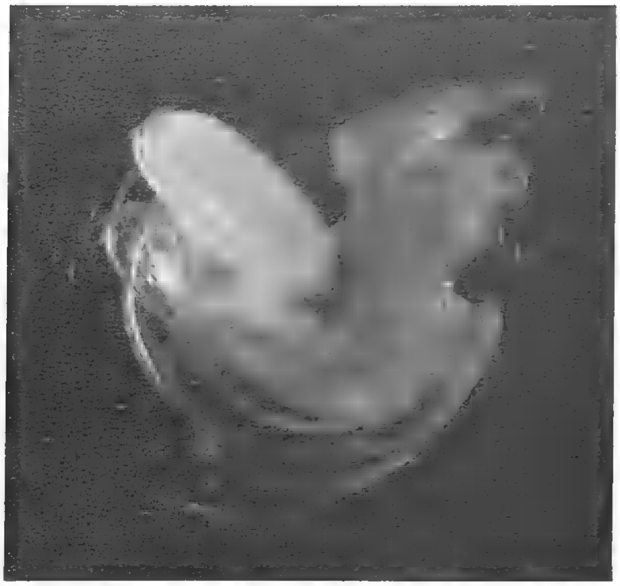


Figure 1.53 The ocean strider, *Halobates sericeus* (Gerridae), may lay its eggs on a variety of substrata, including the shell of this heteropod, *Atlanta turriculata* (Atlantidae), on which two elongate eggs, one apparently empty, are visible. (After Seapy 1996) [R. Seapy]

Perhaps holoplanktonic molluscs have become so successful and abundant because they have few space constraints or competitors in the open ocean. They are widespread and cosmopolitan in distribution, yet we know little about their feeding and reproductive biology mainly because of the difficulty of collecting and studying planktonic animals *in situ*.

Cephalopods

Cephalopods live in a broad range of habitats from neritic to oceanic and bathybenthic to epipelagic, in all oceans and seas, except the Black Sea. A large proportion of all taxa are holopelagic, including 80% of all genera recorded from Australian waters.

As in other pelagic organisms, the need to maintain position in the water column has been a primary factor in the development of the diversity of morphology, function and life style shown by various groups of pelagic cephalopods.

At one extreme, in very streamlined squids such as loliginids and ommastrephids, the highly muscular mantle provides the power for jet propulsion (Fig. 1.54D; Wells, M.J. & O'Dor 1991). These animals range swiftly over large areas and maintain their position in the water column by swimming continuously (see also Chapter 11). The mobility of such muscular squids is illustrated by the North Atlantic ommastrephid *Illex illecebrosus*, and the North Pacific ommastrephid *Todarodes pacificus*, which migrate some 2000 km each way on the return journey between the southern spawning grounds and their northern feeding grounds (O'Dor 1983; Okutani 1983).

At the other extreme, a number of pelagic cephalopod groups have achieved neutral buoyancy, with concomitant conservation of energy, in several different ways. In many families, the body weight is reduced by replacement of heavier metallic ions from the body fluids with ammonium ions derived from nitrogenous waste (Clarke, M.R., Denton & Gilpin-Brown 1979). In these ammoniacal squids, the resultant low density fluid may be stored in a large coelom, as in cranchiids (Fig. 1.54A, B; Pl. 18.10; Clarke, M.R. 1962) or in vacuoles in the tissues of the head, arms and mantle, as in *Lepidoteuthis grimaldii* and various species of *Histioteuthis* (Fig. 1.54E, F; Clarke, M.R., Denton & Gilpin-Brown 1969, 1979; Roper, C.F.E. & Lu 1990). Bathyteuthids and gonatids maintain neutral buoyancy by producing oil which is stored in the digestive glands (Denton & Gilpin-Brown 1973; Clarke, M.R. 1988). *Spirula spirula* controls its buoyancy by regulating the volume of gas in its chambered shell (Denton & Gilpin-Brown 1971).

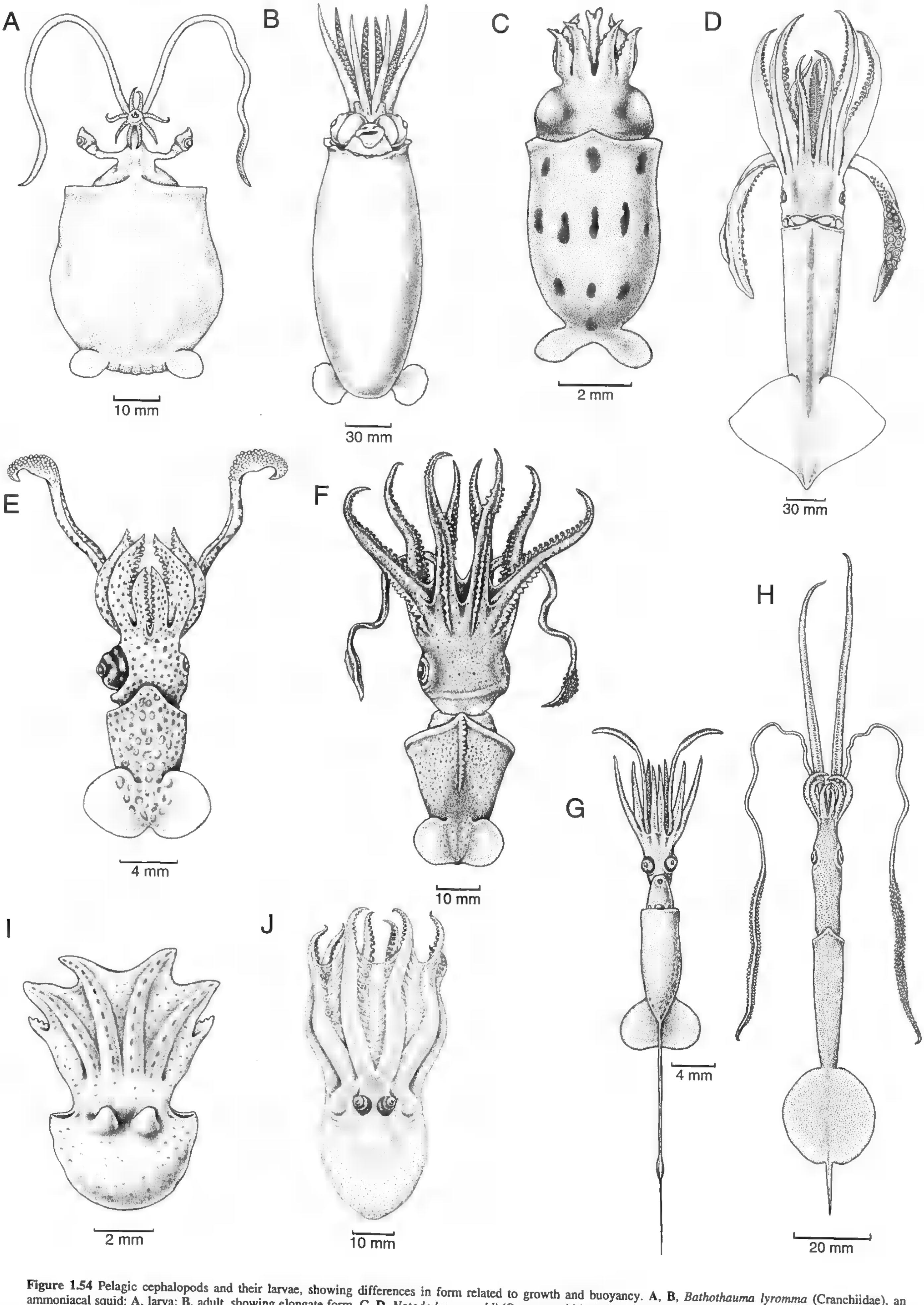


Figure 1.54 Pelagic cephalopods and their larvae, showing differences in form related to growth and buoyancy. **A**, **B**, *Bathothauma lyromma* (Cranchiidae), an ammoniacal squid: A, larva; B, adult, showing elongate form. C, D, *Nototodarus gouldi* (Ommastrephidae): C, rhynchoteuthion larva; **D**, the streamlined form of the adult muscular squid. **E**, **F**, *Histioteuthis miranda* (Histioteuthidae), an ammoniacal squid: E, larva, showing the asymmetrical eyes typical of this family; F, adult. G, H, *Joubiniteuthis portieri* (Joubiniteuthidae), a slender delicate ammoniacal squid: G, larva; **H**, adult. **I**, **J**, *Amphitretus pelagicus*, a pelagic octopod (Amphitretidae): I, larva; J, adult. (B, after Allan 1945; Sweeney *et al*. 1992; F, J, after Allan 1945; C, after Aldred 1974; H, after Sweeney *et al*. 1992) [K. Hollis]

Streamlining is less critical in these neutrally buoyant groups, as they are no longer dependent on their locomotion for respiration, and these animals show a wide diversity of body shapes (Fig. 1.54A, B, E–J). Jet propulsion is required only for occasional escape reactions or rapid manoeuvring, and weak mantle pulses are sufficient for normal slow gill aeration (see also Chapter 11).

Increased buoyancy also carries an increased risk of predation, and a number of different defensive counter-mechanisms have evolved. At the simplest level, some oceanic octopods shelter within or on other organisms. For example, males of *Ocythoe* species live in salps (Hardwick 1970) and argonauts clasp the backs of jellyfish, or each other, forming chains (Nesis 1977). As in other members of the neuston community, the blue colour of epipelagic or neustonic oceanic cephalopods reduces their visibility from above. Examples are immature *Moroteuthis* species (Onychoteuthidae), the ommastrephid *Ommastrephes bartrami* and some epipelagic octopods (Roper, C.F.E. & Young 1975). Young of *Tremoctopus* species may protect themselves with pieces of *Physalia* tentacles held in the arms, and suckers filled with *Physalia* nematocysts (Jones, E.C. 1963).

Most living cephalopods have an ink sac. Ejection of its contents in the featureless pelagic environment can provide a visual barrier behind which the squid may escape. The ink of some species also includes a skin irritant, which may deter predators further. The ink of some loliginids and sepiolids includes luminescent bacteria which sparkle brilliantly for many minutes, confusing the dark-adapted eye of a potential predator (see also Chapter 11).

Cephalopods can change their colour rapidly. Use of colour change for camouflage or in communication between individuals is most highly developed in inshore species. Colour is less useful to mesopelagic and deeper-living cephalopods, which have evolved other anti-predator devices. Many oceanic cephalopods, especially teuthoid squids, have photophores in the skin (Herring 1977, 1988). As a defence against predators, most mesopelagic species are able to produce down-welling light from ventral photophores at an intensity and wavelength that match those of the daylight, and thereby eliminate their silhouette against the highly-directional daylight above (Young, R.E. & Roper 1976, 1977; Young, R.E. & Mencher 1980).

Many pelagic cephalopod species gradually migrate downwards as they grow, a process termed ontogenetic descent (Clarke, M.R. & Lu 1974, 1975; Lu & Clarke 1975a, 1975b; Roper, C.F.E. & Young 1975). For example, juveniles of the cranchiid squid *Teuthowenia pellucida* (Pl. 2) are confined to the upper 200 m of the ocean and descend when adult to depths of 900–2500 m (Voss 1985). A few, such as *Vampyroteuthis infernalis*, undergo ontogenetic ascent from deep water (Roper, C.F.E. & Young 1975). Many species also adopt a pattern of diel vertical migration to depths of several hundred metres during the day (Clarke, M.R. & Lu 1974, 1975; Lu & Clarke 1975a, 1975b; Roper, C.F.E. & Young 1975). This vertical migration may provide protection during the day and access to feeding areas during the night. It may also reduce the energy required to maintain the down-welling light system, by minimising the level of background daylight (Young, R.E. & Roper 1977).

Cephalopods are well equipped to catch swift prey such as small fish, crustaceans and other cephalopods, using their suckered arms and tentacles, speed and agility, and well-developed nervous and sensory system. The structure and function of the large eyes in coleoid cephalopods are comparable to those of vertebrates, and sight appears to be most important for these cephalopods (Messenger 1981). In turn, juveniles and small cephalopod species, especially oceanic ones, are very vulnerable to predation by larger fish or crustaceans. Subadult and adult cephalopods are particularly important sources of food for large fish such as sharks and tunas, for cetaceans and seals, as well as for seabirds near the surface. Ecologically they are extremely important in the food webs of all oceans, and the weight of squid consumed by such predators suggests that their biomass is of the same order as that of fishes (Clarke, M.R. 1986).

Cephalopods are dioecious and exhibit varying degrees of external sexual dimorphism. Males and females of some species also differ markedly in size and shape; males are dwarfs in *Argonauta* and related genera. Generally, males use one or more modified arms, each termed a hectocotylus, to transfer spermatophores to the females.

The spawn of only a few nectonic and oceanic oegopsid squids is known, and may form large gelatinous masses or flat ribbons, and some mesopelagic squids and cirrate octopods lay single eggs (Boletzky 1982; Young, R.E. & Harman 1985). Young, R.E. (1972) suggested that it is likely that all incirrate octopod females brood their eggs until the young hatch. In the genus *Argonauta*, the elaborate shell secreted by the female provides protection and flotation and allows attachment of the eggs (Pl. 21.3; Young, J.Z. 1960).

For many years all coleoid cephalopods were thought to be semelparous, dying *en masse* after a single spawning. Although this occurs in *Loligo opalescens* and *L. bleekeri* (Fields 1965; Hamabe 1973) and probably also in most ommastrephids (see Chapter 13) and some histioteuthids (Clarke, M.R. 1980), multiple spawners apparently exist in all coleoid orders (Harman, Young, Reid, Mangold, Suzuki & Hixon 1989), including oceanic species with small eggs (Mangold 1987).

Development in cephalopods is direct, whereby hatchlings of species with large eggs resemble miniature adults, and those with small eggs only show gradual changes in proportions (Fig. 1.54E–H). Little is known of the development of pelagic species because attempts to rear young oegopsid squid to a stage where they can be identified have been unsuccessful to date (Sweeney, Roper, Mangold, Clarke & Boletzky 1992). Frequently the juveniles are so different from the adults that they have been described as a different species.

Meroplankton

Between two-thirds and three-quarters of all tropical and temperate benthic marine gastropod and bivalve molluscs have a planktonic larval stage as part of their life cycle (Thorson 1950; Ockelmann 1965). Collectively, such passively drifting larvae, along with those of other benthic invertebrates, are known as the meroplankton or ‘temporary plankton’.

Larvae of gastropods and eulamellibranch bivalves are known as veligers. The name refers to the presence of the velum, a ciliated structure common to all veliger larvae. Among gastropods the velum is a thin, transparent, usually bilobed or four-lobed structure, located on each side of the head (Fig. 1.55). Three rows of cilia around the periphery of the velum are used in both feeding

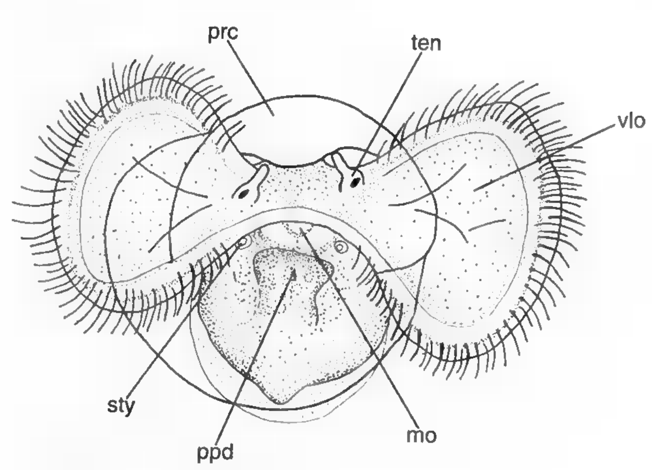


Figure 1.55 Typical swimming caenogastropod veliger larva, *Ilyanassa obsoleta* (Nassariidae). **mo**, mouth; **ppd**, propodium; **prc**, protoconch or larval shell, length *ca.* 0.5 mm; **sty**, right statocyst; **ten**, left tentacle with eye spot at base; **vlo**, ciliated velar lobe. [R. Scheltema]

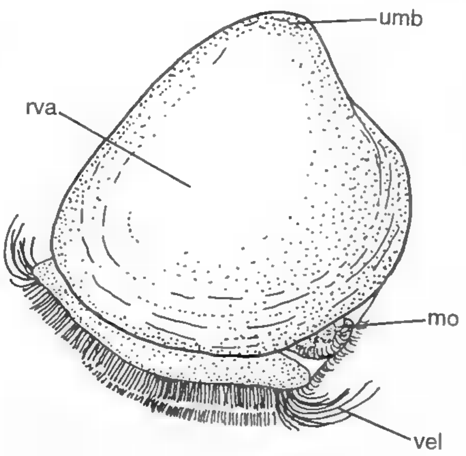


Figure 1.56 Typical swimming bivalve veliger larva, *Crassostrea virginica* (Ostreidae). **mo**, mouth; **rva**, right valve of prodissoconch; **umb**, umbo, where two valves of prodissoconch articulate; **vel**, ciliated velum; the anterior end is to the right; length of valves *ca.* 275 µm. [R. Scheltema]

and swimming (Fretter 1967). These cilia are remarkably coordinated and appear to be under nervous control (Carter 1926; Mackie, Singla & Thiriot-Quievreux 1976). In the marine eulamellibranch and filibranch bivalves, the velum is reduced to lappets and the arrangement of cilia is more complex than that of gastropod veligers (Fig. 1.56). Exceptions are found among teleplanic, or long-distance, bivalve veligers, such as those of the Pinnidae (Scheltema, R.S. & Scheltema, A.H. 1984) and the galeommatoidean, *Planktomya henseni* (Allen, J.A. & Scheltema 1972), in which the vela are thin, bilobed structures much like those encountered among gastropods (Fig. 1.57).

Protobranch bivalves and neomenioid aplacophorans have a characteristic larva termed a pericalymma, which is surrounded by a ciliated test during its development (Drew 1899; Thompson 1960; Gustafson & Reid 1986); these short-lived larvae do not feed and are lecithotrophic. A lecithotrophic larva is present in other aplacophorans, as well as in the Polyplacophora and Scaphopoda, but these lack a test during development (see Nielsen 1995).

The larval shell of gastropod veligers is termed the protoconch and in some 'prosobranchs' may be elaborately ornamented. A marked discontinuity occurs between protoconch I and protoconch II; the first is laid down early during development, usually while larvae are still retained within an egg capsule, and the second is formed subsequently during planktonic life. Protoconch I may have patterns of minute protuberances whereas protoconch II often has striking patterns of axial and spiral cords (for example, in the Cypraeidae) or other kinds of ornamentation (Fig. 1.58). Alternatively protoconch II may be smooth, as encountered among the Architectonicidae (Scheltema, R.S. & Williams 1983). The larval shells of opisthobranch gastropods have a few smooth whorls, and the species are difficult to distinguish from one another (Hadfield 1964). In nudibranchs the shell is lost at metamorphosis.

As in gastropods, a discontinuity is present in the eulamellibranch bivalves between an early larval shell, designated prodissoconch I, and the subsequent prodissoconch II (Waller 1981). The latter is readily recognisable among species with a feeding planktonic larva, in which protoconch II becomes much larger than the initial prodissoconch I (Ockelmann 1965), a condition quite unlike that encountered in non-feeding larvae. Veliger larvae in different bivalve families differ in the structure of their hinge (Fig. 1.59), a character useful for identification to genus (Rees 1950; Lutz *et al.* 1982).

The larval shell appears on the apex of the juvenile or well-preserved adult shell of gastropods, or at the umbo in bivalves. Its structure allows one to infer the mode of development even among fossil specimens, that is, whether or not a species has, or had, a planktonic development (for examples, see Shuto 1974; Scheltema, R.S. 1977 for gastropods; Lutz & Jablonski 1981 for bivalves). Neogastropoda tend to follow a non-planktonic development that follows phyletic lines (Radwin & Chamberlain 1973) and at high Arctic latitudes molluscs seldom have planktonic development (Ockelmann 1965; Thorson 1965). Hain (1990) concluded that most Antarctic gastropods have a 'lecithotrophic intracapsular metamorphosis' and indeed only two exceptions are known. However, unlike those in the Arctic, some of the most abundant Antarctic bivalves are now known to have planktonic development (Hain & Arnaud 1992); of 44 Weddell Sea bivalves examined, 14 (32%) have planktotrophic development and 13 (30%) have demersal lecithotrophic development. Hence, about two-thirds of Weddell Sea mollusc species have a passively drifting larval stage while the remaining third, which includes six families, exhibits brooding behaviour. Information on the mode of development is important in understanding the role of life histories in the evolution, systematics, biogeography, and ecology of molluscan species (Scheltema, R.S. 1978, 1986a, 1989; Jablonski & Lutz 1983; Jablonski 1986; Nielsen 1995).

The manner and rate of feeding in molluscan veligers have been described in a number of gastropod and bivalve species. Feeding is accomplished by the cilia of the velum. Details of the ciliary arrangement on the velum of a gastropod have been illustrated by Fretter (1967) and of the bivalve *Pecten maximus* by Cragg (1989). Precisely how feeding occurs has been described in detail using cinematography (Strathmann & Leise 1979; Strathmann 1987).

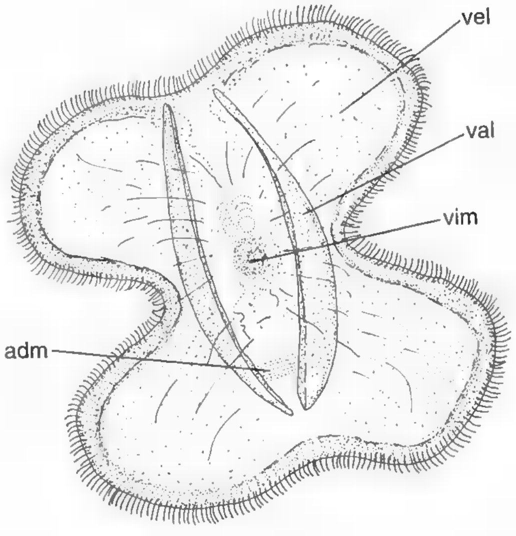
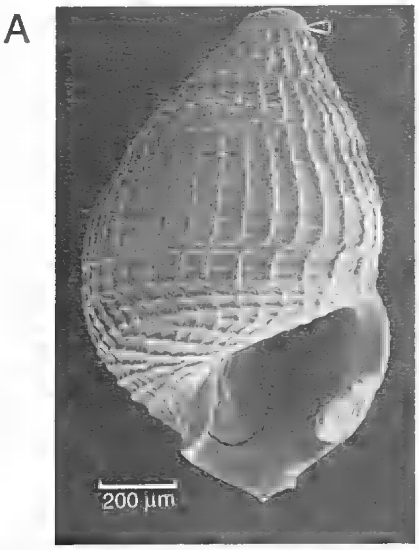


Figure 1.57 Swimming teleplanic bivalve veliger larva of the family Pinnidae, widely represented in the Indo-Pacific and in tropical Australian waters. The velum is a broadly expanded, thin bilobed structure differing markedly from that encountered among oysters and clams (see Fig. 1.56). Pinnid larvae are some of the largest found among bivalve molluscs. **adm**, adductor muscle; **val**, valve of shell; **vel**, velum; **vim**, visceral mass as seen through velum. [R. Scheltema]

Some selection for food particle size apparently is possible. Bonar & Maugel (1982) suggested that particles may be excluded by 'reticulate lamellae in larval gastropod feeding structures' and Paulson & Scheltema (1968) showed that veligers of the caenogastropod *Nassarius obsoletus* apparently can select different species of micro-organisms. Thorson (1946) proposed that the food ingested by larvae is limited by the maximum size of the oesophagus and that molluscan veliger larvae generally are herbivorous, feeding largely, if not entirely, upon pico- or nanoplankton which range from 2–20 µm in size. However, not all larvae are strictly herbivorous.



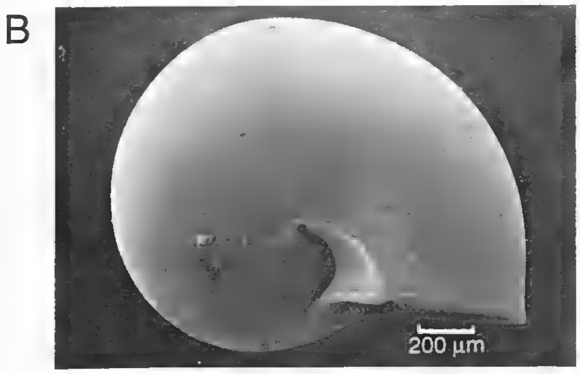


Figure 1.58 Larval protoconch of two teleplanic Indo-Pacific gastropod species, illustrating extreme differences in shell ornamentation. A, the shell of the cowrie *Cypraea isabella* (Cypraeidae), showing demarcation between Protoconch I and II (arrow). B, protoconch of *Philippia radiata* (Architectonicidae). Both species are widely distributed in the Indo-Pacific, including the North Queensland coast; those shown are from the central Pacific Ocean. [R. Scheltema]

Veligers of the oyster *Crassostrea virginica* are omnivorous and readily ingest a wide range of food particles, including Protozoa and bacteria; alternative food sources 'play an important role in larval nutrition' (Baldwin & Newell 1991). Masson's (1977) observations on the larvae of *Mytilus galloprovincialis* were essentially similar.

A variety of large holoplanktonic organisms occur regularly in the digestive tract of large teleplanic gastropod veligers (*ca.* 5 mm length; *Cymatium*, *Bursa*, and *Cypraecassis* species), collected from the mid-tropical Atlantic Ocean. Included are foraminiferans, radiolarians, tintinnids and dinoflagellates, such as *Procentrium* and *Ornithocerus* species, and larger diatoms of 90–100 µm in diameter (Richter 1987). Long chains of diatoms are sometimes ingested by gastropod veligers (Fretter & Montgomery 1968). In laboratory experiments, bivalve larvae are capable of absorbing and utilising dissolved organic material to augment substantially their nutrition from other sources (Manahan & Crisp 1982), but the precise role of dissolved organic matter in the natural environment remains unclear.

Different rates of growth result when various microalgal species are used as food in the laboratory; some microalgal species promote much faster growth than others (Loosanoff 1954). Differences in the nutritional quality of a food organism may, as a consequence of its age and the conditions under which it has been grown, also account for variability in larval growth. Increasing the concentration of an alga or offering more than one species at once produces faster larval growth (Davis, H.C. & Guillard 1958). Boidron-Métairon (1995) concluded that 'quality of algal biochemical composition rather than quantity affects larval growth and survival ... algal nutritive value is not clearly correlated to carbohydrate, protein and amino acid content ... lipid quality rather than quantity affects the nutritional value of microalgae.'

The results of laboratory experiments are only of limited interest to an ecologist for understanding food and feeding requirements in natural populations of larvae, although they are possibly of application for aquaculturists. For example, the concentration of microalgae required for successful growth and development in a standing laboratory culture usually far exceeds that encountered by larvae in their natural environment. Paulay, Boring & Strathmann (1985) questioned whether, in the natural environment, the quality and quantity of food limit growth and survival. Boidron-Métairon (1995) emphasised the need for more evidence on the dynamics of larval nutrition in the field and for understanding natural energy sources available to larvae, whether it be micro-organisms, miscellaneous particulate or dissolved organic matter.

Lecithotrophic planktonic larval development is known for the pericalymma larva of protobranch bivalves and aplacophorans and also for approximately one third of all opisthobranchs for which the mode of development is known (Bonar 1978). Accordingly, they remain planktonic only briefly, usually not for more than a few days. In rare instances, lecithotrophic veligers are facultative planktotrophs known to ingest food, though such larvae apparently derive little or no benefit from doing so (Strathmann 1987).

Predation and disease are two sources of larval mortality. Substantial mortality can also result from hydrographic processes, such as diffusion or advection of the larvae away from any suitable post-larval habitat. In the natural environment, mortality must be very great as the fecundity of species with planktotrophic development is very high. However, only a few data on natural mortality based on actual measurements exist. Estimates have been made in two ways.

Direct estimates are made by monitoring the decline in numbers of larvae within a cohort in a natural environment. Examples of direct mortality estimates within natural cohorts have been summarised by Rumrill (1990). Estimates of instantaneous daily mortality rates for bivalves are 12–28% but no distinction can be made between predation and advection.

Mortality can be estimated indirectly by comparing the difference between fecundity of a species with the number of larvae which subsequently settle and metamorphose. Such estimates are substantially lower than direct estimates, with an instantaneous daily mortality of 3–18%. Indirect estimates of the instantaneous daily rate of mortality for gastropod veligers are 3–16.5%.

The known predators of planktonic gastropod and bivalve veligers are summarised by Young, C.M. & Chia (1987). Predators of gastropod larvae include cnidarians – hydromedusae and siphonophores – and the larvae of polychaetes and decapod crustaceans. The principal known predators of bivalve larvae include ctenophores, hydromedusae and the larvae of polychaetes.

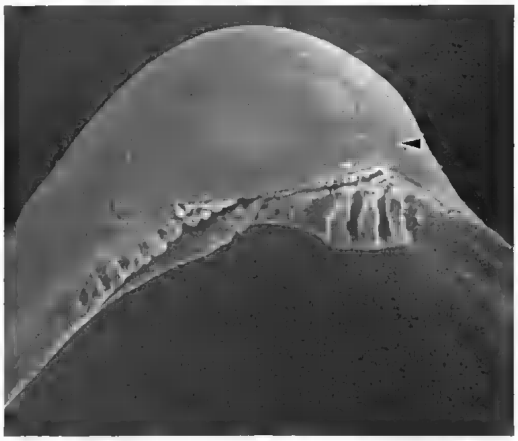


Figure 1.59 Apex of the right larval shell of a species of Pinnidae. The hinge teeth shown interdigitate with those of the opposite valve; they are lost after metamorphosis. The small arrow indicates demarcation between prodissoconch I and II. [R. Scheltema]

Bacterial, viral and fungal diseases are encountered in laboratory culture of bivalve larvae, but almost nothing is known about their role as pathogens in the natural environment, (Davis, H.C., Loosanoff, Weston & Martin 1954; Guillard 1959; Tubiash, Colwell & Sakazaki 1970; Elston 1980).

For convenience, development of planktotrophic larvae can be divided into two periods. During the initial precompetent stage, morphological development and growth occur; in the subsequent competent stage settlement and metamorphosis first become possible (Fig. 1.60). The advent of competence may include changes in behaviour, particularly that related to vertical swimming and testing of a substratum.

The length of the precompetent stage is determined largely by the availability of food, and by seawater temperature, particularly within temperate regions. The earliest laboratory studies of the relationship of water temperature on rate of veliger development were made for the bivalve *Venus mercenaria* (= *Mercenaria mercenaria*) (Loosanoff, Miller & Smith 1951) and the caenogastropod *Nassarius obsoletus* (= *Ilyanassa obsoleta*) (Scheltema, R.S. 1967). The relationship of temperature to growth is known from laboratory experiments for larvae of more than twenty commercially important European and North American bivalve species, but there are data for only a few gastropod species. Laboratory experiments suggest that, within the limits that a larva is likely to encounter in its natural environment, temperature will account for no more than a doubling of the growth rate – or shortening of the precompetent stage by one-half.

The inter-relationship of temperature and food in the natural environment is complex and their respective roles in determining the length of the precompetent larval stage in the field remains problematic. The two can be confounded easily in coastal regions by anthropogenic effects that arise from poor agricultural practices, for example, silts and insecticides, and from industrial pollutants such as heavy metals, acid wastes and other toxic chemicals. The effect of some of the by-products of human activity on molluscan larvae has been examined in the laboratory (Davis, H.C. & Hidu 1969a, 1969b; Calabrese, Collier, Nelson & MacInnes 1973).

During metamorphosis, larvae lose their velum and may either become attached to a hard substratum (for example, oysters), bury into the sediment (clams and protobranch bivalves) or creep upon the surface (most gastropods). The anatomical and physiological changes at metamorphosis may be extensive. In some species, there is a radical change from a herbivorous phytoplankton diet to that of a carnivore, such as occurs in naticids.

The length of the competent larval stage is dependent upon an encounter of a larva with a substratum adequate for survival and development of the newly settled juvenile. Cues for settlement differ with different species and have been the object of both field and laboratory study (Crisp 1974; Scheltema, R.S. 1974; Butman 1987).

Among the earliest observations on settlement cues for a bivalve species were some engagingly simple field experiments by Cole & Knight-Jones (1949); these demonstrated that larvae of *Ostrea edulis* selectively settled and metamorphosed upon hard submerged surfaces bearing a bacterial film in preference to similar surfaces which lacked such a film. Subsequent laboratory experiments show that the cues for settlement of oyster larvae of *Crassostrea virginica* are chemically mediated (Crisp 1967).

Veligers of the caenogastropod, *Nassarius obsoletus*, settle in response to sediment from intertidal flats inhabited by the adults of the species (Scheltema, R.S. 1956). Further laboratory experiments showed that micro-organisms in the sediment provide the cue for this response (Scheltema, R.S. 1961).

Ample subsequent experiments in the laboratory have suggested a variety of cues which may induce settlement and metamorphosis of mollusc larvae. For example, it is not surprising that veligers of 'shipworms' – specialised, wood-boring bivalve molluscs of the family Teredinidae – metamorphose in response to the presence of wood or wood extracts (Harrington 1921; Wilson, D.P. 1952; Kampf, Becker & Kohlmeyer 1959; Turner, R.D. & Johnson 1968) or that the veligers of the opisthobranch *Phestilla sibogae* metamorphose in the presence of mucus secreted by their post-larval prey, reef-building corals of the genus *Porites* (Hadfield & Scheur 1985). Larvae of the caenogastropods, *Bittium reticulatum* and *Rissoa splendida*, and the bivalve, *Brachyiodontes lineata*, respond to the thallus alga, *Cystoseira barbata* (Kiseleva 1966a, 1966b). Larvae of the abalone, *Haliotis* species, are induced to settle in the presence of coralline algae or species of the thallus red alga, *Porphyra*, upon which they feed (Morse & Morse 1984). If a suitable cue is not encountered, larvae (within species-specific limits) can delay settlement and metamorphosis. Some larvae of the opisthobranch *Aplysia juliana* can delay settlement up to 300 days after reaching competence to metamorphose if denied green algae of the family Ulvaceae (Kempf 1981).

The cues for settlement fall into two categories: those requiring contact with the bottom or normal substratum, such as in *Haliotis* (Morse 1985) and those perceived by larvae in the water column and which apparently modify larval behaviour, for example, in *Nassarius* (Scheltema, R.S. 1961), *Crassostrea* (Hidu, Valleau & Veitch 1978; Coon, Bonar & Weiner 1985), *Adalaria* (Lambert & Todd 1994) and *Phestilla* (Hadfield & Scheur 1985). Those chemical cues studied so far appear to be neurogenic compounds (Morse 1985; Hadfield & Pennington 1990).

A 'gregarious' response is shown by the larvae of the European oyster, *Ostrea edulis* (Cole & Knight-Jones 1949; Bayne 1969), and the North American oyster, *Crassostrea virginica* (Crisp

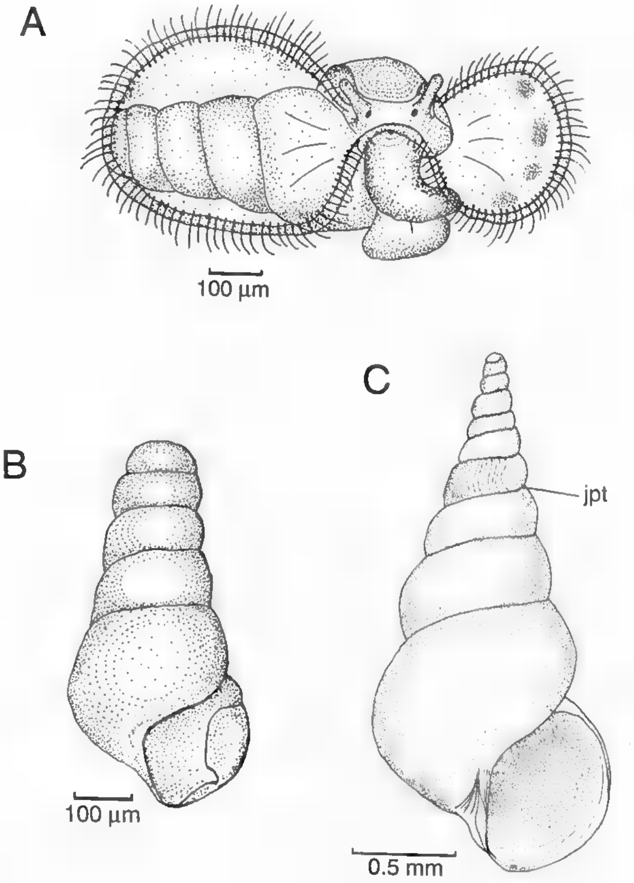


Figure 1.60 A planktotrophic gastropod, probably a species of *Styliferina* (Litiopidae), from Cleveland Bay, off Townsville, North Queensland. **A**, swimming veliger larva, competent to metamorphose; the right lobe of the asymmetric velum has twice the area of the left lobe, which bears lemon yellow pigment spots. **B**, shell or protoconch from larva similar to that in A. **C**, shell of a sexually mature 10-week old individual grown in the laboratory. **jpt**, junction of larval protoconch, as in B, and post-larval teleoconch.
[R. Scheltema]

1967; Hidu 1969; Veitch & Hidu 1971), whereby larvae preferentially settle near members of their own species. Similar gregarious responses have been reported for the caenogastropods *Bittium reticulatum* and *Rissoa splendida* (Kiseleva 1966a).

Although laboratory experiments may reveal the kinds of cues that facilitate settlement, most do not consider the role of hydrodynamic processes found in natural environments, specifically in a region of sheer at the bottom-boundary layer. As water flows along the bottom a characteristic velocity profile develops which can vary according to the phase of the tide, weather, and characteristics of the bottom. How are larvae, capable only of speeds less than 1 mm.sec^{-1} (Chia, Buckland-Nicks & Young 1984), able to settle under temporally and spatially varying current velocities which generally exceed their swimming ability?

Butman (1987) considered the contrasting roles of an *active selection hypothesis*, which supposed that settlement is determined largely by the behaviour of larvae in response to a chemical or physical cue, with an alternative, the *passive deposition hypothesis*, which proposed that larval settlement is primarily the consequence of hydrographic processes. She concluded that the two are not mutually exclusive, such that '... Larvae may be passively deposited and accumulate at the large spatial scales (> 10 m to > 10 km)' whereas 'active habitat selection occurs over much smaller scales' of 10 mm to 1 m.

Experiments in flumes at a current velocity of about 50 mm.sec^{-1} show in fact that larvae of the bivalve *Mulinia lateralis* are able to select organically rich mud over an inert substratum of fine glass beads, but require near bottom flow to move them between patches of sediment 'so that they can exercise their choice' (Grassle, Snelgrove & Butman 1992). Using sediment traps in the natural environment, Butman (1989) could conclude that 'hydrodynamical processes may determine distributions of larvae in very near bottom waters'. More research obviously is required and it seems unlikely that all invertebrate larvae will be affected similarly – for example, because mollusc larvae are more dense they will sink passively more rapidly than those of polychaete larvae.

Larvae of most Australian benthic molluscs remain undescribed. As a result, veligers encountered in coastal water usually cannot be identified to species (Fig. 1.60), notwithstanding that they constitute a significant fraction of the zooplankton. For example, in the tropical waters of Cleveland Bay, northern Queensland, molluscan veligers may contribute up to 10% of the zooplankton in spring and early summer, about equally divided between bivalves and gastropods.

Knowledge of molluscan larvae is of theoretical and practical importance. For example, Nielsen (1995) relied heavily on larval characteristics in determining evolutionary relationships within the molluscs and between the Mollusca and other phyla. The passive dispersal of larvae helps explain the geographic and temporal distribution of molluscs (Scheltema, R.S. 1986a, 1989, 1995); it enables species to colonise new regions and to maintain genetic continuity between disjunct populations over very large geographic regions. For example, many tropical molluscs that occur in Australia belong to widely distributed Indo-Pacific species with geographic ranges extending from East Africa halfway around the world to the eastern-most Polynesian Islands (Scheltema, R.S. & Williams 1983; Scheltema, R.S. 1986b). Genetic differences and similarities between molluscan populations have been related to gene flow effected by larval dispersal (Scheltema, R.S. 1971; Gooch, Smith & Knupp 1972). From the practical viewpoint, the ecology of larvae has long been of interest to those engaged in such shellfisheries as oysters, clams, and scallops, in instances where the fishery is dependent upon natural settlement and recruitment of the early post-larvae or 'spat'. Finally, a knowledge of larval requirements for survival and growth is a necessary prerequisite for aquaculture, as in the culture of the giant clam *Tridacna* (Govan 1995).

MOLLUSCS ON LAND

The Mollusca originated in the sea. The evolution of freshwater and terrestrial species can therefore be viewed as a series of subsequent colonisations of new habitats. The only group to colonise the land has been the Gastropoda; slugs and snails are now integral components of terrestrial ecosystems.

Stylommatophoran pulmonates – snails and slugs with two pairs of tentacles (Fig. 1.61B–D), of which one pair bears eyes at the tip – comprise the major part of terrestrial molluscan faunas throughout the world. A second group of slug-like forms, the systellommatophoran pulmonates, is also found in tropical regions, including parts of Australia. In addition, there are several terrestrial lines within the Caenogastropoda and Neritopsina. These snails have only one pair of tentacles, with eyes near their base (Fig. 1.61A), and a foot bearing an operculum which is used to close the aperture of the shell. In Australia, only members of the Neritoidea, Cyclophoroidea and Rissooidea are terrestrial. Most occur in Queensland.

The reasons for the dominance of stylommatophoran pulmonates over 'prosobranchs' on land are far from clear (Little 1983). Although the two groups have somewhat different anatomical features, they have both adopted quite similar physiological responses to life on land. In some parts of the world, mostly in tropical rainforests, 'prosobranchs' are nearly as common as pulmonates, but they have never diversified in body form to the extent seen in pulmonates.

Australia's present-day land-molluscan fauna includes native pulmonate species, both snails and slugs, and species introduced from Europe, the Pacific and the United States. Most of the many introduced forms are European, including numerous helicids, such as *Helix aspersa*, the common garden snail, and several other snails, a number of herbivorous slug species in the genera *Limax*, *Arion* and *Deroceras* (Altena & Smith 1975), and the carnivorous slug *Testacella haliotidea*. Among the native species are a wide variety of shelled forms that inhabit almost every environment from the desert regions of central Australia to the tropical rainforests of the north-east. Most are herbivores, but some, for example, rhytidids, prey on other snails, earthworms and insect larvae (Smith, B.J. & Kershaw 1979). Native slugs in the family Rathouisiidae occur in litter of tropical and subtropical rainforest. Athoracophorid (Fig. 1.61D) and cystopeltid slugs occur in damp environments as well as dry schlerophyll forest. The biogeographical relationships of indigenous species have been discussed by Allan (1959), McMichael & Iredale (1959), Smith, B.J. (1984) and by Solem & Ponder in this Chapter.

Adaptations to Life on Land

Terrestrial molluscs can desiccate very rapidly because they have a soft, mucus-covered skin. Consequently, their distribution, and the duration of their activity on land, are severely constrained in areas where humidity often falls below 100%. Despite this limitation, terrestrial gastropods inhabit most known environments from lowlands to mountains, and tropical rainforests to deserts. They owe this almost universal distribution, in part, to physiological and morphological adaptations to the rigours of terrestrial life, as well as to behavioural reactions which maintain them in appropriately humid microhabitats (Little 1990).

Physiological and structural adaptations. The most important problem facing molluscs on land is undoubtedly that of water balance. Terrestrial molluscs lose water by evaporation from the skin, in mucus, and in the urine and faeces. These losses must be balanced by uptake of water through drinking and in food, but the major adaptations concern restricting the rate of loss. A relatively impermeable shell reduces evaporation in many species, but in slugs the rates of water loss can be very high. Secretion of mucus onto the skin moistens the external surface, allowing evaporation to continue, so that to some degree the rate of water loss is related to the rate of mucous secretion. With overall rates of loss that can be as high as 17% of the body weight in 40 minutes, the water content of land pulmonates is very variable. Pulmonates can tolerate the resulting large changes in salt concentration of the blood and tissues, but how this tolerance is achieved is not understood (Little 1983). As a probable 'buffer' against changes in water content, some species carry extra water around in the mantle cavity.

During prolonged dry periods, some pulmonates are able to seal the aperture of the shell with a secreted mucous layer or epiphragm (Fig. 1.62). They then remain dormant, in a state referred to as aestivation, until conditions change. During aestivation, the epiphragm reduces the rate of water loss, and the rate is further lowered by an active process occurring in the mantle edge which reduces the permeability of the epidermis to water. The details of this process are not fully understood (Machin 1975; Riddle 1983). Some 'prosobranchs' can also aestivate, the process commencing simply by closing of the aperture of the shell with the operculum. Very often this operculum has structural modifications that allow some gaseous exchange even when it is tightly closed (Little 1983).

Theoretically, evaporation of water from gastropods may be used to cool the body during hot weather. However, this advantage is strictly limited, as the high evaporative rates lead rapidly to desiccation. The adaptations of desert forms to high temperatures therefore involve different mechanisms which reduce evaporation to a minimum. This may be achieved, for example, when the shell can be closely sealed to the substratum (Machin 1967). Some desert species lie loosely on the soil surface, but no Australian snails are known to do this unless they are sheltered under rocks or logs. In general, desert snails have smaller apertures than others, and this also reduces the area from which water may be lost. With the reduced evaporation rate, internal temperatures may rise greatly. There is probably some ability to acclimate to different temperatures, since desert forms can tolerate higher temperatures than other species (Riddle 1983).

During aestivation, the positioning of the shell may affect the temperature inside, and in desert forms, withdrawal of the body of the snail from the lower shell whorl provides an insulating air barrier between the tissues and the ground. The colour and thickness of the shell also affect the degree to which radiant heat is reflected, and desert forms of *Bothriembryon*, *Sinumelon* and *Pleuroxia* have chalky white shells. The temperature relationships of an aestivating desert snail are shown diagrammatically in Figure 1.63 (after Schmidt-Nielsen, Taylor & Shkolnik 1971).

The kidneys of terrestrial gastropods are also involved in water balance. In pulmonates, urine with a lower salt concentration than the blood can be produced in large quantities when the snails are in wet surroundings, but when the environment dries up the urine is resorbed and only dry nitrogenous waste is excreted. The overall excretory capabilities are similar in neritopsine and cyclophoroidean snails, but the few species that have been examined are incapable of resorbing all the fluid from the urine once it has been produced. These species are unable to tolerate dry conditions. In other groups, such as the littorinoidean family Pomatiasidae (not found in Australia), the snails are incapable of producing dilute urine (Little 1990), but can tolerate very dry environments. The sites of water resorption and nitrogen excretion in 'prosobranchs' differ from those in pulmonates, and some of the features of renal systems of terrestrial pulmonates and 'prosobranchs' are compared in Figure 1.64.

Nitrogen excretion in terrestrial molluscs is also adapted to cope with the stresses imposed by frequent lack of water. Most pulmonates produce uric acid as a major excretory product, which can be excreted as a solid since it has a very low solubility and toxicity. Some snails may excrete urea, but the most interesting adaptation is the production of gaseous ammonia. This occurs primarily during aestivation, when the gas is liberated through the mantle. In this way an extremely toxic substance can be excreted without poisoning the snails themselves (Little 1983).

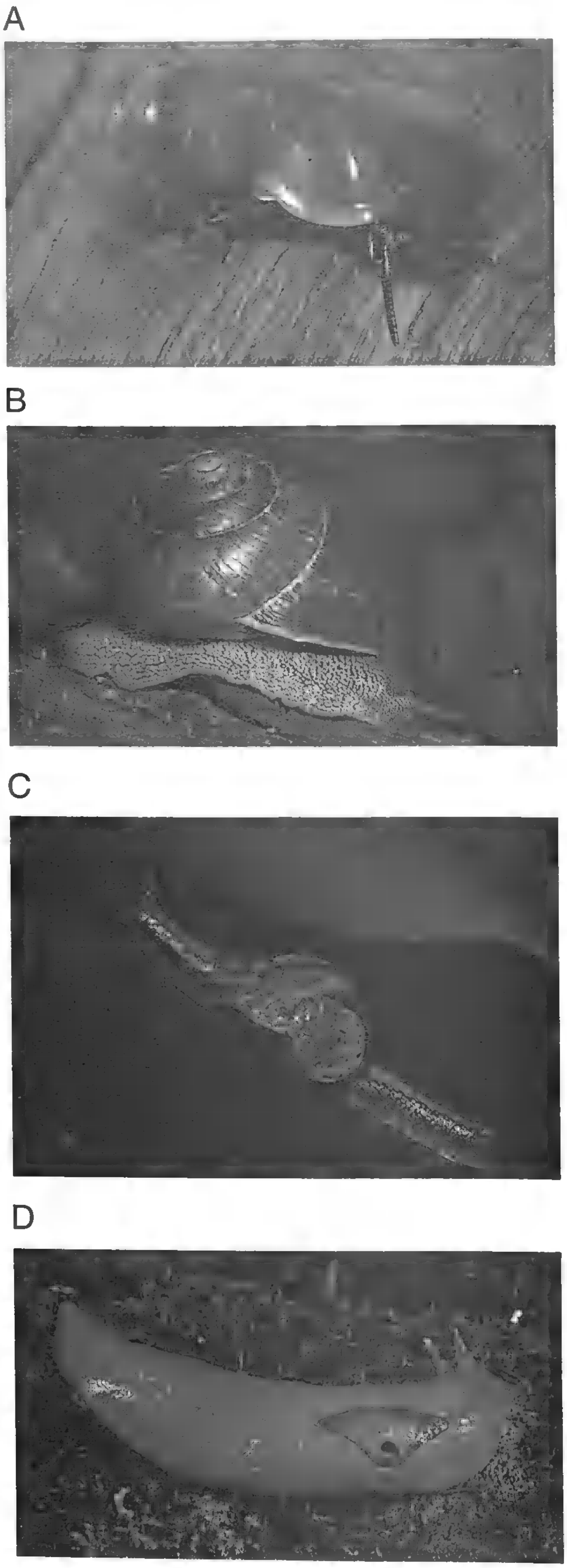


Figure 1.61 Terrestrial gastropods. A, prosobranchs such as *Pupina coxeni* (Pupinidae) bear a single pair of tentacles. B, the camaenid *Meridolum gilberti*, showing the two pairs of tentacles typical of pulmonates. C, a pulmonate 'semi-slug', *Helicarion* sp. (Helicarionidae) has a reduced, fragile shell. D, the shell of the pulmonate *Triboniophorus graeffei* (Athoracophoridae) is reduced to several internal calcareous fragments – note the open pneumostome within the triangle. [A–D, Queensland Museum]

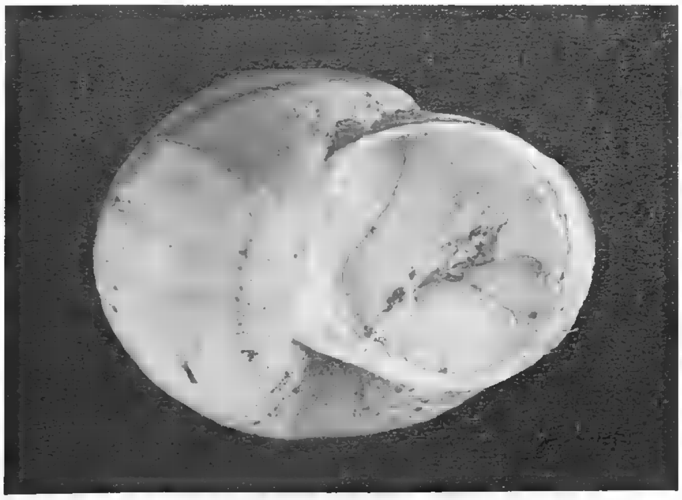


Figure 1.62 *Plectorhagada carcharias* (Camaenidae), ventral view of aestivating snail, showing the epiphragm that seals the shell aperture.
[Clay Bryce/WA Museum]

In all terrestrial 'prosobranchs' and pulmonates, the mantle cavity acts as a lung, thereby differing functionally from the more typical aquatic forms. There are no gills, and the internal surface of the cavity is well vascularised. In pulmonates, ventilation of the lung is controlled by the pneumostome – a sphincter that can open and close (Figs 1.61D, 1.64A). Air is drawn in by lowering the floor of the mantle cavity, and pushed out by raising it. In contrast, ventilation of the 'prosobranch' lung is probably entirely passive; the opening to the exterior is wide, and movements of gas probably occur entirely by diffusion. The rate of water loss from 'prosobranch' lungs is therefore probably much higher than that of pulmonates, although this has not been demonstrated empirically.

Behavioural adaptations. Although terrestrial molluscs show numerous physiological and structural modifications that fit them for life on land, they are not as independent of terrestrial exigencies as many other groups, such as the insects, for example. The behavioural patterns that adapt them for their particular microhabitats are therefore extremely important (Prior 1985). The phenomenon of aestivation has already been mentioned, but in less extreme conditions it is essential that molluscs are active when humidity is high and temperature is not excessive. These behaviour patterns ensure that the majority of terrestrial molluscs emerge from their hiding places after rain or dew has fallen, or at night (Russell-Hunter 1964; Pomeroy 1969). This response is probably actually triggered by falling temperature rather than rising humidity. Slugs in particular are restricted to areas or time periods in which humidity is high (Runham & Hunter 1970; Prior 1985).

In some slugs and snails, behaviour is governed by a circadian rhythm that activates the snails roughly every 24 hours even when external conditions are made constant, as shown by *Helix aspersa* and *Limax* species in the laboratory (Riddle 1983). Longer term activity patterns such as annual reproductive cycles are also geared to environmental conditions. The introduced snail *Cernuella virgata*, common in some areas of southern Australia, breeds annually when the rainy season opens in the autumn (April/May), and each year the timing of the breeding season is governed by the weather (Pomeroy 1969). Similarly, camaenid pulmonates in the Kimberley region of north-western Western Australia are born in the wet season, and their subsequent life cycles are geared to the succeeding annual wet seasons (Solem & Christensen 1984). The timing of life cycles of terrestrial molluscs can, however, vary greatly from one environment to another. In desert forms, for instance, annual emergence from aestivation may be suppressed when the rainy season fails, and desert snails are capable of living for years without replenishing food or water (Schmidt-Nielsen *et al.* 1971).

Distribution

Physical factors governing distribution. It has been emphasised above that availability of water is one of the most basic factors governing the abundance and distribution of land snails. Together with temperature, it determines to a great degree the species composition of land snail communities. The influence of 'climate' cannot be overstressed: the molluscan communities of different regions with different climates may have many similarities in terms of the total numbers of species present, diversity, and some taxonomic features, but invariably a large proportion of the species will be different.

In this regard the study of microclimates is also important, being the climate of the exact microhabitat of the animals, as distinct from the climate measured by meteorologists. These microclimates will differ for each species, even when these are found in the same daytime retreats. Cameron (1978) has shown how snails emerge at night and how different species utilise quite different surfaces for foraging. Perhaps the best series of studies of the effects of climate on distribution of land snails is that on *Cepaea nemoralis* and *C. hortensis* in Britain (Peake 1978; Cain 1983). These two species overlap in distribution, but in general *C. nemoralis* is found on drier and warmer sites, whereas *C. hortensis* dominates in wetter, cooler areas such as valley floors. These climatic factors seem to be much more important than the types of vegetation in the areas concerned.

Two further physical – or strictly, chemical – factors are of major importance in governing land snail distribution. These are the supply of calcium, and the level of acidity or alkalinity (pH) of the soil. A source of calcium is essential for shelled species, and in general there are more species of snail in limestone areas than in any others. This was clearly highlighted in Boycott's (1934) survey of land molluscs in Britain, which showed that there was only one calcifuge, or lime-avoiding, species, but over 20 calcicoles – those most abundant on lime-rich soils. This is in distinct contrast to the situation with slugs, which have either no shell or only a rudimentary one: in Britain slugs show no preference for either calcareous or non-calcareous soils. Apart from the direct supply of calcium, however, limestone soils may have other characteristics beneficial for terrestrial molluscs, such as differences in texture and a generally warmer microclimate (Peake 1978).

The effect of calcium may also be confused with the effect of soil pH. Generally the number of species declines in acid soils. This was shown, for example, for terrestrial 'prosobranchs' in Papua New Guinea (Andrews & Little 1982). The roles of soil calcium and soil pH are, however, still not entirely clear, and may in any case be affected by other physical factors such as rainfall. Excessive rain, for instance, may cause leaching of calcium from surface soil, and unsuitable conditions for snails then result even when the soil overlies limestone.

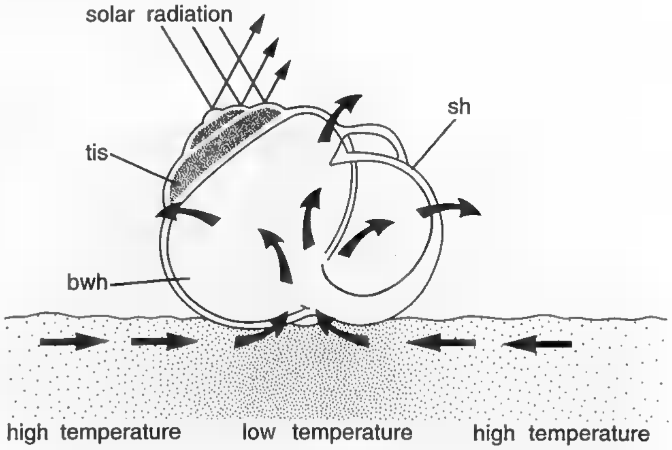


Figure 1.63 Temperature relations in an aestivating desert snail. The arrows show the direction of heat flow. Tissues withdrawn into the upper whorls are insulated from the heat of the soil by the empty lower whorls; a white shell reflects a large proportion of the intense solar radiation. **bwh**, body whorl; **sh**, shell; **tis**, body tissues. (After Schmidt-Nielsen, Taylor & Shkolnik 1971)
[C. Eadie]

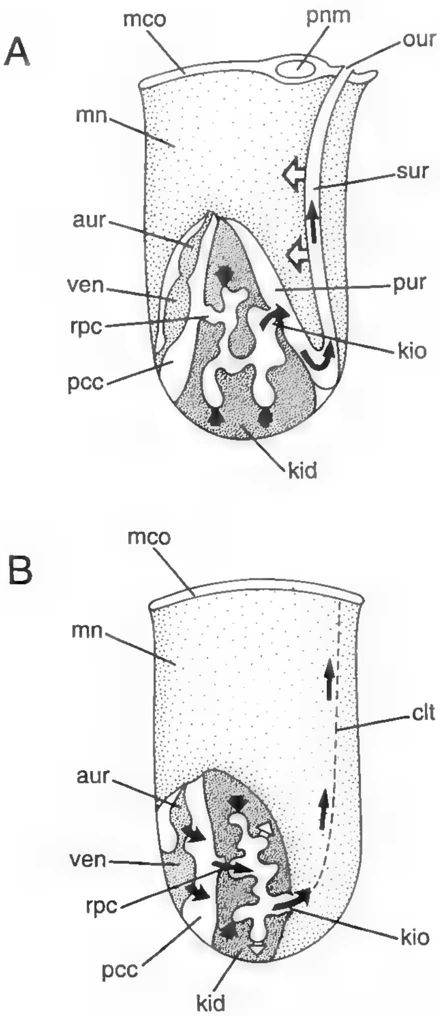


Figure 1.64 Excretory and respiratory routes in terrestrial gastropods. Broad solid arrows show excretion of urate concretions. Broad white arrows show salt and water resorption. Longer arrows show fluid flow. A, in terrestrial pulmonates, primary urine is secreted in the kidney, and the renopericardial canal is closed; urine receives urate concretions in the kidney and leaves the mantle cavity through the ureter, which also resorbs salts and water; as urate secretion and water resorption are spatially separate, the final urine is dry, and some nitrogen is excreted as gaseous ammonia from the mantle. B, in prosobranchs, primary urine is formed by ultrafiltration from the heart. It passes through the renopericardial canal into the kidney, where urate concretions are added, and some salts and water are removed; the urine remains liquid and is removed from the mantle cavity by ciliary tracts. Ventilation in pulmonates is controlled by a pneumostome, but in prosobranchs there is a wide opening to the mantle cavity. **aur**, auricle; **clt**, ciliated tract; **kid**, kidney; **kio**, kidney opening; **mco**, mantle collar; **mn**, mantle; **our**, opening of ureter; **pcc**, pericardial cavity; **pnm**, pneumostome; **pur**, primary ureter; **rpc**, renopericardial canal; **sur**, secondary ureter; **ven**, ventricle. [C. Eadie]

Figure 1.65. The posterior placement of the shell and the elongate head of *Strangesta ramsayi* (Rhytididae) allow for the large buccal cavity used to engulf prey (Solem 1974a). [Queensland Museum]

Biological factors governing distribution. As pointed out by Cain (1983) and Peake (1978), the study of molluscan ecology, and particularly of biological interactions, is a very recent one. Much remains to be investigated, and in this section four points will be briefly discussed, namely the influences of food, competition, predation and dispersal.

Although there is little doubt that food supply can be a limiting factor in marine intertidal molluscan communities, the same cannot be said for terrestrial molluscs. Many land snails eat dead or decaying vegetation, which casual inspection usually suggests is in excess in most snail habitats. This, however, may reflect a lack of critical study, and it is likely that in specific habitats a finite food supply may become limiting.

Whether or not food supply is a limiting factor bears directly on the question of whether there is competition between, or within, species. If food supply is in excess, competition for it is unlikely; but there may, of course, still be competition for some other limiting resource, such as sites suitable for aestivation or egg-laying.

The possibility that competition occurs between species of snails has been closely scrutinised for *Cepaea nemoralis* and *C. hortensis* in Britain, and the findings have been discussed by Cain (1983). The two species occupy separate niches with different climatic characteristics, as discussed above, but in places their distributions overlap. It has been suggested that in these areas of overlap the two species might compete, but the evidence is inconclusive. In summary, competition between some species of land snails may well occur, but it has not yet been demonstrated and is thought not to be very important.

The importance of predation is, in contrast, in no such doubt. Land snails have many predators, including birds and rodents. Other molluscs, such as the slug *Testacella haliotidea* and snails of the genus *Strangesta* (Fig. 1.65), are carnivores, and many more species probably eat the eggs of snails – both their own and other species.

Substantiated situations in which predation has been shown to affect population density are, however, rather few. The impact of the introduced carnivorous snail *Euglandina rosea* on native snail species on Hawaii, Moorea, Tahiti and other Pacific islands and the Mascarene Islands is well documented (Clarke, B., Murray & Johnson 1984; Murray, Johnson & Clarke 1988; Kinzie 1992; Griffiths, Cook & Wells 1993). In Britain, the snail *Aegopinella nitidula* preys on other snails, and it has been suggested, but not proven, that this species is responsible for the low densities of *Nesovitrea hammonis* in specific areas (Mordan 1977). Rodent predation has been shown to reduce population density in a desert snail *Sphincterochila boisseri* in the Negev (Yom-Tov 1970). The effects of thrush predation on *Cepaea hortensis* and *C. nemoralis* have been discussed by many authors (Cain 1983). Thrushes have colour vision, and select those colours and patterns of shell that stand out against the background. While there is no doubt that they do this, the effects that such selective predation may have on the population are difficult to quantify because of the interfering effects of the physical selection imposed by climate. Overall, it is likely that predation is probably important for many species of land molluscs, but the effects of predation by other molluscs, by rodents and by birds probably vary greatly, and much more information is required before any generalisations can be made.

The eggs of terrestrial molluscs hatch as juvenile individuals, in contrast to the situation in many aquatic molluscs. This probably contributes, in part at least, to the restricted distribution of many Australian terrestrial mollusc species, as discussed by Solem in this Chapter. In particular, the colonisation of islands not connected during periods of low sea level must depend upon passive dispersal means. Mechanisms of dispersal other than by crawling are therefore rather important for land molluscs. Several mechanisms have been shown to occur (Rees 1965; Peake 1978), varying from aerial dispersal by wind (Vagvolgyi 1976) to attachment to flying insects or birds. In recent times, the appearance of many European species in Australia has demonstrated the importance of humans in dispersal. Unfortunately, little is known of the rates of successful transport by any of these means. It is possible that within Australia a study of the dispersal of imported species could provide clues about how these dispersal mechanisms function.

MOLLUSCS OF INLAND WATERS

Few books offer details about Australian freshwater molluscs, and enthusiasts need to pursue information that is scattered widely through the scientific literature. The most comprehensive list of taxa is by Smith, B.J. (1992), replacing the long-outdated standard of Iredale (1943). The handbooks of Smith, B.J. & Kershaw (1979) and Williams, W.D. (1980a) are dated, but very useful for preliminary identification. A great deal of fundamental taxonomic work remains to be done. For most groups there is only fragmentary biological information, and often the most basic ecological data must be inferred from studies elsewhere in the world.

Regional Faunas

A recurrent theme in past work has been the idea that different regions of the Australian continent support distinctive faunas. For example, Iredale & Whitley (1938) suggested that the main river systems are characterised by distinctive assemblages of animals, termed *fluvifaunulae*, in which molluscs are prominent. Much of this early work, however, contains *ad hoc* judgments based on few species, and with some qualifications the putative faunas do not bear close examination (see discussion by Walker, K.F. 1981a). Evidently the physiographic boundaries of the major river systems have not been adequate barriers to prevent faunal exchanges, or have not prevailed long enough to permit evolutionary divergences. The widespread climatic instability and aridity of the Quaternary in Australia also would have discouraged development of distinctive regional faunas (*cf.* De Deckker 1986; Bowler, J.M. 1990).

Nevertheless, some bivalve and gastropod species do have distributions limited to the humid tropics, or to dry inland or coastal areas. Among the freshwater mussels (Hyriidae), for example, *Velesunio angasi* is a tropical species and *V. wilsonii* is typical of inland areas. Several species of *Hyridella* occur only in south-eastern coastal drainages, and *Westralunio carteri* is confined to south-western Western Australia (Walker, K.F. 1981a). Few species are confined to isolated river systems.

Bivalvia

Three bivalve families occur commonly in Australian inland waters: the Hyriidae (freshwater mussels), Corbiculidae (little basket shells or orb-shell mussels) and Sphaeriidae (pea shells). Some of the predominantly marine corbiculids and mytilids occur in coastal environments, but are not considered here (see McMichael 1967; Wilson, B.R. 1968; Wells, F.E. 1984b).

Hyriidae. With some possible exceptions, the freshwater mussels of the Australian Zoogeographic Region (Australia, New Guinea and New Zealand) belong to the Hyriidae, a family shared with South America and distinguished, by larval features, from the Unionoidea of other continents (Walker, K.F. 1981a). Four subfamilies are recognised – Cucumerunioninae, Hyridellinae, Lortiellinae and Velesunioninae.

Hyriid mussels occur in seasonal or permanent fresh water throughout Australia (Fig. 1.66), except in southern and western Tasmania. Some species, like *Alathyria jacksoni* of the Murray-Darling river system, are typical of big-river habitats; others, like the widespread eastern species *Velesunio ambiguus* favour slow-flowing and still-water habitats. *Velesunio angasi* of tropical northern Australia and *V. wilsonii* of northern and inland areas are found in virtually the entire range of habitats. Indeed, *V. wilsonii* is reputed to survive for three years without water (McMichael & Iredale 1959), although it is normally associated with permanent waters.

Figure 1.66 A cluster of freshwater mussels, *Hyridella depressa* (Hyriidae), in Lake Burragorang, one of Sydney's water supply reservoirs. [M. Byrne]

Freshwater mussels display a remarkable variety of intraspecific shell shapes and sizes, reflecting their ability to adapt to local conditions. Shape variation is typical of species found in a variety of environments over a wide geographic area (Walker, K.F. 1981b). The length of adult shells ranges from 40 mm for *Hyridella glenelgensis* in south-western Victoria to 200 mm for the boomerang-shaped shells of *Cucumerunio novaehollandiae*, from the coastal rivers of south-eastern Queensland and north-eastern New South Wales. Members of the Cucumerunioninae and Hyridellinae have sculptured shells; others have smooth shells, at least as juveniles. The shells of most adult mussels are pitted and abraded as a consequence of the burrowing habit.

The availability of a taxonomic monograph (McMichael & Hiscock 1958) and a certain amount of other biological and ecological information mean that the Hyriidae are among the best-known Australian freshwater molluscs. The monograph, however, is in need of revision, and the lack of a key hinders identification of species (but see McMichael 1967 for a key to genera). The assignment of species to the family Hyriidae, rather than the Mutelidae (*sensu* McMichael & Hiscock 1959), was effected by Parodiz & Bonetto (1963).

A future taxonomic revision might take account of allozyme variation (for example, Balla 1984) rather than relying entirely on shell shape and internal anatomy. The glochidia larvae of mussels which normally parasitise freshwater fish (for example, Walker, K.F. 1981b) may also provide additional useful taxonomic information. On this basis, early doubts about the affinities of the Cucumerunionae were resolved by Jones, H.A., Simpson & Humphrey (1986). The glochidia of *Cucumerunio* and *Hyridella* have two-pronged larval teeth, rather than a simple tooth, as in *Alathyria*, *Velesunio* and *Westralunio* (Atkins 1979; Walker, K.F. 1981b; Jones, H.A. *et al.* 1986).

Two species of *Lortiella* (Lortiellinae) from north-western Western Australia were described only from shells, and their membership of the Hyriidae is not well substantiated, although McMichael (1967) suggested that their gross anatomy resembles that of species of *Velesunio*. Two other species of doubtful affinity are of the genus *Haasodonta* from New Guinea and are also known only from shells. McMichael & Hiscock (1958) placed them tentatively with the Rectidentinae, a South-East Asian element of the Unionidae. Once clarified, the affinities of these species may change our ideas about the biogeographic relationships of the Australian fauna. The same may apply following a re-evaluation of the fossil fauna, for Ludbrook (1961) described Mesozoic fossils which she regarded as of unionid stock, contrary to the views of McMichael & Hiscock (1958; see also McMichael 1957). Thus, the origins of the modern mussel fauna still are a matter for debate.

The sedentary, filter-feeding habit of mussels makes them potentially useful as monitors for heavy metals, pesticides, radioisotopes and other pollutants (Ryan, Bacher & Martin 1972; Walker, K.F. & Hillman 1977; Jones, W.G. & Walker 1979; Atkins 1981; Walker, K.F. 1981b; Millington & Walker 1983; Jeffree 1985; Jeffree & Simpson 1986; Storey & Edward 1989; Humphrey, Bishop & Brown 1990; Humphrey & Dostine 1994; Jeffree, Markich & Brown 1993; Humphrey, Faith & Dostine 1995; Negri & Jones 1995). Two obstacles to use of *V. ambiguus* as a monitor for heavy metals are the wide variability of metal loads among individuals and the slow rate of metal excretion (Walker, K.F. 1986). These problems may be of less consequence, however, if the time scale for monitoring is in the order of years rather than months.

Several ecological studies have been of made of freshwater mussels, often in tandem with studies of their potential as pollution monitors. The two common species in the Murray-Darling river system (south-eastern Australia), *Alathyria jacksoni* and *Velesunio ambiguus*, provide interesting ecological contrasts (Walker, K.F. 1981b). The former is found in large rivers in the system, but not in the billabongs, lakes and minor streams that are the habitat of the second species. *Alathyria jacksoni* is less tolerant of environmental changes, and particularly vulnerable to dehydration; thus, whilst *V. ambiguus* may survive out of water for a year or more, *A. jacksoni* succumbs to desiccation after about 12 days. Further information on the physiology of *V. ambiguus* is given by Hiscock (1953a, 1953b) and Ch’ng-Tan (1968). The absence of *A. jacksoni* from slow-flowing and still waters may be explained, at least in part, by its intolerance of low levels of oxygen (Sheldon & Walker 1989). Alternatively, the absence of *V. ambiguus* from fast-flowing water probably is because of its small size, light weight and comparatively weak anchorage. *Velesunio ambiguus* displays a variety of irregular forms, including a distinctive, rounded ‘billabong form’ found in shallow, swampy environments associated with the River Murray in South Australia; the broad shell may provide support on the soft substratum (Walker, K.F. 1981a).

The ‘creek’ form of the northern species *Velesunio angasi* is also swollen (Fig. 1.67A), in comparison with the ‘billabong’ form (Fig. 1.67B), a phenotype thought to be a functional adaptation to aestivation while buried in the creek bed through the dry season (Humphrey & Simpson 1985). In fast-flowing water the shells of *A. jacksoni* have a pronounced dorsal arch, whereas shells from lesser currents have a dorsal margin extended backwards as a ‘wing’ (Fig. 1.67C, D). These features are associated with larger foot musculature and enhanced burrowing ability, providing stronger anchorage in fast currents (Walker, K.F. 1981b; Balla 1984; Balla & Walker 1991). Similar variation in shell form occurs in *Velesunio angasi* in billabongs and flowing waters of the Northern Territory (Fig. 1.67E, F; Humphrey & Simpson 1985).

The habitat preferences of *A. jacksoni* and *V. ambiguus* are least obvious in those parts of the Murray influenced by dams and weirs. Below the Darling confluence, weirs have supplanted a large part of the river with impoundments that are more favourable to *V. ambiguus* than to its riverine counterpart. Comparisons between present mussel populations and those represented in aboriginal shell middens suggest that flow regulation has encouraged *V. ambiguus* at the expense of *A. jacksoni* (Walker, K.F. 1981b). Now *V. ambiguus* is common in the weir pools and along the sheltered river margins, whereas *A. jacksoni* occurs in deeper, more strongly flowing water.

The former exploitation by aboriginal Australians of mussels for food and implements is indicated by the prominence of mussel shells in archaeological investigations. The earliest confirmed evidence of human occupation in Australia includes shells associated with bones and other debris from Lake Mungo, New South Wales (Bowler, J.M., Jones, Allen & Thorne 1970). Hale & Tindale (1929), Simpson & Blackwood (1973), Feary (1981), Balme (1983) and Clarke, P.J. & Hope (1985) published related studies.

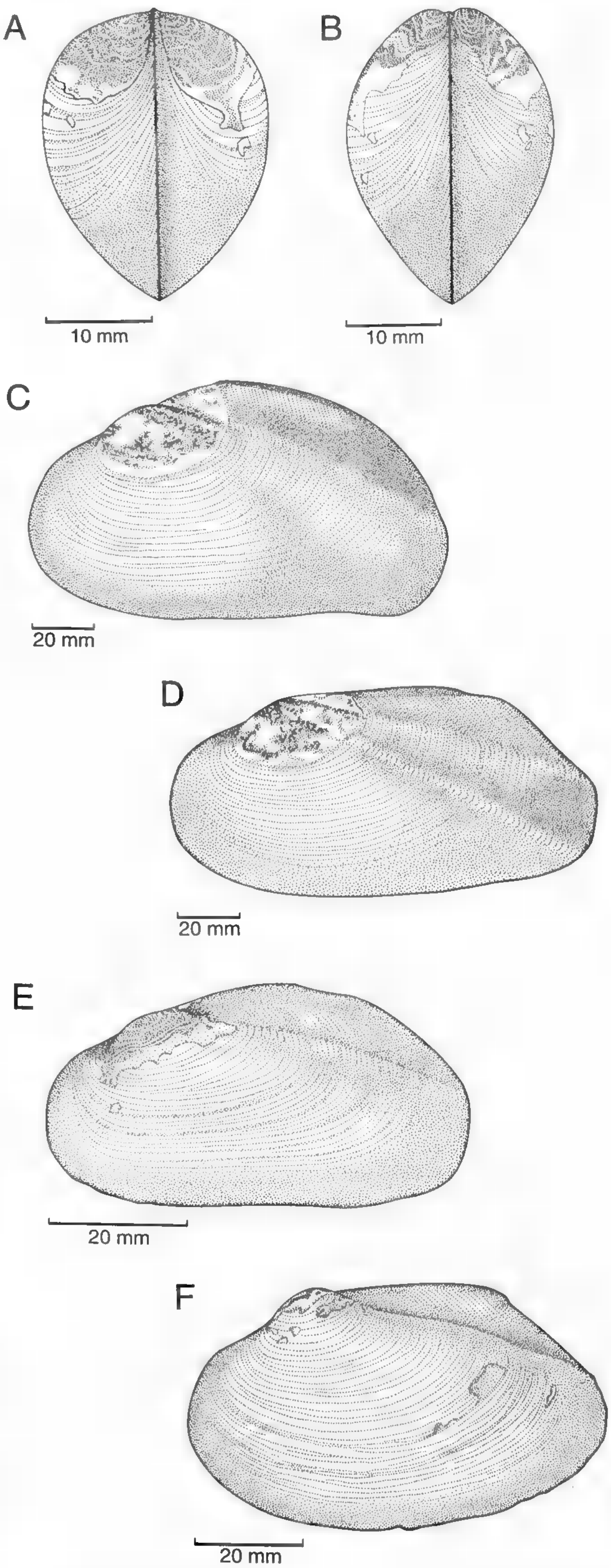


Figure 1.67 Variation in the shell of two Australian hyriid species. **A, B**, anterior views; **C–F**, lateral views. **A**, the swollen, creek form of *Velesunio angasi*, Magela Creek, Northern Territory. **B**, the normal form of *Velesunio angasi*, Magela Creek, Northern Territory. **C**, the arched form of *Alathyria jacksoni* from the River Murray, South Australia. **D**, the ‘winged’, straight-hinged form of *Alathyria jacksoni* from the River Murray, South Australia. **E**, the arched form of *Velesunio angasi*, Mudginberri Billabong, Magela Creek, Northern Territory. **F**, the ‘winged’, straight-hinged or ‘billabong’ form of *Velesunio angasi*, Island Billabong, Magela Creek, Northern Territory. (C, D, after Walker, K.F. 1981a) [C. Eadie]

There is no evidence that increased salinities in the Murray Valley have affected freshwater mussels (Vickery 1978; Walker, K.F. 1981b), except in evaporation basins used to store irrigation return water (Caldwell Connell Engineers 1981). In south-western Western Australia, however, salinisation associated with land-clearing is implicated in the disappearance of the mussel *Westralunio carteri* from the Avon River (Kendrick 1976).

Humphrey & Simpson (1985) made a comprehensive study of *Velesunio angasi* in Magela Creek in the Northern Territory, where there are three distinct shell forms in billabong and stream habitats (Fig. 1.67A, E, F). Their observations of the reproductive cycle and population dynamics of *V. angasi* are the most complete data available for any Australian species. The distribution, abundance and growth of this species in a range of habitats along Magela Creek, are correlated primarily with oxygen concentration (Fig. 1.68A, B), and secondarily with mean food availability as measured by the concentration of surface chlorophyll *a* (Fig. 1.68C; Humphrey & Simpson 1985).

Other valuable studies are those of Jones, H.A. *et al.* (1986), concerning *Cucumerunio novaehollandiae*, three *Hyridella* species and *Alathyria profuga* in the Macleay River, northern New South Wales, and Wirtado (1994), concerning *V. ambiguus* in the Ross River, northern Queensland. Roper, D.S. & Hickey (1994) provided comparable data for *Hyridella menziesi* in the Waikato River system, New Zealand.

Freshwater mussels invariably are hosts to parasitic mites (Unionicolidae) that may cause considerable damage to gill tissues (Gavey 1979; Viets 1980). Trematode parasites also are common in the reproductive organs of mussels, and may cause sterility (Angel 1961; Walker, K.F. unpublished data).

Mussels could be considered unlikely targets for special conservation measures, but at least one species warrants protection. *Hyridella glenelgensis* occurs in localised, very sparse populations in the Glenelg River system of south-western Victoria. Live specimens have not been reported since 1991 (Walker, K.F. unpublished data), and the species appears to be threatened by water diversions and salinisation (K. Heffernan, Casterton, Victoria, personal communication).

Corbiculidae. Nominally four species represent the Corbiculidae in Australia. *Batissa violacea* and *Polymesoda coaxans* are found in northern Australia but with extralimital distributions and/or close relatives in South-East Asia, *Corbicula australis* is widespread and *C. ovalina* is found in northern coastal rivers. The taxonomy of the group is uncertain and there are many dubious synonyms (Smith, B.J. 1992). Species of *Batissa* and *Polymesoda* live in estuaries, but also extend well into the freshwater reaches of coastal rivers. *Corbicula ovalina* also is a coastal species, but one found primarily in fresh water.

Corbicula australis is a small form (< 27mm) found in sandy, shallow streams throughout Australia, apart from south-western Western Australia and Tasmania. It might be mistaken for a juvenile hyriid mussel, but the shell is distinguished by well-marked concentric ridges – hence termed the 'little basket shell'. There is scant biological information on the species (see Tham 1971; Woolford 1984), although the females are known to brood the young to the pediveliger stage in the gills (Fig. 1.69A; M. Byrne personal communication); inferences might also be drawn from the extensive literature on the related *Corbicula fluminea*, an Asian species that is a pest of waterways in the United States (see Stites, Benke & Gillespie 1995). The Australian species is also a pest in irrigation pipelines associated with the River Murray (Fig. 1.69B; Woolford 1984). Brooding of the young may predispose this species for life in pipeline habitats where there is little shelter for free-swimming larvae. It is susceptible to treatment with chlorine and copper sulphate, but these are costly measures and may be unsafe where the water is used for stock or human consumption, as well as toxic to other molluscs and invertebrates. This species, and other Australian corbiculids, are prime targets for ecological studies.

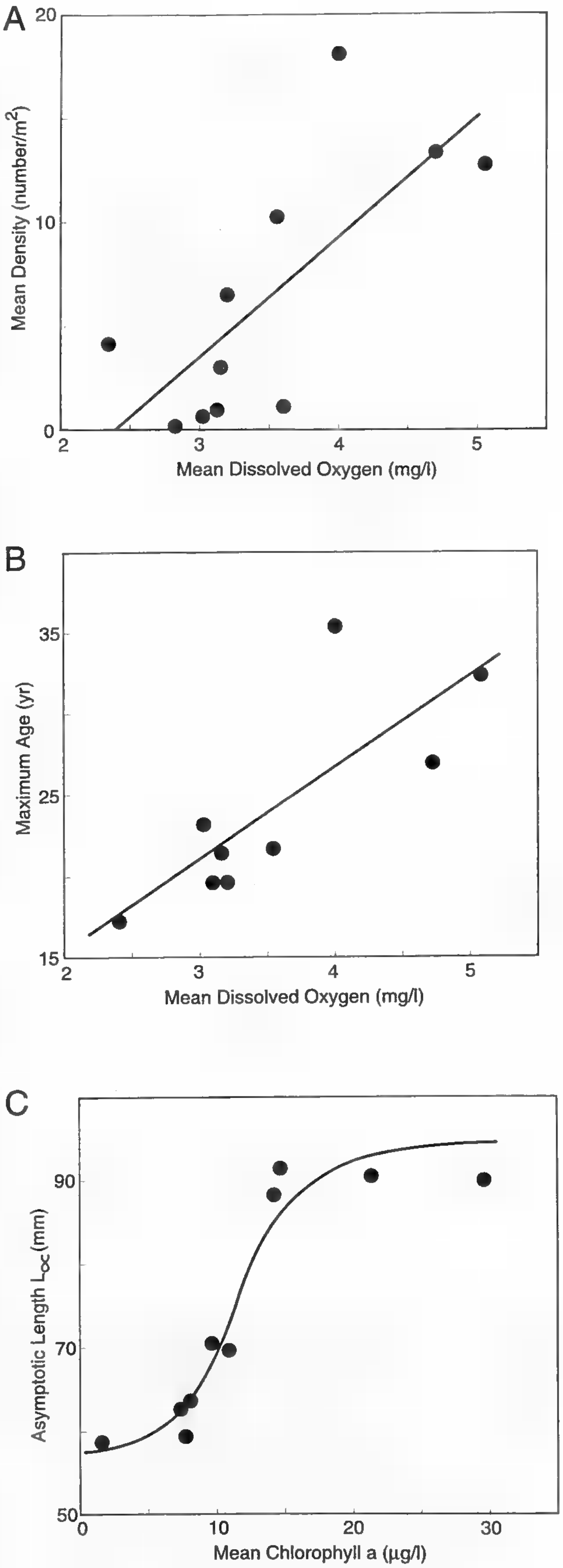


Figure 1.68 The distribution, abundance and growth of the hyriid mussel, *Velesunio angasi*, are correlated primarily with oxygen concentration, and, secondarily, with food availability as indicated by the concentration of surface chlorophyll *a*; both vary widely in billabongs along the Magela Creek, Northern Territory. **A**, the density of mussels is greater in more highly oxygenated water. **B**, mussels live longer in more highly oxygenated billabongs. **C**, mussel growth is correlated with surface chlorophyll *a* levels less than 15 μg/L. (After Humphrey & Simpson 1985)

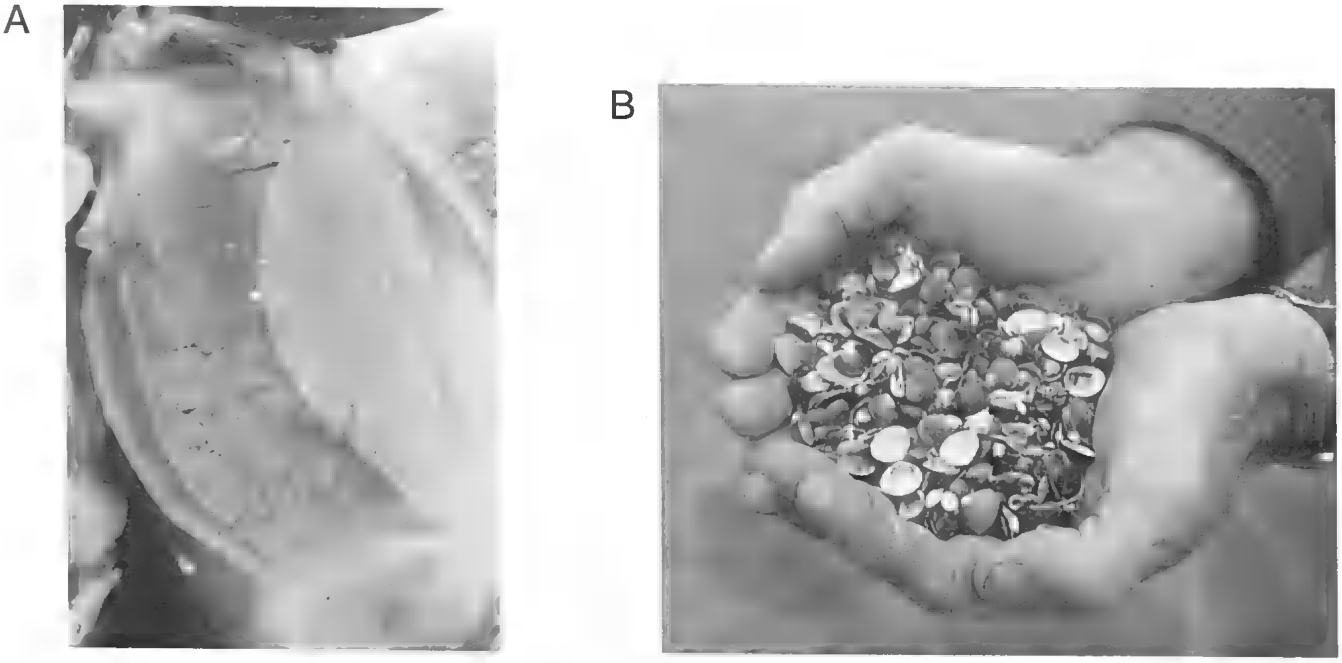


Figure 1.69 *Corbicula australis* (Corbiculidae). **A**, a gill cut to show a brood of pediveligers (*ca* 250 µm in diameter). **B**, shells taken from a basket filter in pipes near Mildura, north-western Victoria, in the mid-1970s. [A, M. Byrne; B, courtesy of Department of Natural Resources and Environment, Victoria]

Sphaeriidae. Five species of *Sphaerium* and seven species of *Pisidium* (Kuiper 1983) represent the cosmopolitan family Sphaeriidae in Australia. Known as 'pea shells', all have small (< 10 mm), fragile shells, and are common on soft sediments in virtually all kinds of permanent freshwater habitats. They are easily dispersed (for example, in mud carried by water birds), which partly accounts for their wide distribution. Apart from the cosmopolitan *Pisidium casertanum*, all Australian species are endemic. *Pisidium aslini* is notable for being endemic to the Glenelg River system in south-western Victoria (Smith, B.J. 1992). Kuiper's (1983) review, although based entirely on shell morphology, is a basis for ecological studies, but very little is known of the Australian species. Extrapolating from work elsewhere (for example, Heard 1977), they are likely to show a variety of life history patterns.

Gastropoda

Gastropods are a large and very important component of freshwater and saline lake communities throughout Australia. Like bivalves, they have a remarkable capacity to adapt to particular environmental conditions. The larger caenogastropods and pulmonates in particular tend to be widely distributed, morphologically variable species. This has caused much taxonomic confusion, and revisions are overdue for several major families. It is difficult to trace ecological and biological information through the literature, and an effective synthesis must await further progress in taxonomy and systematics. Most of the available information is for members of the Lymnaeidae, implicated in transmission of sheep liver fluke (see below).

Ten gastropod families are prominent in Australian inland waters, aside from the essentially marine or estuarine families – Assimineidae, Hydrococcidae, Iravadiidae, Neritidae and Stenothyridae – which may occur in brackish water (see McMichael 1967; Ponder 1984; Smith, B.J. 1992). The main families are the Bithyniidae, Hydrobiidae, Pomatiopsidae, Thiaridae and Viviparidae among the Caenogastropoda, and the pulmonates Ancylidae, Planorbidae, Lymnaeidae, Physidae and Glacidorbidae.

Although the genera *Coxiella* (Pomatiopsidae), *Austropeplea* (Lymnaeidae) and *Larina* (Viviparidae) appear to be zoogeographically distinctive, most of the Australian families have near-relatives in the South-East Asian or Indo-Pacific regions (McMichael 1967). There is evidence of Gondwanan origins, however, in the presence of *Glacidorbis* in southern Australia and South America (Meier-Brook & Smith 1975; Bunn & Stoddart 1983; Boulton & Smith 1985).

The gastropod fauna of the River Murray in South Australia has declined dramatically in diversity and abundance in recent decades. Of some 18 species represented in shell middens, museum collections and published records (Smith, B.J. 1978; Sheldon & Walker 1993a), only one native species, the freshwater limpet *Ferrissia* (Ancylidae), remains abundant in the river (Botting 1995; see below). The introduced *Physa acuta* (Physidae) also is sporadically abundant.

There are probably three reasons for this decline. The first factor is predation and habitat destruction by common carp (*Cyprinus carpio*), which became widespread in the Murray-Darling system after an invasion by imported wild-strain fish in the late 1960s (Brumley 1991). Carp have degraded wetlands along the lower Murray by their habit of sifting sediments and undermining water plants, and they prey directly upon snails and other invertebrates (Fletcher, A., Morison & Hume 1985). The second factor is alienation of river and wetlands through constraints on flooding caused by intensive flow regulation (for example, Walker, K.F. & Thoms 1993). A third factor is speculative, and presumes a change in the biofilms of algae, bacteria and fungi that provide food for snails. Sheldon (1994) speculated that a shift in the relative abundance of algae, at the expense of bacteria, has reduced the nutritional value of the biofilms to a point below that necessary to maintain the growth and reproduction of the native snails. A comparable shift has been reported in other regulated rivers.

A surprising aspect of the decline of the lower Murray snails is that several species have invaded irrigation pipelines to become pests by causing blockages (Woolford 1984; Sheldon & Walker 1993a; Wishart 1994). The presence of snails in these pipelines argues against roles for salinity or any water-borne pollutants in the decline, as the pipelines are fed directly from the river. Further, salinities prevailing in the river are somewhat below the tolerance limits of several snail species (Evans, D.L. 1981). Within the pipes, the snails have access to a bacterial biofilm that is nutritionally superior to that now found in the river (Sheldon & Walker 1993a; Walker 1996).

Figure 1.70 Large numbers of *Fonscochlea aquatica*, occur in Blanche Cup, South Australia, and other nearby artesian mound springs. This limited distribution is typical of many hydrobiid species in such habitats. [K. Lowe]

With one exception, the snails that have disappeared from the lower Murray are represented elsewhere in the Murray-Darling system, although their conservation status is not well known. The exception, the viviparid *Notopala hanleyi*, is believed to be extinct in the natural environment, but remains abundant in three irrigation pipelines in the South Australian Riverland, where it has the paradoxical status of both pest and an endangered species (Sheldon & Walker 1993a). Strenuous efforts are being made by the pipeline authority to remove the snails by chlorination (Wishart 1994).

It is in the nature of the River Murray that, with successive seasons of strong flows, snails are likely to reappear sporadically (*cf.* Walker, K.F. & Thoms 1993), or to persist in isolated wetland refuges. The fact of the decline, however, is well established, and the virtual elimination of an entire trophic group should be a matter for concern. In fact it may be difficult to raise community concern, as invertebrates rarely are accorded the importance given to other animals in conservation issues (for example, New 1995). Similar declines in other molluscan populations may be happening in other rivers, but too little information on their status is available.

Ancylidae. The ancylids are small (< 5 mm), limpet-shaped shells that, given their cryptic habit of clinging to stones, wood or vegetation, are easily overlooked. They are distributed throughout Australia, usually in flowing water but occasionally in stagnant pools. The group was revised by Hubendick (1967), who worked almost exclusively with shell material and based his assignments on 'form groups' rather than species. Two such groups are recognised for the genus *Ferrissia* (*F. petterdi*, *F. tasmanica*), both widespread in Australia. The form of the shell in *Ferrissia* is affected by environmental factors – in some species, for example, the shell may develop a distinct septum, evidently in response to drought conditions (Richardot 1977). A third, distinctive taxon is *Stimulator consetti*, known only from the Harding Ranges on the north-west coast of Western Australia (Iredale 1944a; Smith, B.J. 1992).

The only biological study of ancylids in Australia appears to be that of Botting (1995), who questioned why *Ferrissia* species, alone among native taxa, should remain common in the lower River Murray (see above). She concluded that by virtue of their small size and radula morphology, *Ferrissia* species may feed upon minute particles associated with biofilms that are not accessible to other larger snails. When working with limpets from the Murray at Blanchetown, South Australia, Botting was unable to distinguish the 'form groups' *F. tasmanica* and *F. petterdi* reliably, and preferred to regard them as *Ferrissia sensu lato*. She reported also that in the lower Murray *Ferrissia* appears to be commonly associated with ribbonweed, *Vallisneria spiralis*.

Bithyniidae. The Bithyniidae are a worldwide family represented by several unnamed species in tropical Australia (W.F. Ponder personal communication) and by *Gabbia australis*, a small (8–12 mm) inhabitant of seasonal streams and billabongs in eastern parts of the continent. *Gabbia australis* favours weedy, lentic habitats (Smith, B.J. & Kershaw 1979). It has a considerable ability to resist desiccation, as McKay (1926) found that 25% of a laboratory population survived more than 200 days out of water.

Glacidorbidae. Snails in the distinctive, planispiral genus *Glacidorbis* are operculate, notwithstanding their placement among the Pulmonata. The genus was formerly included with the Hydrobiidae, but was assigned to its own family by Ponder (1986a). *Glacidorbis* occurs in mountain lakes and acidic alpine bogs in south-eastern mainland Australia and Tasmania (Meier-Brook & Smith 1975; Smith, B.J. 1979b; Fulton 1983), in intermittent streams in southern Victoria (Boulton & Smith 1985), and in permanent and intermittent streams in south-western Western Australia (Bunn, Davies & Edward 1983; Bunn & Stoddart 1983). The family is known from southern Chile (Meier-Brook & Smith 1975) and as Miocene fossils from central Australia (Bunn & Stoddart 1983), and so has special zoogeographic significance.

Hydrobiidae. The Hydrobiidae, like ancylids, are widely distributed. The family comprises at least twelve Australian genera (*Ascorhis*, *Beddomeia*, *Fluvidona*, *Fluviopupa*, *Fonscochlea*, *Hemistomia*, *Jardinella*, *Phrantela*, *Posticobia*, *Potamopyrgus*, *Tatea*, *Trochidrobia*), and is especially well-represented in Tasmania. Hydrobiids usually have small (< 10 mm), dark-coloured shells and are found in estuaries and a wide variety of freshwater environments. Two main groups of genera are recognised: the *Beddomeia* and *Fluvidona* groups (Ponder 1992a). The former occurs in Tasmania and eastern Victoria (Ponder, Clark, Miller & Toluzzi 1993), and the latter is widespread in south-eastern Australia, Tasmania, Queensland, Western Australia and elsewhere in the South Pacific region (Smith, B.J. 1992; Ponder 1992a). The taxonomy of the family has been extensively revised in recent years following anatomical investigations and applications of allozyme electrophoresis (for example, Ponder, Colgan, Clark, Miller & Terzis 1994; Ponder, Colgan, Terzis, Clark & Miller 1996).

Figure 1.71 An adult *Austropeplea tomentosa* (Lymnaeidae) (shell length 14 mm), the only endemic intermediate host of the liver fluke *Fasciola hepatica*, showing the broad, ear-like cephalic tentacles characteristic of lymnaeids. [J. Boray]

Figure 1.72 *Glyptophysa concinna*, a planorbid with a helical shell, from south-eastern Australia. [J. Walker]

Hydrobiid species are an important element of aquatic communities associated with mound springs in the Great Artesian Basin (for example, Ponder 1986b; Ponder, Hershler & Jenkins 1989; Ponder & Clark 1990; Ponder, Eggler & Colgan 1995). In South Australia, springs in the Lake Eyre Basin are home to groups of hydrobiids that have radiated into a number of species (*Fonscochlea* (Fig. 1.70), six species; *Trochidrobia*, four species). Dalhousie Springs, and another group of springs nearby, support their own endemic hydrobiids (Ponder 1989; Ponder *et al.* 1996); associated snails include widespread species of *Austropeplea*, *Thiara* and *Isidorella*. A similar radiation of *Jardinella* is reported for springs in Queensland (13 species; Ponder & Clark 1990). As these springs are threatened by depletion of aquifers and excessive stock use, their snail assemblages too are under threat (Ponder 1986b, 1995a).

Potamopyrgus antipodarum is a small (3–5 mm) hydrobiid introduced to Australia from New Zealand early last century (Winterbourn 1970; Ponder 1988). It is especially common in freshwater streams and occasionally brackish waters of south-eastern Australia, where it may be responsible for the decline of native hydrobiid populations. In Victoria, Kefford (1994) compared the grazing roles of *P. antipodarum* with native species in regard to variable stream flows. Generally, *P. antipodarum* favours disturbed habitats, and has been called a molluscan 'weed'. The morphology of the species is highly variable; the features of Australian and New Zealand populations were compared by C. Wallace (1978). He found that males are rare (< 5%) in most populations, indicating that the species is mainly parthenogenetic.

Lymnaeidae. The Australian species of the worldwide family Lymnaeidae generally have been referred to the genus *Lymnaea*, but there is immunotaxonomic and cytotaxonomic evidence to support their referral to a distinct genus *Austropeplea* (Inaba 1969; Blair & Finlayson 1981; Smith, B.J. 1992). Exotic lymnaeids are represented, however, by *Lymnaea stagnalis* and *Pseudosuccinea columella*, both introduced as aquarium snails and now patchily distributed in south-eastern Australia and Western Australia (Smith, B.J. 1992), and *Austropeplea viridis* (see Molluscs and Parasitic Diseases of Animals, this Chapter).

The literature on the Lymnaeidae is comparatively large, owing to the importance of some species as intermediate hosts of the sheep liver fluke, *Fasciola hepatica*. The introduced *Pseudosuccinea columella*, for example, is a potent fluke vector (Ponder 1975).

The native species *Austropeplea tomentosa* is another important vector (Fig. 1.71; Boray & McMichael 1961; Boray 1964, 1966, also Economic Significance, this Chapter) and occurs in streams, ditches and ponds throughout south-eastern Australia, including Tasmania. It has been common in riparian swamplands of the lower reaches of the River Murray in South Australia (Lynch 1965, 1966), but is not common in the main river channel.

The species varies morphologically under different environmental conditions (Boray & McMichael 1961). It is capable of aestivation over several months, and is able to endure dry summers in semi-arid environments. Aestivation is preceded by burrowing, which is stimulated by an initial loss of at least 10% of body weight (Lynch 1965). Burrowing is essential, as active snails will die in a matter of hours if removed directly from the water.

Austropeplea lessoni, a larger relative of *A. tomentosa* (15–20 mm versus 5–15 mm), is found in similar habitats but has a patchy distribution that excludes Tasmania. It is not a vector of liver fluke, but is an intermediate host for avian schistosomes in northern Queensland (Blair & Finlayson 1981; Hurley, Hearnden, Blair & Kay 1994). The schistosomes are responsible also for a form of dermatitis (swimmers itch) in humans. An unusual, undescribed lymnaeid species occurs in the Franklin River, south-western Tasmania (W.F. Ponder personal communication).

Neritidae. A few species of this predominantly coastal family occur in the fresh and brackish streams and rivers of northern Australia (Smith, B.J. 1992). Little is known of the status or biology of these herbivorous snails in Australia.

Physidae. One introduced species, *Physa acuta*, represents this Northern Hemisphere family in Australia (Smith, B.J. & Plant 1981; Smith, B.J. 1992). It is an air-breather, retaining a small bubble of air in the mantle cavity, and so needs ready access to the water surface. It is abundant in disturbed areas throughout south-eastern Australia and occurs in shallow ponds and along the edges of lakes and rivers. As noted earlier, it is occasionally abundant in the main channel of the River Murray in South Australia.

Planorbidae. Members of this cosmopolitan family form the dominant group of gastropods in Australian inland waters. The shells may be grouped on the basis of shell shape (after Smith, B.J. 1992) – planispiral (*Gyraulus*, *Planorbarius*, *Helicorbis*), helical (*Amerianna*, *Bayardella*, *Glyptophysa* (Fig. 1.72),

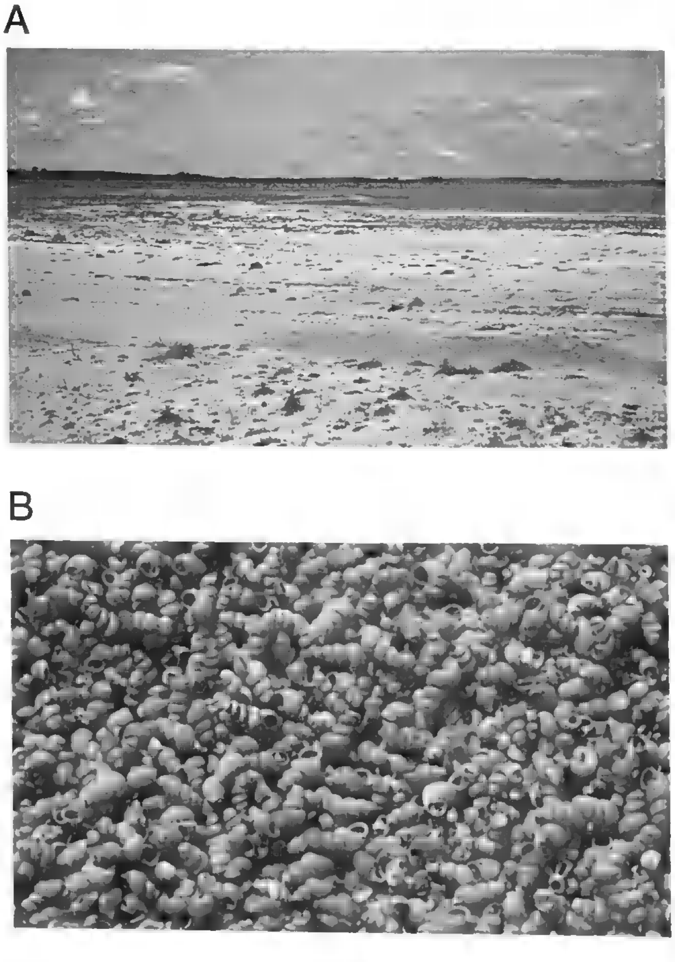


Figure 1.73 *Coxiella striata* (Pomatiopsidae) inhabits hypersaline waters, sometimes in huge numbers. **A**, accumulated shells from such populations forming low 'dunes' at Lake Corangamite, Victoria. **B**, detail of dune composition. [B. Smith]

Figure 1.74 *Melanoides aspirans*, a thiarid from the upper reaches of the Mowbray River, far North Queensland. Like many freshwater taxa, this species' biology is unknown. [B. Collins]

Isidorella, *Leichhardtia*, *Pygmanisus*) or patelliform (*Ancylastrum*). *Bayardella johni* from north-western Western Australia has a disproportionately large body whorl that could be an adaptation to life in turbulent water (Burch 1977).

The variety of planorbid shell forms has engendered a great deal of taxonomic confusion (for example, Smith, B.J. 1992), and many incorrect names are perpetuated in the ecological literature. Reviews have been completed, however, for some planate species (Brown, D.S. 1981) and the non-planate genera (Walker, J.C. 1988).

There is little biological and ecological information for the family, although its members are frequently cited in faunal surveys. Some apparently are tolerant of dry conditions (*Bayardella cosmeta*, Smith, B.J. & Burn 1976; *Isidorella newcombi*, Smith, B.J. & Kershaw 1979). *Planorbarius corneus*, found in parts of Victoria, has been introduced from Europe *via* the aquarium trade (Smith, B.J. 1969; Smith, B.J. & Kershaw 1979). Cotton (1933b) reported the occurrence of the North American *Planorbis campanulatus* in the River Murray, South Australia. This species probably arrived in association with imported materials used in building the weir (Lock 1) at Blanchetown. It has not been reported since.

Pomatiopsidae. Members of this family are found in Australia, North and South America, South Africa, India and Asia, reflecting Gondwanan origins (Davis, G.M. 1979). One genus, *Coxiella*, occurs in Australia. *Coxiella* species are unique in their occupancy of inland saline waters (Kirton 1971; Williams, W.D. & Mellor 1991), where they are able to avoid desiccation and osmotic stress by closing the operculum tightly when unfavourable conditions prevail. The shells are sometimes abundant enough to form beaches and dunes (Fig. 1.73). Although a modern revision is required, currently *Coxiella* is thought to be represented by seven species in Western Australia (one shared with South Australia) and by *C. striata* in eastern Australia including Tasmania (Smith, B.J. 1992).

Stenothyridae. Three species of *Stenothyra* are recorded from a number of coastal streams in Northern Australia and Queensland (Smith, B.J. 1992). These snails usually live in estuarine environments but some species extend into fresh water. They feed on decaying vegetation.

Thiaridae. The Thiaridae are a major family of freshwater operculate snails in Australia. They have virtually a cosmopolitan distribution (Stoddart 1985), perhaps because the species are parthenogenetic (males are rarely found), so that new founder populations are readily established (McMichael 1967). The most widespread genus is *Thiara* (*Plotiopsis*), including the large (25 mm) *T. balonnensis* from the Murray-Darling river system. Four other genera occur in coastal northern Australia, including *Melanoides* (Fig. 1.74). Despite the range and abundance of thiarids, virtually no biological or ecological studies of Australian populations have been made. In south-eastern Asia, but perhaps not Australia, they are important vectors for human diseases (Stoddart 1985).

Viviparidae. Viviparids, termed 'river snails', are cosmopolitan, with six species in Australia (Smith, B.J. 1992). As their name suggests, they are ovoviparous: the female retains the eggs until they hatch as miniature adults. Revision is needed, but currently the genus *Notopala* is thought to contain two species (*N. essingtonensis*, *N. waterhousii*) in northern Australia, and two others in the Murray-Darling Basin (*N. hanleyi*, *N. sublineata*), with an extension to the Lake Eyre drainage (*N. sublineata*). *Centrapala* is represented by a single species, *C. lirata*, found in the Lake Eyre Basin. The northern Queensland species *Larina strangei* is a somewhat aberrant member of this family (*cf.* McMichael 1967; Smith, B.J. 1992).

All are large (20–25 mm), globose forms found on mud bottoms in lowland rivers and lakes (Cotton 1935b, 1935c). Stoddart (1982) described the physiological and morphological features of species from Western Australia in relation to survival in permanent and seasonally dry habitats. Sheldon & Walker (1993b) examined the value of shell morphology for separating species of *Notopala*. They drew attention to the apparent extinction of *N. hanleyi* and *N. sublineata* in the Murray-Darling Basin, although the former persists in irrigation pipelines in South Australia (see above), and the latter still occurs in the Lake Eyre Basin.

Conclusion. The underlying need for taxonomic revisions has been emphasised repeatedly in the foregoing discussion, but despite the fragmentary supporting data many other interesting problems await biologists. What are the impacts of introduced snails on native snails and communities (for example, *Lymnaea*, *Physa*, *Potamopyrgus*, *Pseudosuccinea* and perhaps *Planorbarius*) and what are the mechanisms for the apparent decline of snails in the lower River Murray and perhaps other river systems? What ecological and physiological adaptations enable some gastropod and bivalve species to survive months and even years out of water, whereas others are intolerant of desiccation?

Finally, the precarious status of snails like *Notopala hanleyi* and other species in the lower River Murray, the hydrobiids of the mound springs, and the status of bivalve species like *Hyridella glenelgensis* indicate that the conservation status of Australian freshwater molluscs warrants much more attention than it has been given until now (see also Conservation this Chapter). Indeed, the paucity of information about distribution and abundance may conceal threats to many species.

ECONOMIC SIGNIFICANCE

Molluscs and Parasitic Diseases

Molluscs may cause appreciable economic loss in Australia by serving as obligatory intermediate hosts of many helminth parasites, and of digenic trematodes in particular. Infection with these parasites seriously affects the livestock industry and may also be responsible for diseases in humans. Substantial direct economic loss can also be attributed to molluscs in the horticultural and crop industries of Australia.

A molluscan intermediate host is essential for the development of many parasites which may cause serious diseases in animals and people. Liver flukes (*Fasciola* species) cause losses to the livestock industry estimated at some US$2000 million worldwide as a result of fasciolosis (Boray 1985). Serious losses also occur due to paramphistomosis caused by stomach flukes (paramphistomes) in ruminants, particularly in subtropical and tropical regions. These ruminants, particularly in subtropical and tropical regions. These two major snail-transmitted diseases are endemic in Australia and are responsible for an estimated loss of A$150 million annually to the sheep and cattle industries. Infection with other trematodes and several species of tapeworms and nematodes transmitted by molluscan hosts may be less important for the livestock industry but they also require expensive treatment and control measures.

Schistosomes (blood flukes), transmitted via freshwater planorbid snails, infect 200 million people worldwide and result in poor health, death and economic hardship. In some parts of Australia the climatic conditions are suitable for the disease but fortunately the specific intermediate host snails are absent. In Australia, *Fasciola hepatica* and some less important trematode and nematode parasites occasionally affect humans.

Nine native Australian caenogastropod and pulmonate snail species from freshwater and estuarine environments serve as intermediate hosts of parasites of animals and humans. Of these, only four native species cause serious economic loss (*Austropeplea tomentosa* and three planorbid species). Amongst the introduced molluscs, two lymnaeid species, eight species of slugs and at least four terrestrial snails are also intermediate hosts for parasites.

Molluscs and Parasitic Diseases of Animals

The common liver fluke, ***Fasciola hepatica.*** A quarter of all Australian sheep and cattle graze on pastures where the digenean trematode *Fasciola hepatica* (Fasciolidae) and its most important intermediate host, the native pulmonate snail *Austropeplea tomentosa* (Fig. 1.71) are present. The areas affected are mainly in southern Queensland, New South Wales, Victoria and Tasmania. Economic loss due to fasciolosis was reviewed by Dargie (1986). Acute, subacute and chronic fasciolosis results in impairment of liver function, reduced lambing percentages and poor growth of lambs, depressed production of wool and decline in wool quality, and increased replacement of sheep. In cattle, production and quality of milk are reduced and poorer feed conversion rates have been reported. Fluke drenches alone cost Australian producers approximately A$10 million annually, and the estimated total annual losses under suitable climatic conditions could be A$100 million.

In the life cycle of *F. hepatica* (Fig. 1.75) the most essential factors in the establishment of the fluke are the presence of a suitable snail intermediate host, moisture and favourable temperatures for the larval development of the fluke within the snail. The metacercariae excyst in the small intestine of the primary host, such as a sheep or cow. The young flukes burrow through the intestine wall into the peritoneum and subsequently into the liver tissue, causing haemorrhages and fibrosis. Six weeks later they enter the bile ducts, grow to maturity and produce large numbers of eggs. The adult flukes cause anaemia by sucking blood and by excretion of metabolic products.

The only native intermediate host of *F. hepatica* is the freshwater snail, *Austropeplea tomentosa* (Fig. 1.74). It reproduces vigorously and, under optimum conditions, one snail may produce 3000 eggs per month with a generation time of about one month. The snail aestivates in dry mud for at least a year and also can survive at low temperatures in mud or under ice. The snail can migrate actively against a water current and may drift passively with a current for long distances (Boray 1969a).

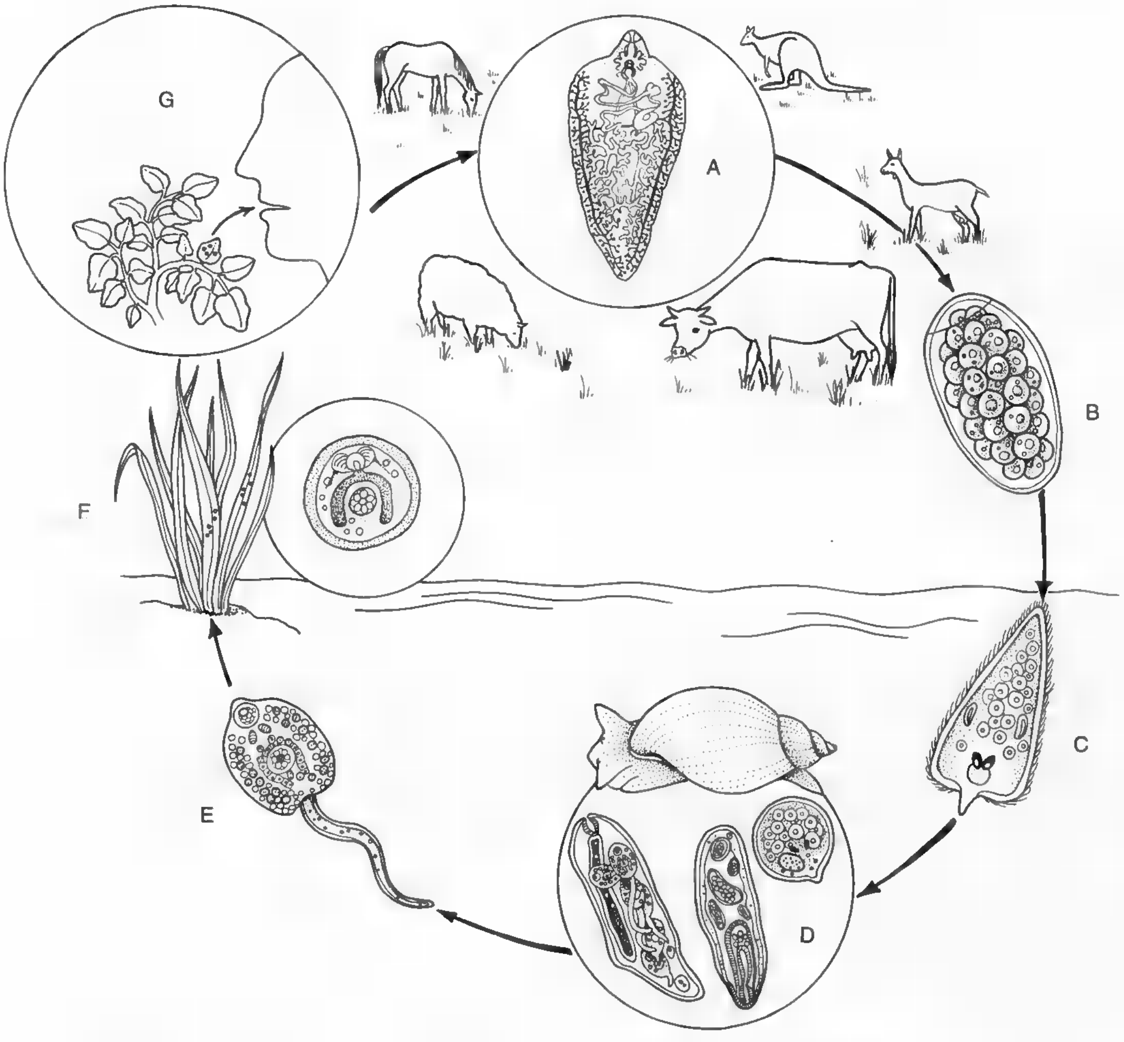


Figure 1.75 The life cycle of *Fasciola hepatica*. **A**, adult fluke occurs in the bile ducts of sheep, cattle and other mammals. **B**, eggs of the fluke pass via faeces to wet areas of pasture. **C**, miracidia hatch from eggs. **D**, miracidia penetrate snail, and other larval stages develop in the snail. **E**, cercariae leave snail and swim in water. **F**, cercariae encyst on grass, to be ingested by herbivorous animals. **G**, humans infected from contaminated watercress. [S. Weidland]

Table 1.1 Some trematodes and their hosts in Australia.

Species	Definitive hosts	First intermediate hosts	Second intermediate hosts
Echinostoma revolutum (Echinostomatidae)	Goose, duck, wild fowl, human (intestine)	Many pulmonate & operculate snails	Snails or clams
Sphaeridiotrema globulus (Psilostomatidae)	Duck (intestine)	*Gabbia australis* (Bithyniidae)	Freshwater snail
Tracheophilus sisowi (Cyclocoeliidae)	Ducks (trachea)	Planorbidae	Same snail
Opisthorchis sp. (Opisthorchidae)	Water rat (bile ducts)	Freshwater snail	Freshwater fish

In addition to this very versatile indigenous snail host, four exotic lymnaeid species have been found in Australia, often in tropical fish and aquatic plant nurseries or urban parks. They are *Austropeplea viridis*, *Lymnaea auricularia rubiginosa* (Boray 1978), *L. stagnalis* and *Pseudosuccinea columella* (Ponder 1975; Salisbury, Harkin & Smith 1976; De Chaneet 1977). Fasciolosis became more widespread following the introduction of *P. columella* into New Zealand (Pullan 1969; Pullan, Climo & Mansfield 1972; Harris & Charleston 1980), and it is evident that this species is a potent vector of liver fluke. This snail has been recorded from grazing properties in north and south coastal New South Wales (Boray, Fraser, Williams & Wilson 1985). All four species were probably introduced recently through the tropical fish trade and distributed by transportation of aquatic plants. The impact of the introduced lymnaeids on the epidemiology of fasciolosis in Australia was discussed by Boray (1978, 1982).

Until recently, Western Australia was free of both fasciolosis and lymnaeid snails susceptible to *F. hepatica*. *Pseudosuccinea columella* is now abundant in the irrigation system south of Perth and the first autochthonous infections of cattle with *F. hepatica* have been found. The eradication of the fluke by frequent anthelmintic treatments was achieved at the properties originally affected and in a nearby area. There is no hope, however, of eliminating the snails from the irrigation system (G. De Chaneet personal communication 1992) and strict and costly quarantine regulations are required to prevent the introduction of the disease from the eastern states. Exotic lymnaeid snails could spread fasciolosis to districts where *Austropeplea tomentosa* is not present, but where suitable habitats for lymnaeids are available.

Stomach flukes (Paramphistomidae). Paramphistomes are ruminant parasites found in the rumen and reticulum. The most important primary hosts of ruminal paramphistomes are sheep, goats, cattle and buffalo. Normally, adult trematodes do not cause clinical disease, but the migrating immature flukes cause acute parasitic gastroenteritis of the small intestine with high morbidity and mortality. Dramatic outbreaks may occur because of massive infection with immature flukes in young calves and sheep (Boray 1959, 1969b; Rolfe, Boray, Nicholls & Collins 1991). The annual economic loss due to paramphistomes may be in the vicinity of A$50 million.

The life cycles of paramphistomes are similar to those of *Fasciola* species. The larval development occurs in a suitable intermediate host snail of the family Planorbidae. Once shed, the larvae encyst on herbage. After consumption by the ruminant the young flukes excyst in the small intestine and migrate to the rumen and reticulum. Usually maturity is reached in about six to seven weeks but the migration is delayed in heavy infections and the immature flukes remain sustained in the small intestine for several months.

The planorbid snails, *Gyraulus scottianus*, *G. gilberti* and *Helicorbis australiensis*, serve as intermediate hosts, respectively, for *Calicophoron calicophorum*, *Orthocoelium streptocoelium* and *Paramphistomum ichikawai*, the three species of paramphistomes present in Australia. The susceptibility of the snails is highly specific, though studies show that *H. australiensis* can be infected with *C. calicophorum* in the laboratory (Rolfe 1987).

Other digenetic trematodes. Trematodes belonging to the families Echinostomatidae, Psilostomatidae, Cyclocoeliidae and Opisthorchidae in Australia were reviewed by Boray (1982); some of these are listed in Table 1.1. Many pulmonate and prosobranch snails can serve as the first intermediate host. The second intermediate host may also be a snail, possibly of the same species as the first intermediate host, or a freshwater fish or bivalve. Only heavy infections cause enteritis in the definitive hosts.

Table 1.2 Snails are intermediate hosts for some intestinal heterophyid trematodes in Australia.

Species	Definitive Hosts	First Intermediate Hosts	Second Intermediate Hosts
Heterophyes nocens	Dog, cat, human, rat	*Thiara* spp., fresh-brackish & marine snails	Several fish species
Stellantchasmus falcatus	Human, cat, dog, birds, mouse, water rat	*Thiara* spp.	Fresh/brackish water & marine fish
S. aspinosus	Water rat	*Thiara* spp.	Freshwater fish
Stictodora lari	Cat, birds	*Batillaria australis*	Marine fish
S. caballeroi	Cat, pelican	Marine snail	Marine fish
S. manilensis	Dog, cat, tern	Marine snail	Marine fish
Haplorchis sprenti	Water rat	Thiaridae	Freshwater fish
H. parataichui	Rat (experimental)	Thiaridae	Freshwater fish
H. yokogawai	Dog, water rat, birds	Thiaridae	Freshwater fish
H. pumilio	Dog, human, water rat, birds	Thiaridae	Freshwater fish
H. vanissimus	Human, birds	Thiaridae	Freshwater fish
Procerovum varium	Water rat, birds	Thiaridae	Freshwater fish
P. batillans	Water rat	*Melanoides* sp.	Freshwater fish

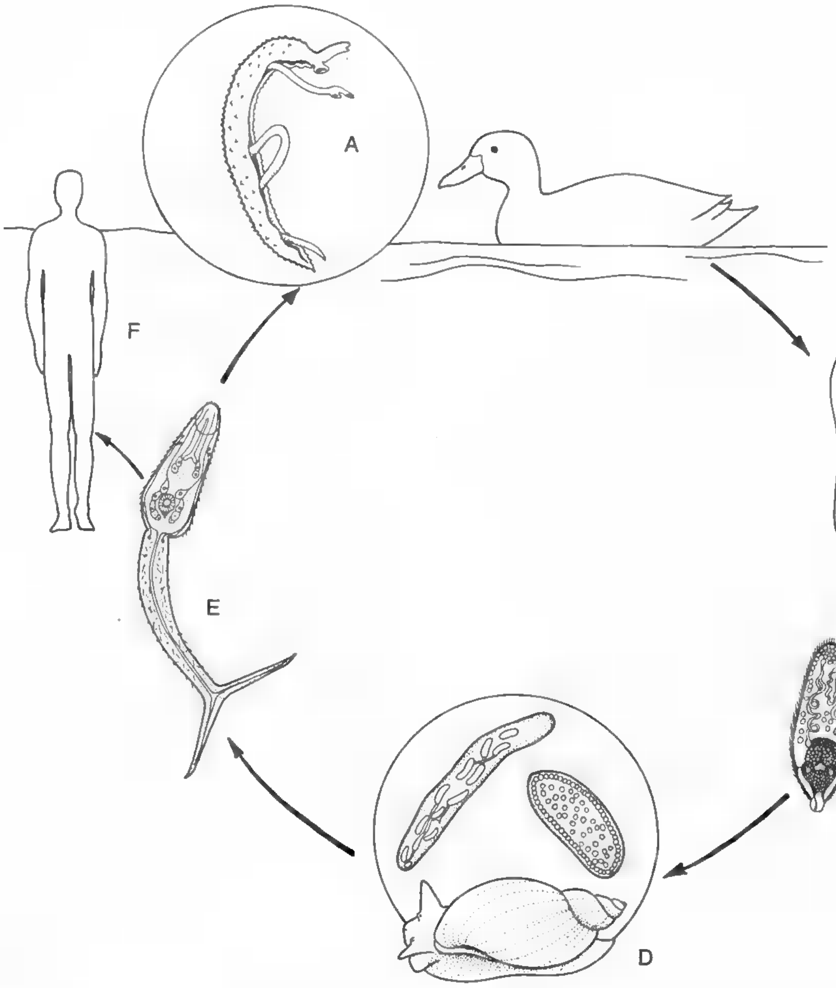


Figure 1.76 The life cycle of schistosome species causing dermatosis in humans. **A**, the adult fluke, parasitic in duck and other water birds. **B**, the eggs of the fluke pass into the water in the host's faeces. **C**, miracidia hatch from eggs and penetrate snails. **D**, sporocysts and cercariae develop in snails. **E**, cercariae emerge from snails and swim in the water. **F**, cercariae penetrate the skin of humans, but develop no further – those penetrating the skin of birds develop to maturity in blood vessels.
[S. Weidland]

Some species of the family Heterophyidae, all parasites of the intestinal tract of mammals and birds, are present in Australia (Pearson 1960, 1964). The first of the two intermediate hosts is usually a freshwater snail of the family Thiaridae, and the second is a freshwater fish. Two species are transmitted by marine snails and fish (Table 1.2). The infection occurs through ingestion of raw fish.

Cestoidea (Davaineidae). Modern husbandry methods have almost eliminated *Davainea proglottina*, one of the common tapeworms causing serious infections in poultry, though 'free range' chicken rearing may increase the occurrence of infection. The larvae develop in introduced slugs (species of *Arion*, *Deroceras*, *Limax*, *Milax* and *Lehmannia*). The same slugs also serve as intermediate hosts for the tapeworm *Aporina delafondi* in pigeons.

Nematoda: Phasmidia (Metastrongylidae). Lungworm infections caused by metastrongylid nematodes in sheep and goats can be a serious problem in European countries. *Muellerius capillaris*, a species present in Australia, causes nodular lesions in the lung tissue, resulting in bronchopneumonia and secondary bacterial infections (enterotoxaemia). Goats are particularly susceptible and the disease may cause economic loss in the goat industry in certain areas. About 20% of the 700 000 fibre-producing goats are affected, amounting to an annual loss of A$500 000 (production loss and chemotherapy).

Terrestrial snails (Helicidae) and slugs in the genera *Deroceras*, *Milax* and *Lehmannia* species act as intermediate hosts. The infective larvae develop in the snails and slugs; sheep are infected by accidental ingestion of the molluscs.

The lungworms, *Angiostrongylus vasorum* and *Aelurostrongylus abstrusus*, of dogs and cats, respectively, are present in Australia and may cause respiratory problems in the hosts, particularly in cats. The larvae become infective in terrestrial snails and slugs. There is no host specificity in molluscs. Another metastrongylid nematode of dogs, *Filaroides osleri*, is common in Australia, and causes haemorrhagic tracheobronchitis, a particularly serious problem sometimes observed in large kennels. Infection occurs by ingestion of infected terrestrial snails or slugs. Infections of rats and domestic animals with *Angiostrongylus cantonensis* is described below in association with human infections.

Molluscs and Human Parasitic Diseases

Parasitic diseases transmitted by molluscs are one of the most important problems affecting millions of people in the tropical regions of the third world. Particularly serious disease is caused by *Schistosoma mansoni*, *S. haematobia* and *S. japonica*. In Australia, people are either transient hosts of some of the parasites of animals (schistosome dermatosis) or only obtain infections occasionally, as a result of different eating habits or improved hygienic conditions. People may become infected with human schistosomes during visits to countries where these parasites are endemic.

Schistosome dermatosis. Freshwater and estuarine snails such as Planorbidae, Lymnaeidae, Thiaridae and Potamididae are suitable intermediate hosts for several members of the digenean trematode family Schistosomatidae. These blood flukes parasitise the nasal or mesenteric veins of birds. After development in the snail host, the emerging cercariae infect birds by intradermal penetration (Fig. 1.76). They also attack mammal hosts unsuitable for full development and cause allergic dermatitis in humans known as 'bathers itch', 'swimmers itch', 'surfers itch', 'weed itch' or 'paddy itch', and produce a vigorous allergic dermatitis on repeated infections.

Species of *Trichobilharzia* are known to occur in several duck species (Johnston, T.H. 1941; Bearup 1956; Blair & Islam 1983; Islam 1986). The larval stages and cercariae are common in *Austropeplea lessoni* and *A. tomentosa*. Cercariae have been found also in species of the freshwater snail genera *Glyptophysa* (Planorbidae) and *Thiara* (Thiaridae). Another common species causing dermatoses of humans, *Austrobilharzia terrigalensis*, has been described from the portal veins of the seagull *Larus novaehollandiae*. The intermediate host snail was found to be the common estuarine potamidid snail, *Batillaria australis* (Bearup 1956).

Fasciolosis. Human fasciolosis is a rare disease caused by *Fasciola hepatica* and produces serious pathological changes as cholangitis, fibrosis and liver cirrhosis. Few cases are reported each year in Australia. Infection occurs by ingestion of metacercariae on watercress obtained from creeks in areas supporting infected sheep, cattle and the intermediate host snail, *Austropeplea tomentosa* (Laird & Boray 1992).

Infection with the intestinal fluke *Echinostoma revolutum* may occur in humans through ingestion of inadequately cooked clams or mussels, and causes enteritis. Lymnaeid and planorbid snails act as first and second intermediate hosts, but the cercariae may also encyst in tadpoles, clams or mussels.

Angiostrongylosis. The metastrongylid lungworm of rats *Angiostrongylus cantonensis* causes eosinophilic meningitis or meningoencephalitis in humans. The lungworm occurs in China, southern Asia, Taiwan, Indonesia, Australia and some Pacific Islands, including Fiji, and is spreading via accidental introduction of infected rats. The life cycle of the parasite was described first in Australia (Mackerras & Sanders 1955). The adult worm is usually found in the pulmonary arteries of rats after an obligatory migration to the brain tissue. The first stage larvae emerge with the faeces of rats and actively penetrate snails.

Snails and slugs serve as intermediate hosts with practically no specificity. Many species of terrestrial and freshwater snails are suitable for the development of infective larvae. In Australia the common garden snail, *Helix aspersa*, some native snails and several slug genera in the introduced families Arionidae, Limacidae and Milacidae may serve as intermediate hosts. In Hawaii, the most important snail host is *Achatina fulica*, the giant African snail. There more than 80% of snails were found to be infected, harbouring 2000–3000 larvae (Wallace, G.D. & Rosen 1969). These infective larvae can be transmitted to transport hosts, such as prawns, frogs and crabs.

Consumption of raw and incompletely cooked intermediate or transport hosts leads to human infections. In South-East Asia, the large freshwater snails, *Pila ampullacea* and *P. polita* (Ampullariidae), are frequently eaten raw, and *Achatina fulica* is abundant. The parasite is present in Australia and some cases of meningoencephalitis have been reported in humans (Prociv & Tiernan 1987). The disease occurs in suburban dogs in Brisbane and Sydney (Mason, Prescott, Kelly & Waddell 1976; Collins, Rothwell, Malik, Church & Dowden 1992) and in horses (Wright, Kelly, Waddell & Hamilton 1991).

Exotic snails and potential exotic diseases. With increased international mobility of people and commercial goods, exotic molluscs may be inadvertently introduced to Australia, and may serve as additional intermediate hosts for parasitic diseases already present. Some of those molluscs may have a wider habitat and temperature tolerance than the local snail hosts, and could extend distributions of parasites. Some parasitic disease can be introduced by human migration or together with the intermediate host of the parasite, and native or previously introduced molluscs may act as intermediate hosts.

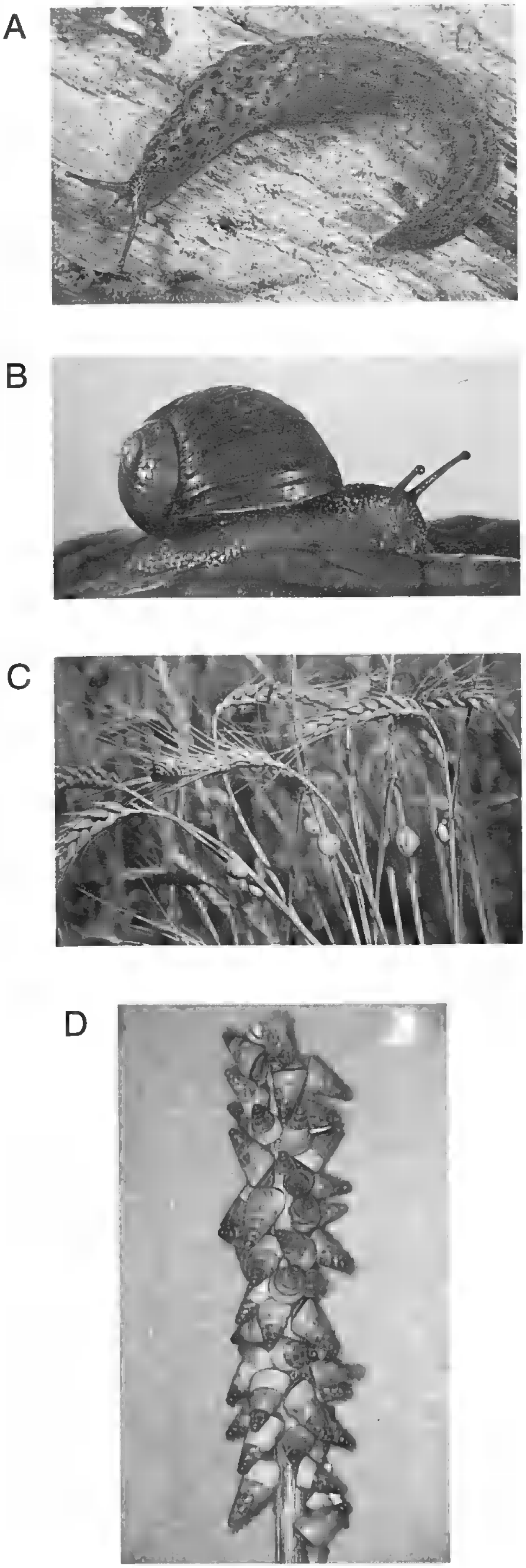


Figure 1.77 Terrestrial snails and slugs of economic significance in Australia: members of the introduced families Helicidae and Limacidae are important as intermediate hosts for parasites, or as major crop pests. **A**, *Limax maximus* (Limacidae). **B**, *Helix aperta* (Helicidae), a garden pest in south-western Western Australia. **C**, *Theba pisana* (Helicidae), an agricultural pest common in wheat crops. **D**, *Cochlicella acuta* (Helicidae), shown in aestivation on a wheat stem, is a crop pest in southern Australia (Baker 1986). [A, Queensland Museum; B, C. Bryce/Western Australian Museum; C, D, G. Baker]

Figure 1.78 Cleaning of pearl oysters, *Pinctada maxima* (Pteriidae) at Aru Island, Irian Jaya. The encrusting growth is scraped off the shells before and during the pearl culture process, usually by hand; however, machine cleaning has increased in recent years. [R. & V. Taylor/ANT]

Tropical fish and aquatic plant importation, particularly from Hong Kong and Singapore, often results in the introduction of snails, with the ever present risk of the accidental introduction of exotic flukes. The potential dangers of the introduction of trematode diseases to the Pacific region were reviewed by Boray (1982).

The introduction of the highly pathogenic Asian liver fluke *Fasciola gigantica* in the snail *Lymnaea a. rubiginosa* would have serious consequences for the sheep and cattle industry. The snail is often intercepted in consignments of tropical fish. The introduction of the Asian liver fluke (*F. gigantica*) would be particularly dangerous because the Australian indigenous *Austropeplea tomentosa* and the introduced *Pseudosuccinea columella* are fully susceptible to this fluke (Boray 1966, 1978).

In a similar way, paramphistome species which are absent from Australia may be introduced in planorbid snails; at least four native species in the genera *Helicorbis* and *Gyraulus* are potential intermediate hosts.

The intermediate host of *Schistosoma mansoni* in South America, *Biomphalaria straminea*, was introduced to Hong Kong and four of these snails have been intercepted in a consignment of tropical fish by Customs at Sydney airport. Other species found under similar circumstances are *Indoplanorbis exustus* (vector of ruminant schistosomes), *Gyraulus* species (vector of paramphistomes), *Semisulcospira* and *Physa* species (Walker, J.C. 1985; Boray unpublished data). Eggs of the flukes *Opisthorchis viverrini* and *Schistosoma mekongi* have been found in the faeces of a South-East Asian person during routine examination (Walker, J.C. & Scott 1982).

It is also possible that the highly pathogenic lung fluke, *Paragonimus westermani* and the Chinese liver fluke, *Clonorchis sinensis*, could be introduced from South-East Asia into the subtropical and tropical regions of Australia. Native thiarid species and *Gabbia australis* (Bithyniidae), respectively, may be suitable hosts for these flukes.

The dicrocoeliid cat liver fluke, *Platynosomum fastosum*, is present in Papua New Guinea, the United States of America and Malaysia. Suitable intermediate hosts, a terrestrial snail and a lizard, are present in Australia.

The giant African snail, *Achatina fulica*, may cause serious plant damage and is also an extremely successful intermediate host for *Angiostrongylus cantonensis*. The snail was introduced to North Queensland (Colman 1977), but was eradicated.

The recent introduction of the snail, *Helix aperta*, native of North Africa and Italy, for culinary purposes resulted in substantial damage to vegetable gardens in Western Australia. The Department of Agriculture, Western Australia, has made considerable efforts to eradicate the snail using methiocarb (P.R. Davis personal communication, 1987). Action by State and Commonwealth department officers successfully controlled these two species, but eradication of *H. aperta* was not achieved. Further monitoring of the areas is essential (P. Colman personal communication, 1992).

Table 1.3. The weight and value of catch for Australian mollusc fisheries, for the seasons 1988–89 through 1993–94. (After ABARE 1992, 1994)

Season	1988–89	1989–90	1990–91	1991–92	1992–93	1993–94
Catch (tonnes)						
Abalone	5464	5133	4888	5039	4659	4723
Scallops	5445	6785	9744	29802	33363	21820
Cephalopods	1742	1739	1781	2352	2464	2739
Donax	364	465	439	692	613	597
Mussels	218	338	280	124	37	40
Mariculture production (tonnes)						
Oysters	8104	6620	9267	8092	9710	2879
Mussels	700	650	600	300	140	140
Landed value (A$ million)						
Abalone	85.6	91.3	83.7	94.6	122.2	176.5
Scallops	21.3	27.0	36.9	82.8	96.0	67.0
Cephalopods	4.2	5.6	5.7	5.5	6.2	7.7
Mussels	0.3	0.6	0.5	0.3	0.1	0.1
Donax	0.5	0.4	0.5	0.7	0.7	0.7
Value of aquaculture products (A$ million)						
Oysters	40.6	34.7	43.2	44.3	47.2	49.5
Mussels	1.4	1.4	1.5	0.6	0.5	0.5
Export value (A$ million)						
Pearls		102.3	103.1	142.1	129.4	126.9
Abalone		122.2	114.8	129.6	168.4	187.4
Scallops		22.5	30.8	44.9	79.0	82.1
Oysters		0.3	0.3	0.2	0.3	0.6

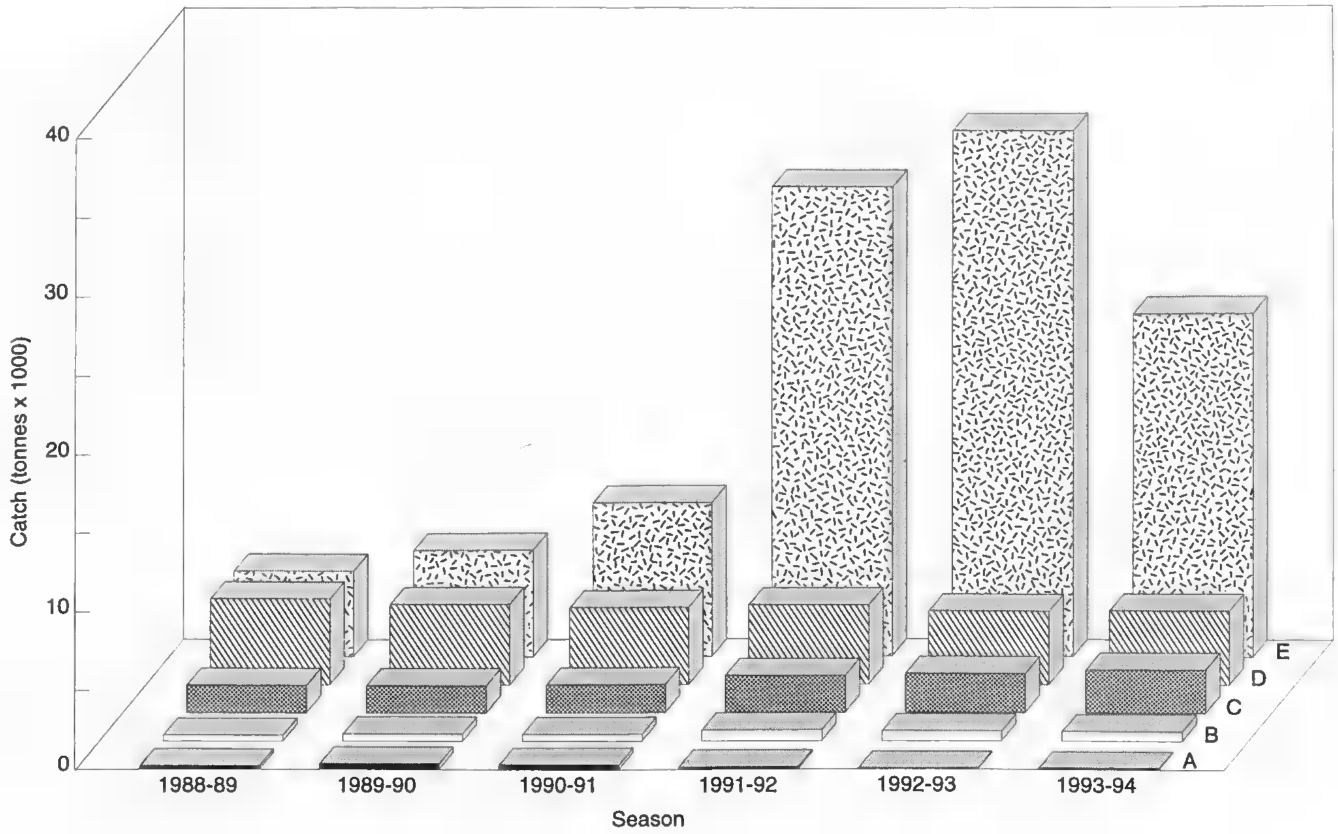


Figure 1.79 Annual harvest for the major Australian mollusc fisheries, in tonnes, 1988–89 through 1993–94. **A**, blue mussel, *Mytilus edulis planulatus* (Mytilidae). **B**, pipi, *Donax (Plebidonax) deltoides* (Donacidae). **C**, all squid, cuttlefish and octopus. **D**, abalone, *Haliotis ruber*, *Haliotis laevigata* and *Haliotis roei* (Haliotidae). **E**, all scallops, *Pecten fumatus*, *Amusium balloti* and *Amusium pleuronectes* (Pectinidae). (After ABARE 1992, 1994)

Molluscs as Plant Pests

Terrestrial snails (Helicidae) and slugs, (Arionidae, Limacidae and Milacidae) (Fig. 1.77) cause considerable damage to plants. In some areas of Australia, the snails have reached population densities requiring chemical control. High moisture and temperature favour the multiplication of snails, with increased damage to crops, but dry plantations can also suffer damage if moist shelter is available for the snails during dry periods. Snails can aestivate for many months during dry periods. Native snails are normally present only in rainforests and other non-agricultural areas and, unlike the highly fecund introduced snail and slug species, their reproduction rate is low. These snails have never been recorded as agricultural pests.

Much information is available on the role of molluscs as agricultural pests in Europe and the Americas (Godan 1983). Baker (1986) reviewed the role of introduced 'white snails' of the Family Helicidae (*Candidula*, *Cernuella*, *Cochlicella* and *Theba* species) as agricultural pests in Australia. Molluscs may cause substantial economic loss to agriculture, horticulture, the fruit growing industry, viticulture and forestry. Damage to products in cellars and agricultural warehouses has also been recorded.

Horticulture. Damage is observed most commonly in small or commercial gardens with ornamental plants, vegetables and strawberries, where frequent watering keeps the plants moist. The major pest is *Helix aspersa*, particularly in temperate to subtropical areas during the humid summer periods. Many arionid, limacid and milacid slug species may also contribute to the damage.

Agricultural crops. The introduced helicid snails *Cernuella virgata*, *Helix aspersa* and *Theba pisana* often aestivate attached to the heads and stalks of wheat and other cereals (Fig. 1.77) and can clog harvesting machinery; contamination of the grain results in its rejection by the handling authorities. Similar problems have been reported with crops of oil seeds, peas and beans. South American quarantine officials have rejected contaminated barley from South Australia because of live *C. virgata* (Baker 1986). In certain areas up to 400 snails per square metre have been recorded. Furness (1977) reported that *H. aspersa* caused serious damage to about 43% and 9% of the citrus orchards in the South Australian Riverland in 1974 and 1975, respectively, and *Cochlicella acuta* caused some minor damage. Also in South Australia, *C. barbara* was responsible for considerable damage to legume pastures (Baker 1986). This species has occasionally caused serious damage to lucerne in New South Wales. It has a wide distribution throughout south-eastern Australia and Tasmania. Similar damage may be caused by *T. pisana* and *Cernuella* species in Victoria, South Australia, Western Australia and Tasmania.

Snails feeding on legume-based pastures and seedling crops either destroy the crop completely or cause rejection of hay by stock because of contamination with snails and their slime (Baker 1986).

The architaenioglossan family, Ampullariidae, is represented by the genus *Pomacea*, of which at least one species is common as an aquarium animal. However, it is not 'officially' recognised as introduced in Australia as it is not yet known to have become established in the wild. Adult snails cause severe damage to fresh aquatic plant material, especially newly transplanted rice seedlings. Introductions of these snails have caused major problems for rice farmers and for food production in general in the Philippines and some other parts of the world (Acosta & Pullin 1991; Cowie 1993).

Snails and slugs cause considerable damage to commercial crops of berries, apples, pears, stone fruits and grape vines. An estimated A$10 million is spent annually on chemical snail control in home gardens and only A$200 000 on commercial horticultural or agricultural crops. This merely reflects the difficulties of snail control over large areas of agricultural land. The total annual cost of the damage caused by molluscs is estimated to be at least A$50 million.

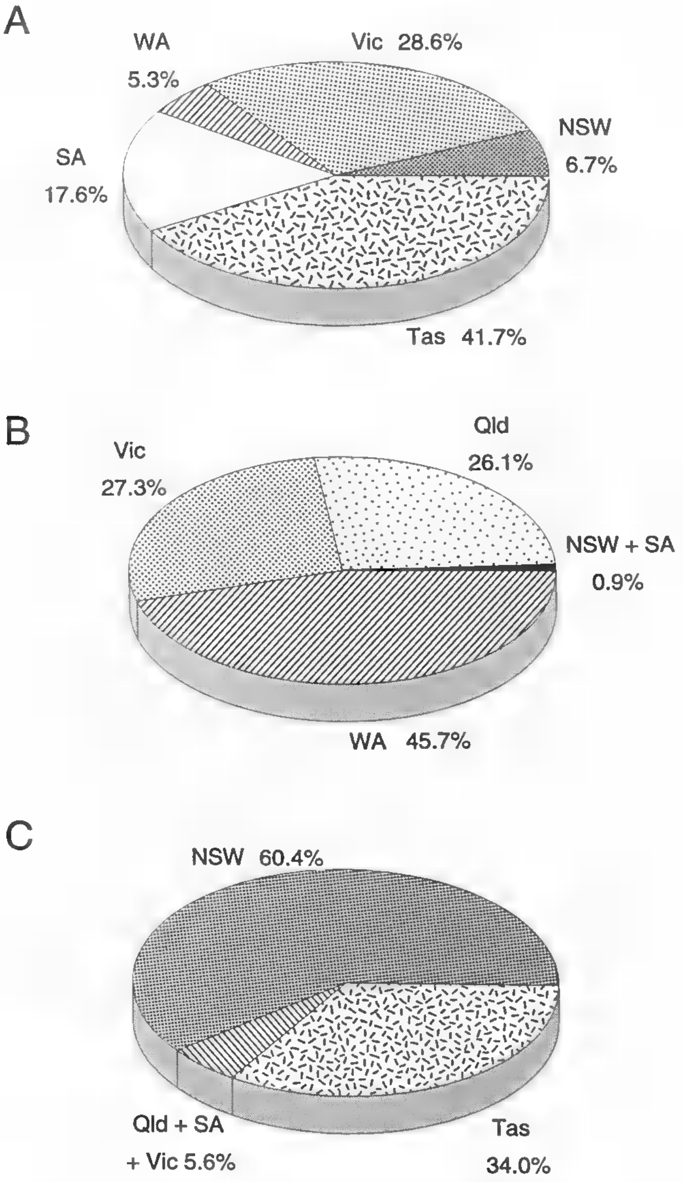


Figure 1.80 The proportion of Australian mollusc fisheries conducted in each State, averaged over six seasons from 1988–89 through 1993–94. **A**, abalone, *Haliotis* species (Haliotidae). **B**, combined scallop fisheries for *Pecten fumatus*, *Amusium balloti* and *Amusium pleuronectes* (Pectinidae). **C**, oyster production, primarily *Saccostrea commercialis* and *Crassostrea gigas* (Ostreidae). **Qld**, Queensland; **NSW**, New South Wales; **Tas**, Tasmania; **Vic**, Victoria; **WA**, Western Australia. (After ABARE 1992, 1994)

Transmission of plant diseases. Experimental evidence for the transmission of plant diseases by molluscs has been reviewed by Godan (1983). Terrestrial gastropods may transmit fungal infections of *Alternaria*, *Fusarium* and *Phytophthora* species (Fromming 1955).

Virus diseases such as 'ringspot' or 'rusty mottle' on cherries, necrotic yellowing of lettuce, and motley dwarf virus of carrots can be transmitted readily by snails and slugs. Evidence of slugs as suitable transport hosts for the Mosaic Virus of tobacco was reported by Heinze (1958).

In Europe, aquatic snails may cause substantial problems in waterworks where large populations of the prolific *Physa acuta* or of lymnaeid species cause blockage of the biofilters (Godan 1983). *Glyptophysa* and *Isidorella* species, and the introduced *Potamopyrgus antipodarum* and *P. acuta* have caused similar problems at the Sydney waterworks. Snails were removed mechanically since the danger of chemical pollution prevented the use of molluscicides. The small freshwater bivalve, *Corbicula australis* (Corbiculidae), has become a pest in inland towns of south-eastern Australia, where it blocks irrigation and domestic water systems (Smith, B.J. & Kershaw 1979).

Snail Control. Chemicals may be applied to reduce populations of molluscs. The use of biological control and repellents is still in an experimental stage (Godan 1983). Terrestrial gastropods are controlled by metaldehyde and carbamates, which are available commercially in Australia. Strategic treatments should be applied, based on the ecology of the molluscs. Eradication should be attempted if a newly introduced snail population is located.

Many molluscicides used to control freshwater snails which transmit schistosomes are useful for the control of fasciolosis and paramphistomosis in Australia. However, eradication is not possible because of the high breeding rate of snails and the extent of their habitats. Molluscicides, such as sodium pentachlorophenate, as an additional measure together with efficient chemotherapy against the parasite in the mammalian hosts may be very useful if applied regularly after a careful survey. However, there is no product registered in Australia for that purpose.

Fisheries and Mariculture

Evidence from shell middens shows that molluscan resources have been exploited ever since humans first colonised Australia (Bailey 1975). The middens in coastal areas invariably contain a wide variety of mollusc shells, mostly taken from the intertidal zone, and it is clear that they formed a significant part of the diets of early coastal dwellers. In the temperate regions, abalone, oysters and mussels were important, while in northern waters several species of giant clams, oysters and mud whelks were sought-after items.

Infaunal bivalves were commonly collected, such as *Anadara trapezia* (Arcidae) in south-eastern Australia (Simmons 1984); the abundant intertidal cardiid *Fragum unedo* in northern Australia; the mactrids, *Mactra rufescens* in Victoria; and *M. eximia*, *M. abbreviata*, *M. rufescens* and *Lutraria rhynachaena* in Queensland (Macpherson & Gabriel 1962). Some freshwater bivalves, such as the hyriid *Velesunio ambiguus*, were also used as a food source by Aboriginal people (Smith, B.J. & Kershaw 1979).

Molluscs continue to form an important dietary component and food resource of many Aboriginal communities in northern Australia; a wide range of gastropods, bivalves and some chitons are utilised (Gray & Zann 1988). Tridacnid clams may also form part of these traditional fisheries (Kailola, Williams, Stewart, Reichelt, McNee & Grieve 1993). Typically molluscs are harvested from the intertidal zone and exceed 20–30 mm in diameter; infaunal species are collected where they occur in high densities (Catterall & Poiner 1988).

Oysters were used extensively by early European settlers in Australia, not only for food but also for the manufacture of lime for mortar (Smith, G.S. 1985), and are now extensively cultivated in south-eastern waters. The pearl shell industry dominated the northern waters of Australia for over fifty years and at its peak made a very significant contribution to Australia's exports. Subsequently the cultured pearl industry developed. Current commercial fisheries exploit various species of scallops, abalone and squid.

Pearl Oysters. The most important mollusc fishery in Australia's history has been that for pearl oysters, particularly for the gold-lipped pearl oyster, *Pinctada maxima* (Pteriidae), from about 1880 to 1950. At its peak, around 1908, the fishery landed pearls and shell valued at many hundreds of thousands of Pounds and employed several thousand people (Bartlett 1954). The fishery was initially focused on Torres Strait but by 1886 these grounds had been seriously depleted and there was a progressive movement to Western Australian waters, centred on Broome (Saville-Kent 1890).

Despite its cumbersome appearance and hazards to the diver, the hard-hat diving equipment used in those days was effective, and skilful manipulation of lines and anchor warps as the luggers drifted with the tides allowed divers to skim over likely areas until pearl oyster beds were located (Idriess 1937). The efficiency of this technique contributed to the progressive decline of the fishery

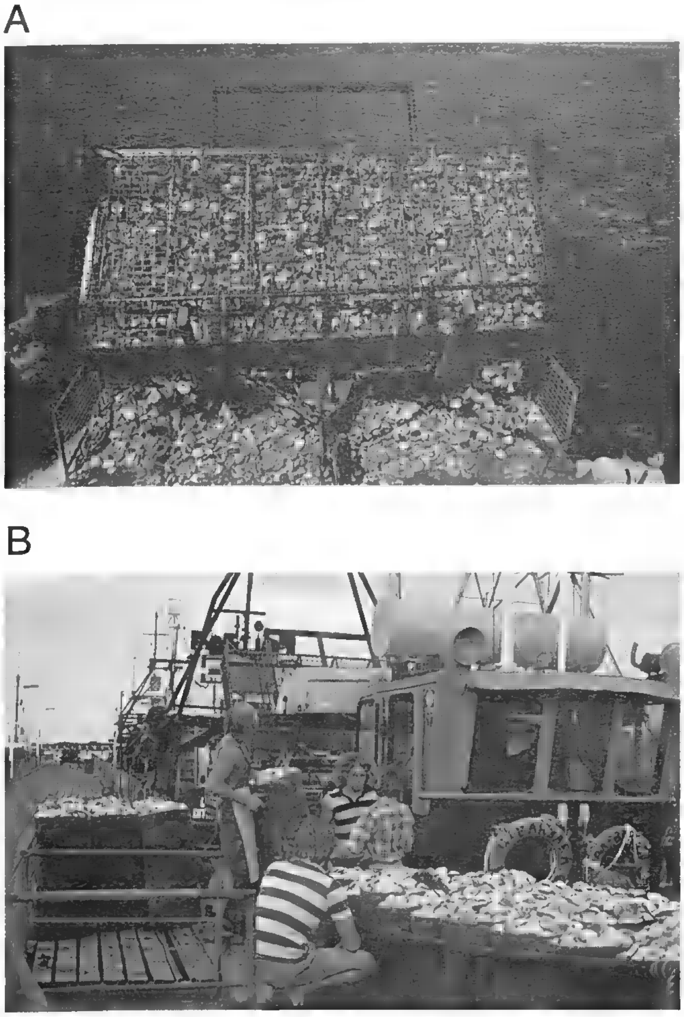


Figure 1.81 Fishing for southern scallops, *Pecten fumatus* (Pectinidae). **A**, emptying the scallop dredge for sorting at the end of a haul. **B**, unloading the day's catch at Lakes Entrance, Victoria.
[courtesy of Australian Fisheries Management Authority]

after 1908 under the twin effects of declining prices for the shell and reduction of the stocks; it ceased to be a significant industry at the start of the Second World War (Bartlett 1954).

The large pearls produced by *Pinctada maxima* in culture led to the development of the pearl culture industry in and around Broome from the 1950s (Kailola *et al.* 1993). The artificial culture of pearls by the introduction of a foreign body to the mantle cavity of pearl oysters is a well-developed technology and is presently actively pursued in several areas centred on Thursday Island in Torres Strait, Darwin and Broome (Fig. 1.78). However, the industry is severely hampered by the scarcity of adult pearl oysters, *Pinctada maxima*, in which to grow pearls; such oysters now fetch extremely high prices. Research aimed at the artificial propagation of pearl oysters is currently underway in Australia and some success by commercial interests has been reported (Dybdahl & Rose 1986). Present activities are directed mostly to the collection of live wild oysters for pearl cultivation. In addition to pearls, mother-of-pearl shell and small amounts of adductor muscle are exported (Kailola *et al.* 1993). The average annual value of this industry was A$120 million between 1989–90 and 1993–94 (Table 1.3). The present fishery for pearl oysters is fully exploited, and stocks of pearl shell appear to be declining in Torres Strait (Kailola *et al.* 1993).

Abalone. Exploitation of abalone (*Haliotis* species, Haliotidae) as a commercial resource is a relatively recent activity and is of importance in all of the southern states. It is currently Australia's most important molluscan fishing enterprise in terms of landed and export value, and the number of issued entitlements (ABARE 1994). The landings comprise blacklip abalone (*Haliotis ruber*, in New South Wales, Tasmania, Victoria, South Australia), greenlip abalone (*H. laevigata*, in Tasmania, Victoria, South Australia, Western Australia) and Roe's abalone (*H. roei*, in Western Australia). Other small, non-commercial species are found in all the reef areas around Australia.

Abalone live on rocky outcrops from the lower intertidal to depths of about 30 m (Shepherd 1973). Harvesting is conducted by divers, usually using hookah apparatus and working from small boats. Abalone are easily over-harvested because they occur in restricted habitats. Strict size limits are enforced in all states, as are limitations on entry to the fishery. Current measures appear to be sufficient to ensure that the abalone fisheries will continue.

The fisheries for green and black-lipped abalone are fully exploited. However, they are highly vulnerable to casual non-professional divers and mortality from this source can be expected to increase. Bag limits and minimum size limits are set for recreational divers and in Western Australia only snorkelling for abalone is permitted. Experimental culture of abalone spat is underway in Tasmania, South Australia and Victoria (Cropp 1989; Kailola *et al.* 1993).

An average of 4984 tonnes of abalone were landed annually in the 1988–89 through 1993–94 seasons, with an annual landed value of A$109 million (Table 1.3; Fig. 1.79). The value of the 2556 tonnes (54% of the catch) exported in 1993–94 was A$187.4 million; as in the previous two seasons, most of this was sold in Japan (84%) and Hong Kong (13%) (ABARE 1994). In 1993–94, the fishery involved entitlements to fish in the Commonwealth and State waters of Bass Strait (144), New South Wales (40), Victoria (71), Western Australia (26), South Australia (35) and Tasmania (125) (ABARE 1994). The number of fishers in each State is roughly proportional to the average catch over six seasons in each State from 1988–89 onwards (Fig. 1.80A).

Scallops. Five scallop species (Pectinidae) are fished commercially in Australia. The southern scallop, *Pecten fumatus*, is fished in Victoria, New South Wales and the Commonwealth waters of Bass Strait (Fig. 1.81). The Tasmanian waters of Bass Strait have been closed for scallop fishing since 1987. At its peak in 1981–82 and 1983–84, this fishery yielded over 23 000 tonnes of scallops per year (Kailola *et al.* 1993).

The queen scallop, *Equichlamys bifrons*, has been fished commercially by divers in South Australia since 1985, and currently yields about 120 tonnes per season. This species and the doughboy scallop, *Mimachlamys asperrima*, are the focus of a recreational dive fishery in Tasmanian waters (Kailola *et al.* 1993).

Figure 1.82 The high value placed on tridacnid clams in South-East Asia for their meat, shown drying on an Indonesian fishing vessel, has led to over-exploitation of all but the Australian populations.
[C. Bryce/Western Australian Museum]

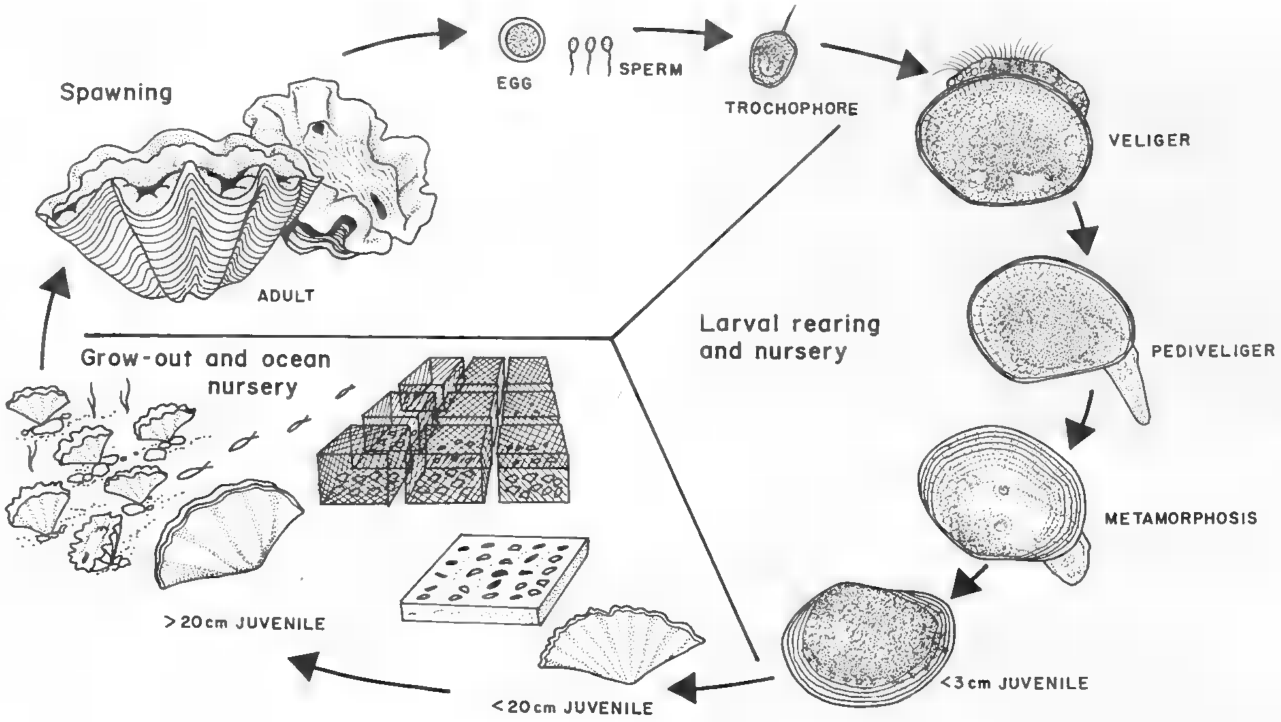


Figure 1.83 Stages in the life cycle and cultivation of giant clams, *Tridacna* species (Tridacnidae). [Australian Centre for International Agricultural Research]

The saucer scallops, *Amusium balloti* and *A. pleuronectes*, form the basis of the subtropical and tropical scallop fisheries. The former species has a disjunct distribution from the Great Australian Bight to north-western Western Australia and from central New South Wales to northern Queensland, and *Amusium pleuronectes* occurs from central Queensland to the northern coast of Western Australia (Lamprell & Whitehead 1992). Where they occur, saucer scallops are important components of trawl catches and in some years are a major source of earnings by the trawlers.

All of the dredge fisheries in southern waters are heavily exploited; they form discrete resources managed by the State fisheries departments (Sanders, M.J. 1970). Overall the southern scallop fisheries are over-exploited, and some areas in Tasmania and Victorian waters are closed to fishing in order to promote recovery. Reduction in density of saucer scallops in some areas of Queensland indicates intense fishing pressure, though the stocks are considered to be secure (Kailola *et al.* 1993).

The scallop fisheries are currently the second most important of the active mollusc fisheries (in contrast to the cultivated oysters). However, recruitment of young scallops to the fisheries tends to be very erratic and production is therefore spasmodic (Gwyther & McShane 1984). On average, 17 827 tonnes of scallops were caught annually in Australia between 1989 and 1994, with a landed value of some A$55 million (Table 1.3; Fig. 1.79). In 1993–94, 4739 tonnes of scallops valued at A$82.1 million were exported, mostly to Hong Kong (40%), the United States (14%) and Singapore (9%) (ABARE 1994; Table 1.3). The proportion of scallops caught in each State, averaged over six seasons to 1993–94, is shown in Figure 1.80B. During the 1993–94 season, the fishery was conducted by five Queensland trawlers, 14 boats in Western Australia and 112 license holders in Victoria.

Cephalopods. Squid, cuttlefishes and octopuses of the families Loliginidae, Ommastrephidae, Sepiidae and Octopodidae have always been a part of the bycatch of trawlers, and landings have increased in recent years as a result of increased demand and acceptability to the Australian public. Though most of the catch was used for bait, the proportion consumed by Australians has increased significantly. The catches include a large number of species (Roper, C.F.E., Sweeny & Nauen 1985). Most of the increase in production between the mid 1970s and early 1980s was due to Taiwanese demersal trawling in northern waters for loliginids and sepiids. Under various joint ventures or licensing agreements, Japanese, Taiwanese and, more recently, Korean squid jigging vessels have targeted ommastrephids off the southern coast since 1971. The arrow squid, *Nototodarus gouldi*, was the most important species. There appears to be much potential for expansion of Australian squid fisheries (Dunning & Brandt 1985). These fisheries are discussed in more detail in Chapter 13.

Australian catches of all cephalopods ranged from 1739 to 2739 tonnes per year from 1989–90 through 1993–94 (Table 1.3). Although the total catch has been much larger in some seasons, for example, over 10 000 tonnes in 1979–1980, most found its way to the home markets of the foreign fishing nations involved (Dunning 1982; see Chapter 13). The landed value of cephalopods over six years ranged from A$4.2–7.7 million (Table 1.3), about half of the value of the 24 375 tonnes of cephalopods imported for human consumption from 1988–89 through 1993–94 (ABARE 1992, 1994).

Oysters. Apparently, when the first European colonists arrived in Australia nearly 200 years ago oysters (Ostreidae) were widespread throughout the cooler regions, often in enormous quantities. Smith, G.S. (1985) has reviewed the history of the oyster industry in Queensland and chronicled the decline of the industry to insignificant levels over the period since 1824 as a result of the combined effects of loss of habitat, ineffective management, disease and wasteful exploitation of both living and dead oysters for lime (Smith, G.S. 1985). This history appears to have been paralleled elsewhere in Australia. The Sydney rock oyster (*Saccostrea commercialis*), the blacklip oyster (*S. echinata*) and the milky oyster (*S. cucullata*) have been the main species harvested.

The oyster industry gradually progressed from an open access fishery, to one in which leases were allocated to individuals to actively cultivate shallow beds by laying solid substrata upon which larval oysters can settle. Dredging for wild oysters – mainly *Ostrea angasi* – in subtidal areas continued for many years but is no longer a significant activity. The Pacific oyster, *Crassostrea*

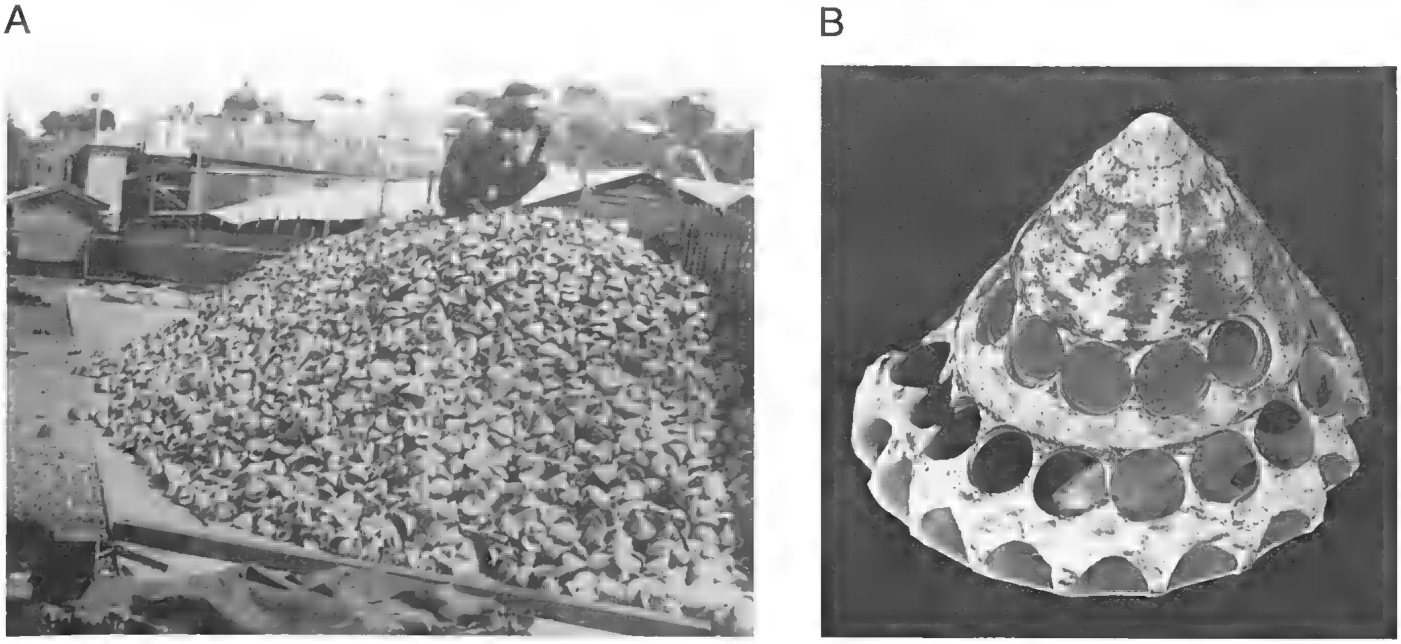


Figure 1.84 Trochus shell, *Trochus niloticus*, was fished intensively for use in button manufacture. **A**, a large pile of graded shell at Townsville in 1954, shortly before the industry collapsed. **B**, a shell after the removal of circular blanks for button manufacture.
[A, W. Fitzpatrick; B, W. Nash/courtesy Australian Fisheries Management Authority]

gigas, is now well established in Victoria and New South Wales. Considerable concern has been expressed for over 20 years that this species may compete successfully with indigenous oyster species, to the detriment of the latter (Bennett 1992).

Oysters are currently the only molluscs which are extensively cultivated for food on a commercial basis in Australia. The Sydney rock oyster, *Saccostrea commercialis*, is the principal species of interest but the Pacific oyster, *Crassostrea gigas*, introduced into Tasmania in the 1940s (Bennett 1992), has also been cultivated on a significant scale since 1967, particularly in Tasmania. This species is also farmed in Victoria and South Australia where native crassostreine oysters are sparse or absent (see Chapter 6).

Early cultivation methods relied upon natural spatfall onto shellbeds or onto rocks. However, the modern industry uses a combination of sticks and trays to maximise efficiency and production. Larval oysters settle upon sticks assembled in frames set out in shallow water, where they grow for a year. The sticks are then separated and placed on racks. The oysters are left to grow to saleable size (between 30–60 g whole weight) and then marketed or transferred to trays for further growth (Malcolm 1987; Kailola *et al.* 1993).

Although much research has been conducted on the larval biology of oysters, the oyster cultivation industry still relies on natural settlement of spat to produce successive crops. This makes the industry vulnerable to catastrophic failure if settlement is unsuccessful for any reason. Nevertheless, the production of oysters, particularly in New South Wales, has been sustained for many years, despite conflicting claims on estuarine areas for recreational and industrial purposes. The potential for subtidal culture of *C. gigas* and of *S. commercialis* is being evaluated as an alternative to the traditional intertidal farming, as used for *S. commercialis* and the more tropical *S. echinata* in New South Wales, Queensland and Western Australia (see Chapter 6).

The production of farmed oysters averaged 7110 tonnes between 1988–89 and 1993–94 (Table 1.3), with an average market value of A$41.7 million. Almost all oysters are farmed in New South Wales and Tasmania (Fig. 1.80C). Most are for domestic consumption, and on average only 28 tonnes were exported annually from 1988–89 through 1993–94 (4%), with an average value of A$0.34 million (Table 1.3).

Giant clams. There is much current interest in the cultivation of giant clams stemming largely from the recognition that, as a result of their symbiotic association with a dinoflagellate algae, giant clams are potentially the world's only self-feeding farm animals (Munro & Heslinga 1983). Six of the seven giant clam species (Tridacnidae) are common in coral reef areas in Australia, of which the three largest species, *Tridacna gigas*, *T. derasa* and *Hippopus hippopus* are of prime interest for cultivation by virtue of their relatively high growth rates. Mariculture of giant clams will also reduce the destruction of reef habitats and stress caused by exploitation of natural populations (Fig. 1.82; Alder & Braley 1989).

Cultivation methods for clams are now established (Fig. 1.83; Crawford, Nash & Lucas 1986) and it is probable that a significant Australian industry will arise as a result of these developments. Two commercial clam hatcheries for tridacnids have been developed recently near Cairns on the Great Barrier Reef (Heslinga & Fitt 1987). In some early mariculture efforts, giant clam mass cultivation was very successful, producing up to 22 tonnes/ha/year of meat with 140 tonnes of shell as an additional product (Heslinga & Watson 1985; see also Chapter 11). The adductor muscle of giant clams is valued at over A$25/kg in South-East Asia, Hong Kong and Taiwan. Shells are also valuable for the tourist trade and the aquarium trade is being supplied now with maricultured clams.

Trochus snails. The fishery for trochus snail, *Trochus niloticus* (Trochidae), began in 1912 as a cheap alternative to pearl shell, and rapidly became an integral part of that fishery (Fig. 1.84; Ganter 1994). Trochus fishing declined in the 1950s as stocks were reduced (Fig. 1.84); prices rose to £260 per tonne in 1958, but production was unsteady and the fishery could not compete with synthetic button manufacture in Australia from 1956 onwards (Nash 1988; Ganter 1994). However, demand for natural products increased in the 1970s, and the market revived. A small market for the shell still exists, and although the fishing is labour-intensive in Australia and prices fluctuate, there has been a resurgence of interest in trochus fisheries.

The Australian trochus fishery is conducted in north-western Western Australia and along the Queensland coast. The Western Australian component is licensed exclusively to the four indigenous communities in and close to King Sound (J. Barrington, Fisheries Department of Western Australia, personal communication). In Queensland, annual quotas for the Torres Strait region and the east coast are presently 100 tonnes and 400 tonnes, respectively, limited to shells between 80 and 125 mm in diameter; 50 tonnes of this total are reserved for

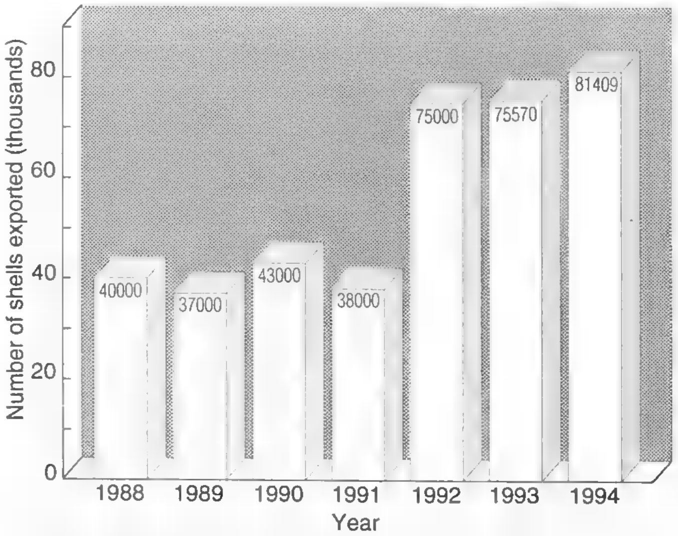


Figure 1.85 Annual exports of mollusc shells from Australia, 1988 through 1994. (After Davey 1993; Biodiversity Group, Environment Australia, unpublished data)

operators from nine indigenous communities. The remainder is fished by seven commercial operators (M. Elmer, Queensland Fisheries Management Authority, personal communication).

Market fluctuations in the price of shell drive the performance of the fishery. Prices per tonne rose through the 1980s from A$1200 in 1982 to A$1795 in 1985 and A$4000 in 1986 (Ganter 1994). By the end of the decade the export value of shell was about A$10 000 per tonne (1989, 1990), then declined to A$4500 in 1992 before rising steadily to about A$5500 in 1995 (R. Louden, Australian Trochus/Bêche-de-Mer Association, personal communication). The meat is also marketable (Nash 1986), and is an important product in parts of South-East Asia. It is removed from the shell by cooking for 10–15 min, then cleaned before it is frozen, canned or dried.

Mussels. Wild stocks of the blue mussel, *Mytilus edulis planulatus* (Mytilidae), are presently harvested by divers in Jervis Bay, New South Wales, at Lakes Entrance, Victoria, and in Cockburn Sound, south-western Western Australia. The total harvest peaked at about 1450 tonnes in 1981–82. Mussels are farmed at several southern Australian localities, using spat which settles naturally on suspended ropes (Kailola *et al.* 1993). The total annual production from both sources was less than 1000 tonnes between 1988–89 and 1993–94, with average annual landed value of A$0.32 million (Table 1.3).

Pipis and other molluscs. The 'pipi', *Donax (Plebidonax) deltoides* (Donacidae) is fished commercially in New South Wales (Macpherson & Gabriel 1962), where some 360–700 tonnes were collected annually between 1988–89 and 1993–94 (Table 1.3). Arks, *Anadara trapezia* (Arcidae), are also collected in Victoria and New South Wales, and appear for sale in markets. Small local fisheries exist for the venerids *Katelysia scalarina* and *K. rhytiphora* along southern shores. Annually, some 15 and 10 tonnes are harvested commercially in Western Australia and Tasmania, respectively. Turban shells, *Turbo undulatus* (Turbinidae), harvested from the intertidal zone as well as by divers from subtidal areas, form a small stable Tasmanian fishery (Kailola *et al.* 1993).

Shell collecting. Shell collecting is often pursued on a casual basis and forms a significant activity in relation to tourism. However, a substantial component of such collections eventually passes through commercial channels. Rare shells taken by trawlers in relatively deep waters are of sufficient economic importance that some trawling companies now regard them as a normal component of catches and not as a casual perquisite of the deck crew.

Annual export figures indicate that this commercial trade, worth an estimated A$2.5 million (Willan 1986), is expanding (Fig. 1.85). According to the permits issued for 1994, exporters resident in Queensland, Western Australia and South Australia accounted for 51%, 29% and 19% of the 81 409 exported shells. Gastropods dominated exports in 1994 (84.4%), as in previous years (Davey 1993). Bivalves (12.5%) and chitons (2.5%) formed only a small part of the total, and the few cephalopods (213) and scaphopods (8) were an insignificant component. Exports of four species each exceeded 1000 individuals – *Zoila friendii*, 1409; *Amoria zebra*, 1090; *Conus 'zebra'*, 1084; *Neotrigonia bednalli*, 1046. In total, 112 families were represented; six comprise 72% of these shells – Cypraeidae, 26.5%; Volutidae, 19%; Conidae, 8.8%; Muricidae, 7.1%; Pectinidae, 5.7%; Trochidae, 4.6% – reflecting the preferences of shell collectors and dealers overseas and in Australia (Willan 1986).

Taxa at most risk from collectors are those which are endemic, those with direct development and those that are relatively rare (Willan 1986). By these criteria, cowries in the genus *Cypraea*, subgenera *Notocypraea*, *Austrocypraea* and *Zoila*, volutes and muricids are most threatened. In his review of the *Wildlife Protection (Regulation of Exports and Imports) Act 1982* in relation to export of shells, Stanisic (1991) noted that no Australian marine mollusc can be considered rare or endangered. However, he recommended that each state should manage molluscs with a focus on habitat protection. Reserve areas with no collecting, bag limits per species, licensing of commercial collecting and possibly export quotas for some species were considered appropriate management options. Implementation of these recommendations was initiated with the declaration of native marine molluscs as controlled specimens in Queensland, South Australia and Western Australia (*Commonwealth of Australia Gazette*, 22 February 1995 and 7 June 1995). Collecting of molluscs in these states will be in accordance with management plans now in force in Queensland and Western Australia (Barrington & Campbell 1996) and in draft form for South Australia (MacDonald 1996).

Other Economic Issues

Shipworms are important in the recycling of wood in the littoral environment. However, they also cause considerable damage to wooden structures in the sea, and measures to protect pilings, piers and vessels against the teredinid wood borer, *Martesia striata*, cost several million dollars each year (Turner, R.D. 1971).

Suspension-feeding coastal bivalves are useful bioindicators of water quality because they accumulate suspended particles on their gills (see Chapter 4). In southern Australia *Mytilus edulis planulatus* is used extensively as a bioindicator to monitor levels of bacteria and pollutants such as trace metal and organochlorin pollutants in coastal waters (Talbot, V.W., Magee & Hussain 1976a, 1976b; Harris, Fabris, Statham & Tawfik 1979). *Saccostrea commercialis* is used in a similar manner by the New South Wales Environmental Protection Agency (Talbot, V. 1985, 1987).

The biocidal agent in many anti-fouling paints, tributyltin, has been implicated worldwide in sublethal effects on various molluscs and fishes, and mortality of invertebrates in some seagrass systems (Nias, McKillup & Edyvane 1993). Restrictions on use of tributyltin were introduced in New South Wales in 1989 primarily because it affects shell shape and reduces growth in oysters (Batley, Fuhua, Brockbank & Flegg 1989). The sensitivity of some dioecious gastropod species to this pollutant has prompted evaluation of their use in bioassays, based on the extent to which imposex, a form of pseudohermaphroditism, develops in the assayed population. Australian studies have been conducted on *Conus* species on Rottnest Island, Western Australia (Kohn & Almasi 1993), muricids, *Thais orbita* and *Morula marginalba*, along the New South Wales coast (Wilson, Ahsanullah & Thompson 1993) and on another muricid, *Lepsiella vinosa*, in South Australia. All these studies indicated that the proportion of females showing imposex was related to the level of boat usage at sampling sites, but Nias *et al.* (1993) cautioned that this deformity may also be induced by other factors such abnormal ionic concentrations and environmental stress.

DISTRIBUTION AND RELATIONSHIPS OF MARINE AND ESTUARINE FAUNA

Alfred Russell Wallace (1876) provided the first treatment of biogeography in its accepted sense. Wallace and Darwin and many others after them, considered that the continents and oceans were fixed in position. The concept of dispersal was essential to explain the observed distributions of closely related plants and animals.

The biotas of the southern continents were considered to be old survivors pushed south by the more vigorous, newer animals and plants that evolved in the north. This classical historical biogeography assumes that species dispersed from their 'centres of origin' and that the composition of species in any particular area is largely dependent on which species were able to disperse there (Ekman 1953; Darlington 1957).

Following the acceptance of plate tectonics in the mid 1960s there emerged three schools of thought. Dispersal biogeography was essentially an extension of the earlier ideas of a mobile biota with a mobile earth replacing land bridges and some of the other means of dispersal. The second approach, the equilibrium theory, inspired by MacArthur & Wilson (1967), is otherwise known as the theory of island biogeography. These biogeographers aim to analyse rates of dispersal, colonisation and extinction on islands or island-like habitats. Unlike dispersal biogeography it yields testable predictions. The third school, vicariance biogeography, began with Leon Croizat, the father of panbiogeography, in the 1950s, who argued that life and earth have evolved together. Panbiogeography is now a separate school and employs different methodology from that of other vicariance biogeographers.

From the onset of its investigation by Europeans, the temperate marine Australian biota was recognised as being largely unique. The botanist, Sir Joseph Hooker was the first to try to explain the distribution patterns he observed in his travels in the southern part of the world in the middle of last century. Other early attempts to account for these distribution patterns include those of Hedley (1896) and W. Hutton (1896).

Since the time of Hooker the origins and relationships of the Australian biota have received considerable attention. Various theories involving the problems of biotic relationships and geological phenomena preceded the now generally accepted tectonic history of the region – for review see Barlow (1981) and Frakes, McGowran & Bowler (1987). Several major biogeographic synopses have been published in the last thirty years (Keast, Crocker & Christian 1959; Keast 1981; Archer & Clayton 1984; Wilson, B.R. & Allen 1987; Poore 1995) to which the reader is referred for more detail.

Molluscan taxa have not been utilised in the biogeographic studies in the Australasian region as much as they might have been, given that many are relatively well known and conspicuous. Charles Hedley made several important contributions relating to western Pacific and Australasian biogeography around the turn of the century (Hedley 1884, 1893, 1899d), proposing ideas well ahead of his time. Some more recent major studies include those of Dartnall (1974) and E.A. Kay (1980, 1984) on marine molluscs of the western Pacific region. Darragh (1985) provided a detailed biogeographical analysis of the Tertiary molluscan fauna of south-eastern Australia. B.R. Wilson & Allan (1987) used molluscan examples in their general treatment of the zoogeography of Australia.

Earth History

The key to present distributions is often to be found in the past. Geological and climatological events have radically influenced the distribution of animals and plants. An obvious example is the series of much lower sea-levels during several glaciations in the Pleistocene, the most recent of which occurred around 20 000 years ago. These events would have had a profound influence on the distributions of both the marine and non-marine biotas because of a number of factors.

The land bridges formed by the drying of both Bass Strait and Torres Strait prevented movements between eastern and western populations of marine species, leading eventually to divergence and, in some instances, speciation. This is evident in the number of east-west species pairs or sister species (Fig. 1.86; Dartnall 1974). The land bridges between New Guinea and northern Australia, and between Tasmania and Victoria, would have facilitated the migration of non-marine species between these areas and also would have allowed, through greater continuity of habitat, the migration of shallow water, intertidal and estuarine species. Ocean currents would also have been affected.

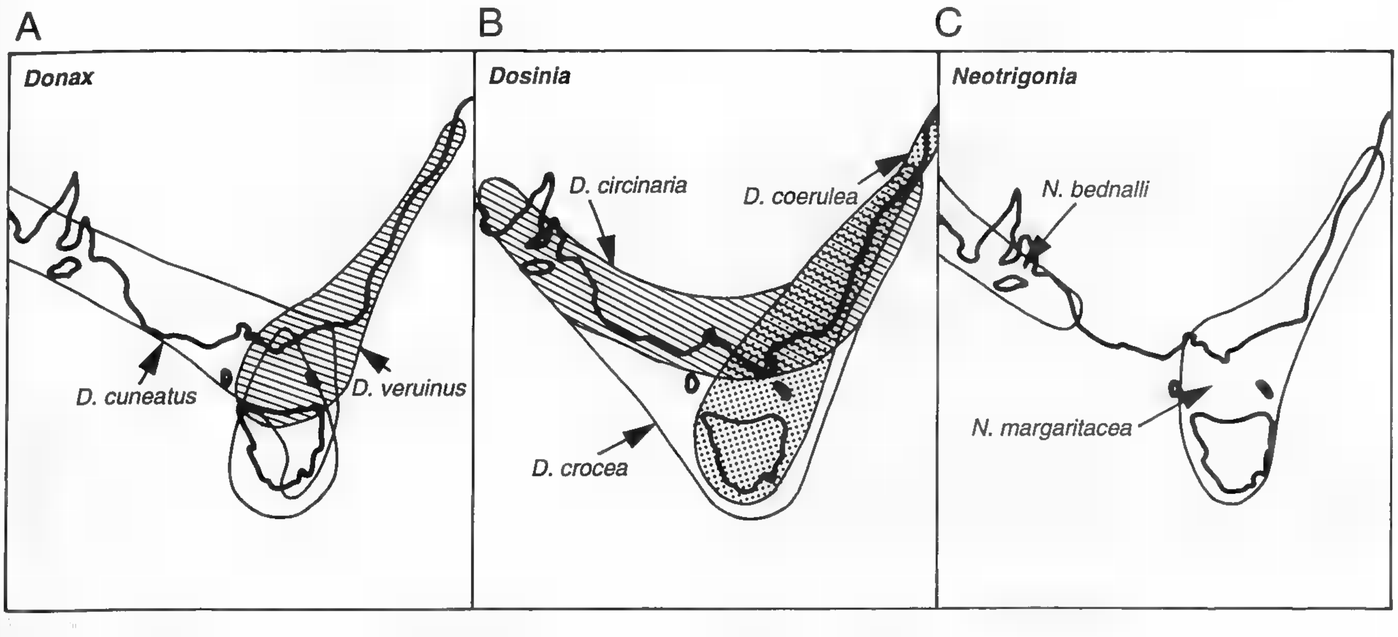


Figure 1.86 The distribution patterns of bivalves, illustrating the evolutionary consequences of the closure of Bass Strait, south-eastern Australia, during glacial periods. **A, B**, subsequent to the re-opening of Bass Strait, congeneric species became sympatric: A, *Donax* (Donacidae). B, *Dosinia* (Veneridae). C, *Neotrigonia* (Trigoniidae) species remain allopatric. (After Dartnall 1974) [I. Hallam]

The drying of the continental shelf would have resulted in longer rivers, relocation of estuaries and, through the connection of previously separated rivers as they flowed towards the new coastline, the merging of estuaries and conjoining of other marine habitats.

The areas that were drying, and newly inundated areas, were colonised by successive communities of animals and plants that would have each interacted with the surrounding communities in different ways, and the cooler air and water temperatures would have affected the ranges of almost all marine, and many non-marine species.

The shelf between the Great Barrier Reef and the mainland would have been dry. The fauna occupying this habitat at present, as with Bass Strait, Torres Strait and the Continental Shelf in general, derives from that which recolonised the area some 18 000 years ago.

Hence this relatively very recent climatic event, and the series of similar events preceding it through the Pleistocene, caused massive upheaval. However, the effects of more profound events further back in geological history also need to be interpreted and understood before any real understanding of biogeographic patterns can be achieved (for summaries of Australia's tectonic history, see Barlow 1981; Frakes *et al.* 1987; see also The Fossil Record, this Chapter).

On a larger scale, the perceived relationship of Australia to other land masses depends on the geological model being used. Various models have been proposed which offer different explanations or different spatial relationships for the reconstruction of land masses in the past. Although the conventional Gondwanaland model is generally involved, there are alternative proposals, such as the Pacifica hypothesis (Nur & Ben-Avraham 1982). The main theories are discussed by C.B. Cox (1990). Some biogeographical evidence can, and has assisted in our understanding of both broad-scale and local geological events, the corroboration of Continental Drift being a good example. While some authors suggest that past geological events can be predicted on the basis of biogeographic analysis (Craw & Weston 1984; Michaux 1989), other writers are more cautious (for example, Seberg 1986).

Marine Provinces

The human need to classify in order to comprehend diversity has resulted in the recognition of faunal and floral regions and provinces. The general boundaries and overlap areas of such provinces in Australian waters have been disputed and alternative schemes have been proposed, based on the distributions of a diverse range of animal groups. These various proposals have been reviewed by Wilson, B.R. & Allen (1987); the following brief comments are limited to the contribution to this debate of several studies based largely or entirely on molluscs.

On a broad scale, the biogeography of the Indo-Pacific region has received considerable attention. Some workers, such as Hedley (1899d) and Ladd (1960), proposed large, now submerged land areas in the Pacific to account for the distributions of, particularly, non-marine fauna. Clearly plate movements have played a large part in shaping modern faunal compositions, as well as the combined effects of climatic and sea level changes (for example, Kohn 1990). Useful reviews in which Mollusca are emphasised include those of Powell (1958), E.A. Kay (1980) and Kohn (1983b).

The first descriptions of Australian faunal provinces based on molluscs were by Hedley (1904, 1926), who divided the Australian marine fauna between two tropical and two temperate provinces. The tropical coastline between Geraldton and Cape York was termed the Dampierian province, and that from Cape York south, the Solanderian province. The warm temperate South coast was divided into a Peronian province in the east and an Adelaidean region in the west; subsequently the latter was renamed the Flindersian province by Cotton (1930).

Other authors who have subdivided the coastline into regions worked on single groups of animals, and the results of their work led to quite different conclusions. Iredale & May (1916) named south-eastern Tasmania the Maugean region, based on their work on the molluscan fauna. Bennett & Pope (1953) extended this region to include the remainder of Tasmania and Victoria. As part of a broader study on distributions of Indo-Pacific cypraeids, Schilder (1961) divided the Australian area into a northern part ('Dampierian' plus 'Queensland', the latter including Norfolk Island and Lord Howe Island) and a southern ('South Australian') part.

Following various divisions of the northern Australian region, based on distributions of fishes (Whitley 1932) and echinoderms (Clark 1946; Marsh 1976), Endean (1957), also working with echinoderms, concluded that this region comprised a single Tropical Australian Province.

F.E. Wells (1980), working with 'prosobranch' gastropods, agreed with Endean on the concept of a single province for northern Australia. He found that 88% of the macro-'prosobranch' gastropods investigated in northern Western Australia also occur in either Queensland or in adjacent parts of the Indo-West Pacific. Subsequently, F.E. Wells (1986a) showed that 'prosobranch' species of offshore coral reefs in northern Western Australia differ significantly from those found inshore, paralleling the situation in Queensland for the Great Barrier Reef. He suggested that the Solanderian province be considered part of the tropical Australian province. A comparison of the macro-'prosobranch' from northern Australia, New Guinea and Indonesia showed a very low level (8%) of northern Australian endemics (Wells, F.E. 1990). Many gastropods, even such well known species as *Dicathais orbita* and *Turbo torquatus*, were originally distinguished as separate species in eastern and western Australia but are now considered representative of single widespread species.

Bennett (1980) recognised a warm temperate province covering most of the west coast and the north coast eastwards to Cape York; a tropical province along eastern Queensland; an eastern warm temperate province covering the coasts of New South Wales, eastern Victoria and north-eastern Tasmania; a cool temperate province for southern Tasmania; and a western warm temperate province for the remainder of southern Australia, including north-western Tasmania.

Dartnall (1974) discussed the faunal provinces of south-eastern Australia and Darragh (1985) provided new insights into the composition of Australian faunal provinces by examining their geological history, especially those of the south-eastern part of Australia (summarised by Wilson, B.R. & Allen 1987).

The current view is that Australian marine species are basically part of the tropical Indo-West Pacific fauna, with low endemicity on the northern coast, or an Australian warm temperate fauna, with high endemicity, on the southern coast (Ekman 1953; Wilson, B.R. & Gillett 1971; Wilson, B.R. & Allen 1987; Poore 1995). The east and west coasts of the continent are overlap zones with a small proportion of endemic species on each coast (Fig. 1.86). Wilson, B.R. & Gillett (1971) suggested that further faunistic subdivision would emphasise differences between regions and obscure the broad faunal overlaps. This is basically the view that Dell (1962) took nearly ten years earlier with New Zealand faunal provinces, which had been largely based on Mollusca. He recognised a northern warm water and a southern cold water fauna, with a central area of overlap, whereas previously (for example, Powell 1961) four provinces had been recognised.

There are two reasons for the differences of opinion in the delineation of biogeographic regions around the Australian coastline. Firstly, different groups of organisms show different patterns; secondly, recognition of biogeographic patterns often hinges on taxonomic judgements, because the determination of provinces is based on the relative number of forms unique to an

Figure 1.87 Major faunal regions of the Australian coast. The northern and southern limits of the overlap zones correspond with mean water temperatures (°C) in January and July, respectively, of 25° and 19° at Brisbane; 19° and 14° at Eden, 24° and 20° at Carnarvon and 19° and 16° at Albany. (After Wilson, B. & Gillett 1971; Bunt 1987) [I. Hallam]

area. Poore (1995) noted that although the broad division of Australia into northern and southern regions is inadequate for making management decisions, more detailed division of the coast and adjacent waters has not been possible. He maintained that resolution of the issue requires more detailed distributional data and phylogenetic analyses of a wide range of taxa at family and genus level, with a focus on the southern fauna.

Marine Distributions

Following B.R. Wilson & Gillett (1971) and B.R. Wilson & Allen (1987), the marine molluscs of Australia can be divided into three zoogeographic components: tropical species, warm temperate species and forms endemic to the east or west overlap zones of the continent (Fig. 1.87). In general, the shallow-water benthic marine molluscs of Australia are widespread species with ranges extending for hundreds of kilometres; only a small fraction of the fauna has restricted ranges. A few taxa have been described only recently and their ranges will probably increase as they become better known. Some of the small-ranged taxa are potentially vulnerable to habitat destruction and over-exploitation (see The Australian Marine Molluscan Fauna, this Chapter).

The tropical fauna on the north coast of the continent extends from North West Cape in Western Australia to about latitude 26°S to the southern tip of the Great Barrier Reef on the Queensland coast. The molluscs of this area are part of the vast Indo-West Pacific faunal region which extends over large areas of the tropical Indian and Pacific Oceans from the tropical east coast of Africa eastwards to the Hawaiian Islands. Species also occurring along the north coast of Australia often also occur in many other areas of the Indo-West Pacific. The money cowrie, *Cypraea moneta* (Fig. 1.88), has an exceptional distribution, and is one of very few Indo-West Pacific species which reach the eastern Pacific (see Emerson 1967 for a review). Such broad distributions are usually attributed to the long-lived planktotrophic larvae of the species concerned which are dispersed long distances by currents (Scheltema, R.S. & Williams 1983). Even some temperate species have surprisingly broad ranges, some extending around most of the southern half of the continent.

The warm temperate fauna of the south coast of Australia is largely endemic. Species in this fauna tend to be widespread from New South Wales along the southern coast to southern Western Australia, though a number have restricted ranges. A few southern Australian species extend into the overlap zones on the east and west coasts where they mix with some tropical species. However, a number of endemics also occur in these overlap zones on both coasts. A few southern African species occur sporadically in south-western Western Australia (Wells, F.E. & Kilburn 1986).

Some endemic Australian species have remarkable distributions. For example, the mud whelk, *Pyrazus ebeninus*, which is found only on the east and south-east coasts, ranges from Bass Strait to the tip of Cape York. A few genera are found around the entire Australian continent but not beyond it. Examples are the relict bivalve genus *Neotrigonia* and gastropod genus *Botelloides* (Ponder 1985).

Estuaries

The brackish waters of estuaries support a specialised fauna that can tolerate a wide range of salinities. In these very dynamic habitats, marked changes in salinity, sedimentation, temperature and water depth often occur over short periods of time. These changes, if persistent, can also rapidly affect the vegetation characteristic of these regions – mangroves, seagrasses, saltmarsh – so that faunas dependent on these plants for their habitat are also affected. The best documented extinction of a marine animal in historical times (Carlton, Vermeij, Lindberg, Carlton & Dudley 1991; Gould 1991) is of a small limpet associated with seagrass. Its extinction was brought about by the disappearance of seagrasses from the habitats within the salinity tolerance of this species. Because estuaries are often seriously disturbed by human activities, which often accelerate these changes, they are particularly vulnerable to major faunal and floral degradation.

Estuarine species tend to have extensive ranges and the geographic patterns of faunal composition in estuaries are similar to those shown by marine animals. Why this should be so, given the isolated nature of each estuary, requires some explanation. Many estuarine animals have planktonic larvae and it is known (for example, Epifanio 1988) that these can disperse between estuaries, although there are few well-documented molluscan examples. Floating mangrove leaves have also been suggested as vehicles of dispersal between estuaries (Wehrtmann & Dittel 1990). Estuaries are the feeding places of a large variety of shore birds, which can accidentally carry organisms between localities, either attached to the body or passed through the digestive system.

Historically, changes in sea level during the Pleistocene have allowed estuaries to interconnect. Ponder, Colgan & Clark (1991) suggested that during the arid conditions of glacials the number of estuaries is reduced by the cessation of flow of many rivers and

Figure 1.88 The money cowrie, *Cypraea moneta* (Cypraeidae), has an exceptionally broad distribution – from Rottnest Island off Perth around northern Australia to mid-New South Wales, through the Indo-West Pacific, from Natal and the Red Sea to southern Japan, Polynesia, Hawaii, Cocos Island and the Galapagos Islands. [L. Newman/A. Flowers]

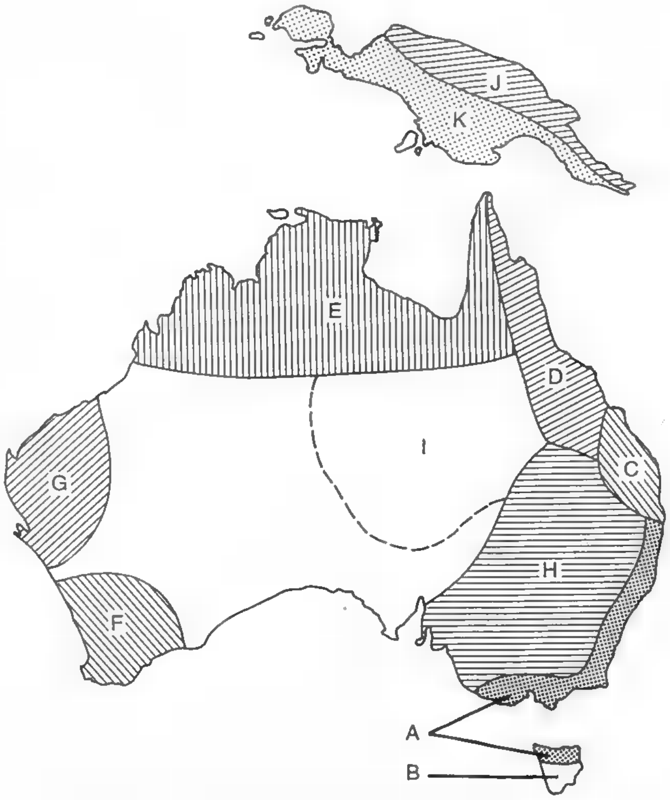


Figure 1.89 The fluvifaunal provinces of Australia and New Guinea. A, Lessonian. B, Tobinian. C, Krefftian. D, Jardinian. E, Leichhardtian. F, Vlaminghian. G, Greyian. H, Mitchellian. I, Sturtian. J, Gaimardian. K, Riechian. (After McMichael & Hiscock 1958) [I. Hallam]

the amalgamation of others by lowered sea levels. Subsequent recolonisation of estuaries from the relatively few remaining populations may explain, in part, why some estuarine species are relatively uniform genetically over large areas.

Deep Water Regions

Although the benthic marine molluscs of shallow waters (< 50 m depth) are relatively well known, benthic animals from depths greater than about 50 m are more difficult to collect, as trawls or dredges operated from vessels are required. Some general aspects of the zoogeography of deep-sea animals were outlined by Ebeling (1967).

The macro-molluscan fauna of the south-eastern continental shelf (50–200 m depth) has been studied in some detail, but very little is known about the shelf fauna from other parts of Australia. The upper slope fauna (200–500 m) from the east and north-west coasts of Australia has been collected in recent years but little work has been done on this material to date. In other parts of Australia the slope faunas are still essentially unknown.

Molluscs living at greater depths (500–2000 m or more) off the Australian coasts are largely unsampled, and much of the material from the handful of stations sampled to date is still unworked.

Pelagic Molluscs

The vast majority of marine mollusc species have benthic juvenile and adult stages. Apart from the bulk of cephalopods, only a few species belonging to four gastropod groups are holopelagic, that is, they complete the entire life cycle in the water column. Holopelagic gastropods include the heteropods, the thecosomatous and gymnosomatous pteropods and a few species of nudibranchs, and comprise fewer than 150 species across all groups (see Holopelagic Gastropods, this Chapter).

Different assemblages of pelagic organisms inhabit tropical, temperate and polar regions. Within these broad zones, defined largely by temperature, species are widespread, often occurring worldwide in areas with the appropriate temperatures. Some of the colder water species are thought to be bipolar, occurring in the northern and southern temperate or polar areas but not in the intervening tropics. The holoplanktonic molluscs recorded from the waters around Australia, including those found off the southern coast of the continent, are almost all tropical species. Further south, temperate species occur, of which two – *Limacina retroversa* and *L. helicina* – are recorded from southern Australia (Wells, F.E. 1989).

A very few molluscs are neustonic, actually living on the surface of the sea. They include the caenogastropod genus *Janthina* and members of the small nudibranch family Glaucidae. Both groups are tropical, though, like the pelagic molluscs, they have been found along the southern coast of Australia. Swimming cephalopods, such as squids, are usually widely distributed but the benthic octopuses, especially those with direct development, are typically more localised.

The developmental mode of a species is often correlated with its distribution, the relationship between planktonic larvae and large geographic ranges being well known (for example, Scheltema, R.S. 1971, 1978, this Chapter; Scheltema, R.S. & Williams 1983).

Introduced molluscs

A few marine molluscs are known to have been introduced to Australia. Several species, including *Neilo australis* (Neilonellidae), *Paphirus largillierti* (Veneridae) and *Maoricolpus roseus* (Turritellidae), may have become established successfully in Tasmania (Greenhill 1965; Dartnall 1974) following an apparently unsuccessful attempt to introduce the New Zealand Foveaux Strait oyster (*Ostrea lutaria*) (Dartnall 1974; Pollard & Hutchings 1990). The Pacific oyster, *Crassostrea gigas*, was introduced successfully into Tasmania during the 1940s, and is now well established in Victoria and New South Wales. *Maoricolpus roseus* is now the dominant molluscan species in parts of south-eastern Tasmania. The New Zealand gastropod *Zeacumantus subcarinatus* was introduced to the Sydney area in the 1930s (Iredale 1936). A listing of known introduced marine invertebrates was given by Pollard & Hutchings (1990).

Many marine animals and plants have been transported around the world on the hulls of ships (*cf.* Allen, F.E. 1953) and, more recently, in bulk carriers in ballast water (Hutchings, van der Velde & Keable 1987; Jones, M.M. 1991; Hutchings 1993). In addition to the sessile animals carried on the hulls of ships, other animals feeding or sheltering in these organisms, such as several nudibranch gastropods, have been distributed widely by such means (see Pollard & Hutchings 1990).

DISTRIBUTION AND AFFINITIES OF NON-MARINE MOLLUSCS

In contrast to the marine mollusc fauna, the non-marine fauna is much less diverse and most species have relatively restricted ranges. Most of the families which occur in Australia also occur on other continents, but there is a substantial degree of endemism at the generic and species level. Because of their generally poor powers of dispersal, freshwater molluscs (for example, Starobogatov 1970; Taylor, D.W. 1988) and terrestrial molluscs (Solem & van Bruggen 1984; van Bruggen 1987) make ideal subjects for biogeographic studies.

Non-marine Zoogeographical Regions

Most of the published studies on the zoogeography of Australian non-marine molluscs have referred separately either to freshwater or terrestrial forms, but they have not considered the two groups together. Tate (1887) was the first to attempt to delineate zoogeographical regions on the basis of the composition and distribution of the Australian terrestrial fauna. Subsequent rearrangements were made by Hedley (1884), Iredale (1937a, 1937b) and McMichael & Iredale (1959). Iredale & Whitley (1938) introduced the concept of a 'fluvifaunula' for a group of species that can be used to characterise each of the various freshwater zoogeographic areas of Australia. The concept was originally based on freshwater molluscs and fish, reflecting the taxonomic interests of the authors.

These two sets of zoogeographic regions have entirely distinct series of names for the different regions, despite the fact that Iredale & Whitley (1938) and McMichael & Iredale (1959) recognised that the patterns for freshwater distribution are in general agreement with those of terrestrial snails.

McMichael & Hiscock (1958) provided a modified version of the fluvifaunal provinces first proposed by Iredale & Whitley (1938) and revised by Iredale (1943) and Whitley (1947, 1959). This is based largely on major drainage systems (Fig. 1.89). Nine fluvifaunal areas are recognised in Australia and two in New Guinea.

The Lessonian fluvifaunula occurs in the southern half of the eastern coastal drainage system, that is, the rivers which flow mainly eastwards off the Great Dividing Range from northern New South Wales to western Victoria and including northern Tasmania. It is characterised by species of *Hyridella*, although the genera *Cucumerunio* and *Alathyria* from the north and *Velesunio* from the inland also occur in the region.

The Tobinian fluvifaunula occurs in southern Tasmania, and lacks hyriids.

The Krefftian fluvifaunula, in the coastal streams of the east coast of southern Queensland, is similar to that of the Lessonian but the genera *Alathyria* and *Cucumerunio* are characteristic; *Hyridella* only occurs in the southern part.

The Jardinian fluvifaunula, which occupies the eastern drainages of Cape York and the rest of northern Queensland, contains no characteristic hyriids, although *Velesunio* is present.

The Leichhardtian fluvifaunula occurs in northern Australia from the western side of Cape York to northern Western Australia; characteristic hyriid genera are *Velesunio* with some occurrences of *Alathyria*, and, in the north-western part, *Lortiella*.

The Vlaminghian fluvifaunula of south-western Australia is characterised by the endemic *Westralunio carteri*.

The Greyian fluvifaunula in the north-west of Western Australia has no hyriids.

The Michellian fluvifaunula occupies the Murray-Darling River system and includes *Velesunio ambiguus* and *Alathyria jacksoni*.

The Sturtian fluvifaunula occupies the Lake Eyre drainage system and contains only *Velesunio wilsonii*.

McMichael & Hiscock (1958) also included New Guinea in their scheme – with two fluvifaunulae recognised – a northern Gaimardian fluvifaunula, with *Velesunio sentaniensis*, and a southern Riechian fluvifaunula which contains species of *Alathyria*, *Hyridella*, *Westralunio* and *Microdontia* as well as two endemic genera, *Virgus* and *Haasodonta*.

B.J. Smith & Kershaw (1979) outlined six faunal regions for non-marine molluscs. These zones are not distinct; there are transitional areas between adjacent zones (Fig. 1.90).

The Leeuwinian Region, in south-western Western Australia is the most distinct of these faunal regions. Characteristic molluscs are the land snail genus *Bothriembryon* and the freshwater mussel *Westralunio carteri*.

The Dampierian Region in northern Western Australia includes the Kimberley and Pilbara areas, and is characterised by a number of camaenids, including the genus *Rhagada*. Previous authors have tended to include the Kimberley in a northern Australia unit with the Pilbara as a related area.

The Solanderian Region includes the northern part of the Northern Territory through eastern Queensland. The dominant snails are the camaenid genera *Bentosites* (= *Varohadra*) and *Xanthomelon*.

The Centralian Region covers the centre of the continent and almost all of South Australia. Characteristic genera include the camaenid genera *Sinumelon*, *Pleuroxia* and *Semotrachia* and the viviparid genus *Centrapala*. In Palm Valley, *Bothriembryon spenceri* is an important relict species.

The Oxleyan Region extends across south-eastern Queensland and north-eastern New South Wales. The dominant genera are *Meriodolum* (Camaenidae), *Hedleyella* and *Pedinogyra* (both Caryodidae).

The Peronian Region of south-eastern Australia, Victoria and Tasmania is characterised by charopids and hydrobiids.

Lord Howe Island and Norfolk Island both have largely endemic faunas which are quite distinct from those on the mainland and thus these islands could be regarded as separate regions also.

Whereas the recognition of provinces such as those outlined above may be a convenient way of viewing a fauna, there is a danger that they can be taken too seriously, with the assumption that they have real biological meaning. This they may have, but to date it has not been demonstrated rigorously. In fact, the utility of these non-marine provinces is probably not much greater than their somewhat discredited marine counterparts.

Doubts have been expressed about the concept and the division of Australia into zoogeographic regions. K.F. Walker (1981b) tested the distributions of freshwater mussels (Hyriidae) against the fluvifaunal provinces and concluded that the earlier literature considered 'faunal distributions only with a preconception of distinctive fluvifaunulae' and that 'the degree of overlap appears too great to warrant recognition of separate zoogeographic provinces'. He contended that 'authors apparently worked from the assumption that discrete fluvifaunulae do in fact occur, each assemblage having a geographic range more or less distinct from that of its neighbours. The selection of "characteristic" species on this basis provides spurious support for the concept as all members of the group must be considered'. Bishop (1981) pointed out the lack of published information on Australian zoogeographic patterns of terrestrial taxa, and suggested that obtaining data on phylogenetic relationships on a global basis within a family would be more fruitful.

Our lack of knowledge of Australian non-marine molluscs is amply illustrated by the monographic works on camaenid land snails in the Kimberley region of Western Australia by Solem

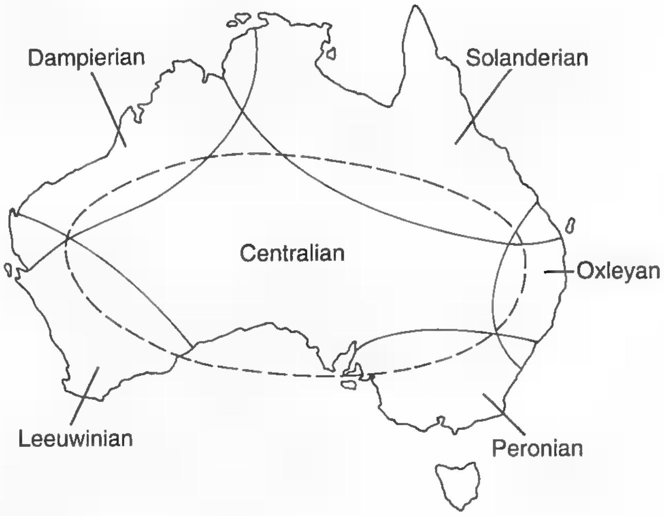


Figure 1.90 The six major faunal regions of Australia, with their transition zones. (After Smith, B.J. & Kershaw 1979) [I. Hallam]

Table 1.4 Freshwater mollusc families found in Australia. Those marked with an asterisk include at least one introduced taxon.

	Order	Family
Class Bivalvia		
Subclass Palaeoheterodonta	Unionoida	Hyriidae
Subclass Heterodonta	Veneroida	Sphaeriidae
		Corbiculidae
Class Gastropoda		
Superorder Neritopsina		Neritidae
Superorder Caenogastropoda	Architaenioglossa	Viviparidae*
	Sorbeoconcha	Thiaridae
		Hydrobiidae*
		Assimineidae
		Bithyniidae
		Pomatiopsidae
Superorder Heterobranchia	Pulmonata	Glacidorbidae
		Lymnaeidae*
		Planorbidae*
		Ancylidae
		Physidae*

(1979, 1981a, 1981b, 1984a, 1985, 1988a). In these papers, Solem monographed 139 species in 29 genera, of which 89 species (64%) and 12 genera were previously undescribed. He suggested in 1985 that only half of the living species had been described. Similarly, Ponder *et al.* (1993) described the freshwater snails of the *Beddomeia* group (Hydrobiidae); these include four genera and 67 species, of which 87% were new taxa, mostly Tasmanian.

The indigenous land and freshwater molluscan fauna of Australia comprises some 1020 described species – 224 freshwater and 796 terrestrial species (Smith, B.J. 1992 and subsequent papers to June 1995; see Table 1.7 in Conservation), excluding species from Lord Howe and Norfolk Islands. In addition there are 52 introduced taxa (Smith, B.J. 1992).

The Australian non-marine molluscan fauna is reasonably well known when contrasted with most other non-marine invertebrate groups, although B.J. Smith (1992) estimated that 30–40% of taxa, particularly small land snails, remain undescribed. A more likely estimate is about 50%, with the total non-marine fauna comprising around 2000 species. Most of the named freshwater species-group taxa (72% of 176) and the named terrestrial species-group taxa (81% of 642) are restricted to a single State or Territory.

The Freshwater Molluscan Fauna

An overview of the freshwater molluscan fauna by Walker is given under Molluscs of Inland Waters (this Chapter). The families represented, and their higher classification, are summarised in Table 1.4. Here we deal briefly with the taxonomic composition and biogeography of each family.

The Hyriidae are the most conspicuous of the bivalve families found in fresh water. They are rather well known taxonomically and show some interesting biogeographic patterns. To date this family has been the group of freshwater molluscs most commonly used for determining biogeographic patterns (see McMichael & Hiscock 1958; McMichael & Iredale 1959; Walker, K.F. 1981a). Hyriids are also found in South America, New Guinea and New Zealand. Triassic fossils are known from North America (Banarescu 1990) and Australia (McMichael 1957; Ludbrook 1961). Of the Australian genera, *Alathyria* (four Australian species), *Westralunio* (one Australian species) and *Velesunio* (four Australian species) are also found in Papua New Guinea, and *Cucumerunio* (one Australian species) and *Hyridella* (four Australian species) also occur in New Zealand. Only *Lortiella* (two species) is restricted to Australia.

The Corbiculidae are represented by a few large species living in mangroves and in brackish water, and some tropical Australian species also extend into fresh water. The only truly freshwater taxon is *Corbicula* found in rivers through much of mainland Australia, but not Tasmania. B.J. Smith (1992) recognised two species, but the taxonomy of the Australian species of *Corbicula* is greatly in need of revision. The genus is also found in Asia.

Members of the third bivalve family, the cosmopolitan Sphaeriidae, are found mainly in temperate Australia, including Tasmania, the Murray-Darling Basin, coastal Queensland (Kuiper 1983) and the Northern Territory (W.F. Ponder personal observations). The only modern review (Kuiper 1983) is based purely on shell characters and substantial changes to the existing taxonomy are likely following revision based on a wider suite of characters. Presently the Australian representatives of the family are thought to represent only two genera, both of which are cosmopolitan. There are seven species of *Pisidium* (one introduced); one species is in the subgenus *Afropisidium* which has a wide distribution outside Australia. The three species of *Sphaerium* are all currently included in the endemic subgenus *Sphaerinova*.

Only two or three species of the widespread family Neritidae occur in freshwater habitats in Australia. They are restricted to the near coastal reaches of rivers and streams in tropical north-eastern and northern Australia (Smith, B.J. 1992). Very little is known of their biology.

The Viviparidae are represented in Australia by at least six species in three indigenous genera (Smith, B.J. 1992). They are mainly associated with major river systems in the northern half of Australia and in the Murray-Darling system (Cotton 1935b, 1935c; Stoddart 1982; Smith, B.J. 1992; Sheldon & Walker 1993b). In addition, an introduced Chinese species has been recorded recently from the Sydney region (Shea 1994). No viviparids are known from Tasmania. Viviparids are found on all continents (Banarescu 1990) and, at the least, it is likely that the genera *Notopala* and *Larina* (?= *Centrapala*) are closely related to taxa in New Guinea and Asia.

The cerithioidean family, Thiaridae, is found throughout Asia, Africa, and the tropical Indo-Pacific islands. In Australia it is represented by five genera (*Brotia*, *Melanoides*, *Ripalania*, *Sermylasma* and *Thiara*) and several subgenera (Smith, B.J. 1992). This arrangement is tentative, as the taxonomy of the Australian members of this family is generally poorly understood. The group is most diverse in northern Australia, but *Thiara (Plotiopsis) balonnensis* is found in the Murray-Darling system and many large coastal rivers, and a similar species, *T. (P.) lirata* occurs in south-western Western Australian rivers. *Thiara amarula*, typical of the genus, occurs across northern Australia and is also found from East Africa and Madagascar to New Caledonia, Fiji and Samoa (Starmühlner 1976). At least one species, *Melanoides tuberculata*, has colonised other tropical areas successfully, including the southern United States of America. Like some other members of this family, it is parthenogenetic and ovoviviparous. It is not clear whether this species, found through much of tropical Australia, has become established in Australia or is native to the area. Other *Melanoides* species, members of the subgenus *Stenomelania*, are native to Australia; two species are found in Queensland, and another in northern New South Wales. According to the present classification (Smith, B.J. 1992), two endemic monotypic genera, *Ripalania* and *Sermylasma*, are confined to rivers in tropical eastern Queensland, and *Brotia (Pseudopotamis) supralirata* occurs on the Torres Strait islands.

Several rissooidean families live in inland waters – the Hydrobiidae, Assimineidae, Pomatiopsidae and Bithyniidae. The Hydrobiidae are by far the most diverse and the most speciose of all Australian freshwater molluscan families. This family is found mainly in south-eastern Australia but has also undergone significant radiations in artesian springs associated with the Great Artesian Basin (Ponder 1986b; Ponder *et al.* 1989; Ponder & Clark 1990) and on Lord Howe Island (Ponder 1982).

Two major hydrobiid groups are represented in Australia (Ponder 1992a). The *Hemistomia* group comprises several genera including *Fluvidona*, *Angrobia*, *Posticobia*, *Jardinella*, *Fonscochlea* and the estuarine *Tatea* which is related to faunas in New Zealand and New Caledonia. The *Beddomeia* group comprises the second major radiation and includes *Beddomeia*, *Phrantela*, *Nanocochlea* and *Victodrobia*; the last of these is found only in Victoria and the remainder occur in Tasmania (Ponder *et al.* 1993).

Within Tasmania, species of *Phrantela* and *Beddomeia* are restricted to the western and northern areas respectively, with the exception of one atypical species of *Beddomeia* found in the Franklin River drainage (Fig. 1.91). This group of genera has no obvious close relationship with any extralimital taxa. The genus *Ascorhis*, which is normally estuarine, was recorded from brackish temporary pools near Lake Eyre South (Ponder & Clark 1988) to which, presumably, it had been transported from the coast by birds. The Hydrobiidae are found in Europe, the Americas, northern and western Africa, Sulawesi, New Zealand, New Caledonia, New Guinea and on a few Pacific oceanic islands.

A New Zealand species, the parthenogenetic, ovoviviparous *Potamopyrgus antipodarum* (Ponder 1988), is widespread in disturbed areas in south-eastern Australia, and is probably now the commonest freshwater snail in south-eastern Australia, including Tasmania; it is also well established over much of Europe and, more recently, has been found in the United States of America. Hydrobiids often have very restricted distributions and can show high levels of genetic structuring in very small areas (Ponder *et al.* 1994).

The cosmopolitan Assimineidae occur mainly in the marine supralittoral, typically in estuarine habitats. The family is represented in fresh waters of south-western Australia by *Austroassiminea letha* (Solem *et al.* 1982), which is found in a few coastal springs and seepages, and by several unnamed taxa from springs in north-western Australia and the Northern Territory (W.F. Ponder personal observations).

The Pomatiopsidae have undergone major radiations in Asia (Davis, G.M. 1979 and subsequent papers) and are also found in the Americas and Africa. In Australia, this Gondwanan family is represented by only a single genus, *Coxiella*, which is confined to salt lakes and saline coastal lagoons and rivers over much of the mainland and, in Tasmania, to coastal ponds. *Tomichia* from southern Africa is a probable sister taxon to *Coxiella*; *Aquidauania* from South America is also related (Davis, G.M. 1979).

Species of the family Bithyniidae are found throughout much of the mainland, but not Tasmania. They are usually found in muddy pools, billabongs and slow, muddy streams or rivers. B.J. Smith (1992) listed only a single species (*Gabbia australis*) but several unnamed taxa are known from northern Australia (W.F. Ponder personal observations). The family is also found in Eurasia, Africa and India and parts of South-East Asia. The genus *Gabbia* is known from Australia and southern New Guinea; although Asian taxa are placed in this genus, according to Starobogatov (1970) they belong to different genera. At present the biogeographic and taxonomic relationships of the Australian taxa have not been determined and more definitive conclusions await further study.

Australian members of the family Stenothyridae are generally found in estuarine waters (Smith, B.J. 1992). However a few taxa occur in the lower reaches of tropical Australian rivers just upstream of brackish areas.

On the basis of our present understanding, it appears that most of the species in the freshwater pulmonate families have rather broad distributions. Members of the cosmopolitan family Lymnaeidae are widely distributed. *Austropeplea lessoni* ranges over much of the Australian mainland – although northern populations are sometimes regarded as a separate species, *Austropeplea vinosa* – and *A. tomentosa* occurs throughout south-eastern Australia and Tasmania into South Australia (Boray & McMichael 1961; Boray 1964; Smith, B.J. 1992). This species is also native to New Zealand (Boray & McMichael 1961; Climo & Pullan 1972). Fossils resembling *A. tomentosa* are known from New Zealand (Climo & Pullan 1972) and Australia (W.F. Ponder personal observations), and Australian and New Zealand populations are morphologically indistinguishable (Boray & McMichael 1961). However, it is unlikely that a freshwater species would maintain sufficient gene flow across the Tasman Sea for speciation not to have occurred so further studies are required to verify the relationships of the New Zealand and Australian populations. Several introduced species are recorded from Australia, four of which are well established (Boray 1978; Kershaw 1991; Smith, B.J. 1992); they include *Pseudosuccinea columella*, an intermediate host of liver fluke (Ponder 1975; Boray 1978),

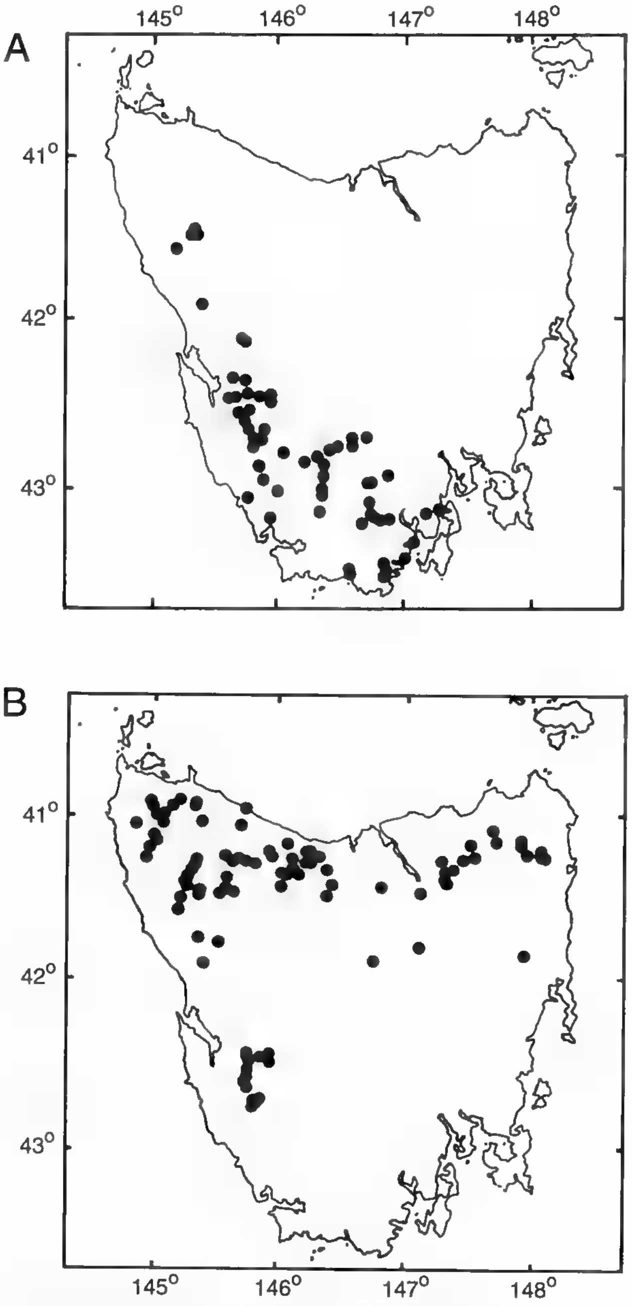


Figure 1.91 Distributions of two hydrobiid genera in Tasmania. A, records of *Phrantela* species. B, records of *Beddomeia* species. (After Ponder, Clark, Miller & Toluzzi 1993) [G. Ross]

Some lymnaeids have limited distributions, as shown by a few species in other parts of the world which have restricted distributions. The only known Australian example is an undescribed genus and species which appears to be restricted to limestone areas in the lower reaches of the Franklin River, south-western Tasmania (W.F. Ponder personal observations).

The cosmopolitan family, Planorbidae, is well represented in Australia by at least nine genera (Smith, B.J. 1992). *Planorbarius corneus* was imported as an aquarium animal and has become established in a few locations in Tasmania (Kershaw 1991; W.F. Ponder personal observations). The introduced and abundant *Physa acuta* (Physidae) is easily confused with species of *Glyptophysa*, with which it often occurs. Fossils attributed to *Glyptophysa*, *Syrioplanorbis* and *Gyraulus* are known from Miocene deposits in Australia (McMichael 1968; Ludbrook 1980; Walker, J.C. 1984). The species-level taxonomy of Australian planorbids is poorly understood as is evident from the listing by B.J. Smith (1992) of 85 available species names under *incertae sedis*.

J.C. Walker (1984) gave a detailed account of the biogeography of the non-planate planorbid genera. The genus *Isidorella*, with two species, is endemic and is found through much of the Australian mainland except coastal Queensland; the only possible near relative is *Protancylus* from Sulawesi. *Glyptophysa*, with several species, is found throughout Australia, including Tasmania, and is distributed through parts of South-East Asia, New Guinea, some Pacific islands, New Caledonia and New Zealand. A monotypic subgenus, *Oppletora*, is restricted to the north-west of Australia. One species of the endemic genus *Bayardella* occurs in the north-west of the mainland, and another mainly in the east. The Tasmanian endemic genus *Ancylastrum* is limpet-shaped but is closely related to *Glyptophysa*. Two species of *Amerianna* occur in northern Australia and the genus is distributed through New Guinea and the Philippines, with a few records in Thailand and Indonesia where it is probably introduced. Walker concluded that *Isidorella* and *Bayardella* are Gondwanan elements. *Glyptophysa* may also be Gondwanan, and this genus may have spread north more recently; whereas *Glyptophysa* may share a common ancestry with *Ancylastrum* and *Oppletora*, the origin of *Amerianna* is uncertain but may have been to the north of Australia. Of the planate genera, *Gyraulus* is cosmopolitan, *Helicorbis* occurs through much of Asia and the Pacific islands and *Pygmanisus* is endemic to the southern half of Australia, including Tasmania.

The Ancylidae are also virtually cosmopolitan but poorly known in Australia. The only revision, that of Hubendick (1967), was based on a small amount of material and only shell characters were used. Hubendick recognised two widespread Australian species groups but did not refine the taxonomy further. Currently the two recognised Australian species are included in a subgenus (*Pettancylus*) of *Ferrissia*, a genus distributed through North and Central America, Africa, South-East Asia and the Pacific islands; the subgenus also has a Pacific distribution (Hubendick 1967). A supposedly endemic genus and species, *Stimulator consetti*, is restricted to north-western Australia. Ponder (1981a) recorded an unidentified ancylid from Lord Howe Island.

The Glacidorbidae (Ponder 1986a) are known from Australia, Chile and South America (one species in the genus *Gondwanorbis*; Meier-Brook & Smith 1975; Ponder 1986a; Starobogatov 1988). In Australia, species of *Glacidorbis* occur in Tasmania, south-western Australia and in the south-east, extending north to southern Queensland. The genus is known also as a Miocene fossil, from South Australia (Buonaiuto in Bunn & Stoddart 1983). A single specimen of an undescribed species probably belonging to this family is also known from New Caledonia (W.F. Ponder personal observations). The distribution of this family suggests it is Gondwanan and that the family might also be expected to occur in New Zealand, but to date it has not been found there. Currently there are four named species from Australia, all included in *Glacidorbis*, but several unnamed species are known from Tasmania and the south-eastern Australian mainland.

The freshwater molluscs of Australia show patterns of distribution which reflect their history, and the history of climatic change, as well as their ability to disperse and to withstand drought. Major elements of the fauna are endemic and, at least, are probably of Gondwanan origin. Some taxa, particularly hydrobiids, thiarids and many of the pulmonates are unable to withstand drying, particularly if it is prolonged. These groups are thus confined largely to permanent water in the eastern and south-eastern drainages of the mainland and Tasmania or are associated with large rivers or artesian springs. Their distributions are often a reflection of geomorphological and climatic history.

Some taxa can survive prolonged drying, for example, under experimental conditions, 25% of *Gabbia australis* specimens survived after being dried for 203 days (McKay 1926) and some hyriids survive for very long periods in dried mud or soil, or even in air (McMichael & Iredale 1959). Other taxa may be good dispersers, living in habitats frequented by birds and adopting behaviour that makes accidental dispersal more likely. Aerial transportation of molluscs has been reviewed by Rees (1965), but none has been documented in Australia. Dispersal of glochidia larvae by their fish hosts is a factor in the distribution of hyriid mussels. Floods, cyclonic storms, and humans and stock also aid dispersal. Taxa that combine good dispersal capability with means of avoiding desiccation often have wide ranges over inland Australia.

The existence of only two species of Hyriidae in Tasmania, confined to only a single river system, is unexplained, especially as this group was present in Australia as early as the Triassic (McMichael 1957; Ludbrook 1961). Tasmania entirely lacks representatives of several families that occur on the mainland – Corbiculidae, Viviparidae, Bithyniidae and Thiaridae. However, all of these families have a predominantly tropical distribution, with high diversity in South-East Asia so their absence from Tasmania may simply be the result of climatic constraints, or their inability to cross Bass Strait, even during times of low sea-level coupled with glacial conditions. Their origin in Australia probably dates from contact of the Australian and Sunda Plates during the Tertiary. They are probably not Gondwanan, as suggested by the lack of these groups in New Caledonia (with the exception of Thiaridae and estuarine corbiculids) or in New Zealand.

One of the more unexpected aspects of Australian freshwater mollusc zoogeography is the absence of the Melanopsidae – an ancient cerithiodian family with freshwater members found in the Mediterranean area, New Caledonia and New Zealand. Australia also lacks radiations of freshwater taxa in families such as Stenothyridae and Neritidae, although these occur in brackish water in estuaries and mangroves. The lack of a conspicuous freshwater neritid fauna in particular is surprising given that they are common in New Guinea, the Pacific islands and throughout South-East Asia. Their presence on relatively recent Pacific islands suggests that they are capable of effective dispersal – so why have only two or three species reached the rivers of the tropical north? Possible explanations include historical accident, unfavourable physical conditions for dispersal, and major drying events with extinction of much of the endemic freshwater fauna in the northern rivers. There are several endemic freshwater fishes (several rainbow fish and gobies, Allen, G.R. 1989) in these drainages, but little is known of most of the invertebrate groups.

Analysis of the hydrobiid genus *Jardinella* suggests that the three closely related species found in coastal drainages are derived from a western radiation (Ponder 1991). If these river systems had been in continuous existence during the last few million years one might expect to see greater diversity and endemicity in groups such as Hydrobiidae.

Presently the analysis of freshwater mollusc biogeography in Australia is hampered by poorly resolved taxonomy and lack of detailed distributional data for many taxa. Given the current rapid changes to our freshwater ecosystems, with evidence that taxa have recently disappeared from some areas, it is essential that such work be undertaken urgently.

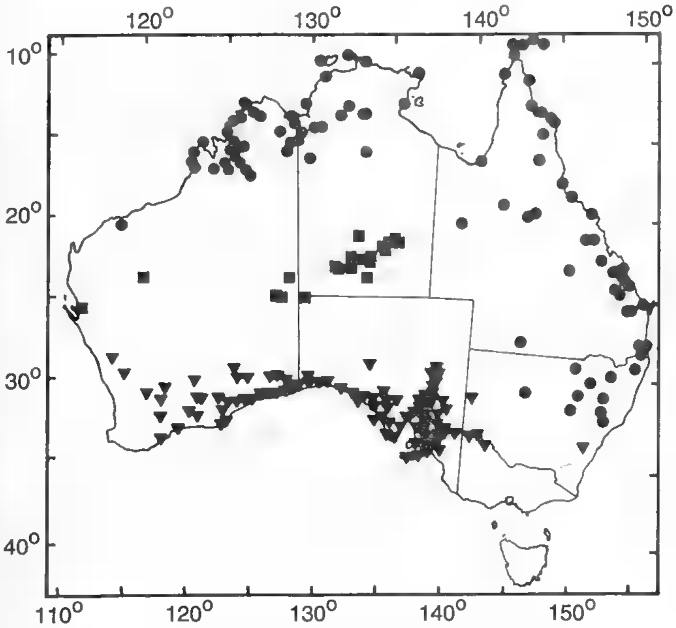


Figure 1.92 Distribution of three widespread species of *Pupoides* (Pupillidae) in Australia. ▼, *Pupoides adelaidae*; ■, *Pupoides beltjanus*; ●, *Pupoides pacificus*. (After Solem 1991) [A. Solem]

The Terrestrial Molluscan Fauna

It is not yet possible to make definitive statements concerning the biogeography of Australian land snails. Most of the basic survey work needed to provide raw distributional data has not yet been accomplished. 'Species' and 'genera' in many groups are recognised as artificial pigeon holes that do not reflect phylogeny, and the critical intercontinental comparative studies to determine genus and family category affinities are still needed. On the simplest distributional levels, major changes in knowledge can be anticipated. For example, two genera previously considered to be restricted to Queensland-northern New South Wales, *Glyptopupoides* and *Georissa*, were found recently in the Kimberley region of Western Australia (Solem 1988c).

Study by J. Stanisic of the spectacular radiation of charopid land snails from the tropical to temperate rain forest patches in Queensland and New South Wales is less advanced than work on camaenids (Stanisic 1990), but he has collected more than 200 species in the last few years. In all, 347 species of indigenous land snails have been described from eastern Australia (Stanisic 1994). Based on material in the Queensland Museum collections, a further 325 species in 16 families are unnamed as yet (Stanisic 1994); most of these are charopids (200), helicarionids (40) and camaenids (35). Based on these data, a total land snail fauna for Australia of 1200 to 1500 native species is a conservative estimate.

Several other families have also radiated extensively, among them the Punctidae, Bulimulidae and Helicarionidae; species and higher level revisions are needed to determine the full extent and directions of their diversification. Perhaps the most poorly known family is the Succineidae. Iredale (1937a) described two new genera and listed 13 species; *Arborcinea* is based on aestivating juvenile specimens, and *Austrosuccinea* has been synonymised with the worldwide genus *Succinea* (see Patterson 1971). None of the Australian species names has been characterised well enough that a series of populations can be grouped, assigned a meaningful range, and separated from other named forms, despite the fact that succineids have been collected in most parts of Australia.

Because of the limitations outlined above, only a 'broad brush' outline of land snail distribution and diversity can be presented. Of the 37 families of land snails and slugs recorded from Australia, 23 contain native species only, and 14 are represented only by introduced taxa (Table 1.5); the Enidae, Subulinidae and Helicarionidae include both native and introduced species.

The introduced taxa are largely synanthropic (associated with humans), restricted to cities, gardens, and field crop areas, where some become major nuisances, if not actual pests. A few species, such as the subulinid *Lamellaxis clavulinus*, several European slugs and the helicid *Theba pisana* have become feral with great success. Fortunately, these are the exceptions, rather than the rule. Their distributions within Australia today reflect the whims of history and commerce, temperature and humidity barriers and patterns of cultivation (Solem 1989).

The native taxa show a variety of distributions that can be clustered, in part at the family level, in part at the generic level. These clusters represent current restrictions of moisture, and thus ranges, during the currently arid period in which we live.

The largest number of families show northern tropical origins. These are mostly Indonesian-Polynesian groups that barely enter the wet coastal margin of Australia. There are a few records of the cyclophorid genus *Leptopoma* in northern Queensland, and recently the Indonesian *L. minus* has been found on Melville Island and the Cobourg Peninsula in the Northern Territory. The Trochomorphidae, which occur from South-East Asia to Tahiti are represented by *Trochomorpha melvillensis* on Melville Island (Solem 1988c) and *Amphidromus cognatus* from the same area. Solem (1983b) recorded a South-East Asian-Indonesian genus of Camaenidae as an Australian resident.

The charopid, *Pilsbrycharopa tumidus*, which belongs to an Indonesian-New Guinean complex, occurs further inland in the Fitzroy River, southern Kimberley (Solem 1988c). More arid areas have their own special taxa. Separate species of the South-East Asian pupilloid genus *Gyliotrachela* occur at Chillagoe Caves, Queensland, the Daly River area of the Northern Territory and both the Napier and Ningbing Ranges in Western Australia. Records of the hydrocenid genus *Georissa*, which occurs from India to Hawaii, are scattered from northern New South Wales to mid-Queensland; an isolated species occurs in the Ningbing Ranges of Western Australia.

The pupillid *Gastrocopta recondita* occurs on various Indonesian islands and as well as on an inland Kimberley range. Another member of the genus, *G. macrodon*, has been recorded from Milne Bay and the Louisiade Archipelago, Papua New Guinea, plus wetter parts of the Kimberley (Solem 1988c), but not from Queensland and the Northern Territory.

Some species known from Indonesia range more extensively into Australia. Both *Stenopylis coarctata* (Helicodiscidae) and *Discocharopa aperta* (Charopidae) occur in the Pilbara and central Australia. The helicarionids *Wilhelminaia mathildae*, *Coneuplecta calculosa*, *Coneuplecta microconus* and *Liardetia scandens* (an endemic), and the genera *Pleuropoma* (Helicinidae) and *Nesopupa* (Pupillidae) all occur inland of the Kimberley, Western Australia-Northern Territory-Queensland coast.

The above situations represent single species or taxa of low diversity with general northern Australian distributions. Other Indonesian-Melanesian taxa have crossed only at Torres Strait. The Diplommatinidae are represented by some seven species; the Pupinidae by 29 species in several genera; the Rathouisiidae by probably two species; and the Athoracophoridae by at most a few species in coastal Queensland and New South Wales; all are largely confined to the east-coast rainforests (Stanisic 1994). Most of the above genera reach a common southern limit of distribution in the Clarence River-Richmond River-Dorrigo area of north-eastern New South Wales.

Much more successful immigrants are members of the subfamily Camaeninae (Camaenidae). In both shell size and species numbers, this group dominates the land snails of the Great Dividing Range and adjacent hills, extending from Torres Strait to southern New South Wales, then with a western shift into the Flinders Ranges, Gawler Ranges, and Eyre Peninsula of South Australia, where a radiation into several genera has occurred (Solem 1992a).

Two essentially tropical Pacific groups require special comment. The Achatinellidae are basically a Polynesian group today, with a few small-sized species widely distributed by commerce. Australian records extend from Sydney north to Torres Strait and then west through the Northern Territory and wetter parts of the Kimberley of Western Australia. We do not know how much of this represents passive transport on plants, the true identity of the Australian populations, or even the proper generic classification for these few species. The taxonomy of the so-called Helicarionidae of Australia is in disarray. There are several wet forest endemics from Queensland to Tasmania, especially the 'semi-slugs' of the *Helicarion* group, but neither species nor generic limits have been established for the northern taxa, although R. Kershaw has clarified the status of several southern taxa. These Indonesian taxa in northern Australia provide evidence of habitat expansion. Similar radiations are seen in the dry country of the Kimberley, Western Australia and Northern Territory (*Westracystis*) and Gawler-Flinders Ranges (identity uncertain) taxa.

The taxa discussed previously have been characterised by relatively clear indications of northern origins and affinities, basically northern or eastern 'wet areas' distributions, and mostly low diversity (Pupinidae and Helicarionidae have moderate diversity). However, the origin and affinities of a few families provide unsolved puzzles.

The Cystopeltidae, occurring from southern Queensland to Tasmania, and comprising a few species, have not been allied convincingly to any other land snail family. The mid- to southern Queensland monotypic genus *Coelocion* is placed in the Megaspiridae together with the living species of *Megaspira* from southern Brazil and fossils from the Paris Basin Eocene; the little known New Guinea genus *Perrieria* may not be related.

The only native species of Enidae, *Amimopina macleayi*, from the northern fringes of Australia, is related to central and South African enids, rather than to the genera living today in India, South-East Asia, or Indonesia. The two species of *Eremopeas*, which range from the Timor Sea and Torres Strait south to the Pilbara, George Gill Range in central Australia, and Claude, New South Wales, cannot be allied at present to extralimital members of the Subulinidae.

The Pupillidae are basically a worldwide group with many species showing substantial ranges within Australia (Fig. 1.92). No anatomical studies have been completed, and the relationships of the Australian *Pupilla*, *Pupoides* and *Gastrocopta* are unknown.

Six further families – Caryodidae, Rhytididae, Punctidae (= Laomidae), Charopidae (= Flammulinidae), Bulimulidae (= Bothriembryonidae) and Camaenidae (= Hadridae, Papuinidae, Chloritidae, Xanthomelontidae and Rhagadidae) – are discussed in approximate order of increasing diversity. All represent significant faunal elements.

The Caryodidae, which Iredale (1937b: 14–19) split into four families, are part of the Gondwanan acavoid complex, which includes taxa from South Africa and Namibia, Madagascar, Mascarene Islands, Seychelles, Sri Lanka, mid-Queensland to Tasmania, and much of South America. Members of each of the several Australian genera are very different from each other in shape and size, and are well differentiated anatomically. Whether they should be maintained as an Australian endemic family or combined on a family level with some of the extralimital taxa remains to be determined. The caryodids form an old Australian group confined to wet forest litter along the east coast, with limited species diversity (13 species; Smith, B.J. 1992).

The Rhytididae (= Paryphantidae) show moderate diversity in areas of South Africa, Seychelles, Mascarene Islands, northern Queensland to Tasmania, New Caledonia, and New Zealand diversity. A few species are known from the Mount Lofty Ranges, South Australia, one from near Pemberton, Western Australia, and there are a few possible relatives from Indonesia to Samoa. No modern revision of inter-area affinities exists. The group may be polyphyletic: homoplasious features associated with adaptation for carnivory may have been mistakenly interpreted as evidence of common ancestry. In Australia, the family occurs mainly in the southern areas and is not very diverse.

The Bulimulidae (= Bothryembrionidae) are primarily a Neotropical family, numbering about 1000 species. There are two Old World centres of diversity: Melanesia to New Zealand, and Western Australia. The *Placostylus* complex is diverse in the Solomon Islands and on the main island of Fiji. Two species are known from New Caledonia and a few species are recorded from Lord Howe Island, Vanuatu (= New Hebrides), and the northern tip of New Zealand. Some apparently more generalised taxa restricted to Vanuatu are anatomically similar to the members of the Australian radiation, the *Bothriembryon* complex.

The last near-comprehensive revision of *Bothriembryon* (Iredale 1939) used only shell features. Intensive field surveys in Western Australia have revealed about 55 species (Solem unpublished data), which range from the Pilbara, south to Cape Leeuwin and then east into South Australia. A few endemic species fringe the Eyre Peninsula and Kangaroo Island, and one species, *B. tasmanicus*, lives along the east coast to Tasmania. Three colonies are known of a remarkable isolated relict, *Bothriembryon spenceri*, in central Australia. No phylogenetic hypotheses have been presented for the family, although the bulimulid distributions suggest intriguing problems for investigation.

The family Punctidae occurs worldwide, with major centres of diversity in New Zealand and south-eastern Australia. A few species live in South Australia, and the humid south-western corner of Western Australia; there are isolated montane records in Queensland and New Guinea, and several species live on Lord Howe and Norfolk Islands. The fauna comprises several hundred species, but nothing can be said about generic clusters or species ranges.

Table 1.5 Land snail families found in Australia.

Class and ordinal groups	Native Families	Introduced Families
Class Gastropoda		
Superorder Neritopsina	Hydrocenidae	
	Helicinidae	
Order Architaenioglossa	Cyclophoridae	
	Diplommatinidae	
	Pupinidae	
Order Pulmonata		
Suborder Systellommatophora	Rathouisiidae	Veronicellidae
Suborder Eupulmonata	Achatinellidae	Cionellidae
	Pupillidae	Pleurodiscidae
	(+Vertiginidae,	Enidae
	Chondrinidae)	Valloniidae
	Enidae	Subulinidae
	Caryodidae	Ferussaciidae
	Subulinidae	Achatinidae
	Megaspiridae	Streptaxidae
	Rhytididae	Arionidae
	Bulimulidae	Zonitidae
	Helicodiscidae	Limacidae
	Punctidae	Helicarionidae
	Charopidae	Milacidae
	Helicarionidae	Testacellidae
	Succineidae	Bradybaenidae
	Athoracophoridae	Helicidae
	Cystopeltidae	
	Trochomorphidae	
	Camaenidae	

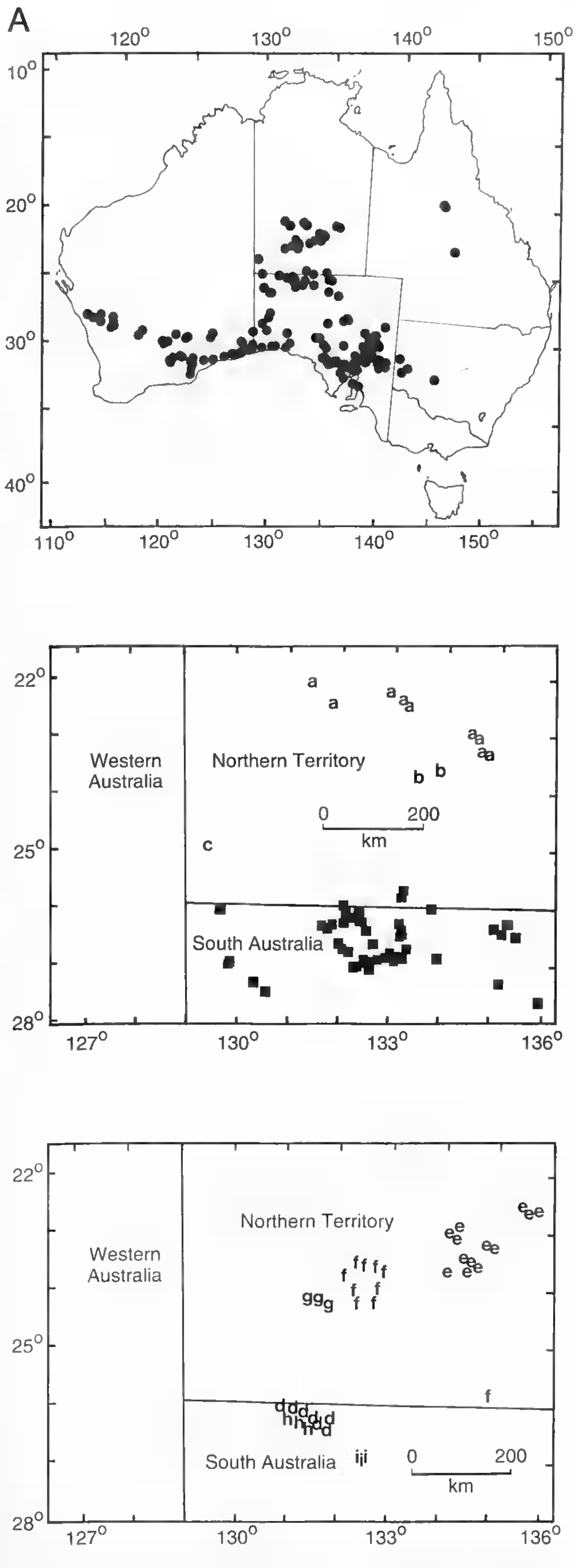


Figure 1.93 Distribution patterns in the camaenid genus *Sinumelon* (Camaenidae). **A**, overall distribution of all Australian species, based on 653 records. **B**, **C**, the northern records of the widespread species *S. pedasum* (squares) and the very limited ranges of nine other species in the same region of Central Australia. **a**, *S. perinflatum*; **b**, *S. bednalli*; **c**, *S. hullanum*; **d**, *S. amatensis*; **e**, *S. dulcensis*; **f**, *S. expositum*; **g**, *S. gillensis*; **h**, *S. musgravesi*; **i**, *S. pumilio*. (After Solem 1993) [G. Ross]

The Charopidae show an extensive Polynesian-Micronesian radiation (Solem 1983a). Species diversity is high in New Caledonia, New Zealand, Tasmania, Victoria, New South Wales, parts of Queensland and South Africa, and there are less extensive radiations in South America, Lord Howe Island, Norfolk Island, and the humid south-west of Western Australia (Solem unpublished). Stanisic (1990) demonstrated the diverse affinities of a number of subtropical east coast taxa. In general, shell and anatomical features were similar to those of New Zealand species. However, *Sinployea intensa* was shown to be a remnant of a large Pacific radiation and the mainly Pacific Basin-North American subfamily Rotadiscinae was recorded for the first time. A more comprehensive understanding of biogeography is dependent on the clarification of several hundred more species in the Australian-New Zealand fauna.

The Camaenidae are somewhat better known. This complex family arose from an early to mid-Tertiary immigrant from Indonesia-New Guinea, undoubtedly in several colonisation waves. In the Cretaceous, camaenids were present in both Utah, United States of America and central China. The extant New World distribution is from Cuba through the Lesser Antilles and from Costa Rica south into Amazonian Peru, substantially south of the Mesozoic distribution. In the Old World, camaenids range from Japan and China through Indonesia and New Guinea into the Solomon Islands, and then over much of Australia. B. Scott (1996) reassessed the family, and restricted the Camaenidae to only the Asian and Australian taxa.

No camaenids are known from Tasmania, much of Victoria, or the humid south-west corner of Western Australia. Because of pre-adaptation to a long dry season, during which the snails aestivate, they do very well in semi-arid regions. They are unique among the Australian biota in that one subfamily, the Sinumeloninae, has its centre of diversity in central Australia, with secondarily derived taxa in the Gawler-Flinders Ranges, on the Nullarbor, and along the west coast of Western Australia.

In summary, except for the Pupinidae and Helicarionidae, most families are derived through or via South-East Asia and are found along the wetter northern and eastern margins of Australia. These families show very low levels of diversity. The Cystopeltidae, Megaspiridae, native Enidae and native Subulinidae are relicts with limited Australian ranges and are of unresolved affinity. The Pupillidae show a low level of speciation, and taxa generally have wide ranges; their origin(s) is(are) unknown. Five families, Caryodidae, Bulimulidae, Rhytididae, Punctidae and Charopidae, show southern continent affinities and may have been involved in plate tectonic dispersions. The most speciose of Australian land snail families, the Camaenidae, appears to be a post-Miocene colonist from the north.

Two additional aspects of Australian land snail biogeography require brief mention. First, extensive geographic ranges are very unusual for Australian land snail species and genera, probably because of limited dispersal (*cf.* Molluscs on Land, this Chapter). Those of the Pupillidae (Fig. 1.92) and some species in the camaenid genus *Sinumelon* (Fig. 1.93A, B) are exceptions; other species of *Sinumelon* have very restricted ranges (Fig. 1.93C). The median linear species range for all Australian land snails is probably less than 40 km. The ranges of 29 camaenid species found in the Ningbing Ranges, in the Kimberley region of Western Australia (Solem 1988a), are 0.1–7 km (median 1.65 km) in length and 0.01–7.45 km^2 (median 0.825 km^2) in area; most are allopatric. A sample distribution of the short species ranges found in this radiation is given in Figure 1.94.

High levels of sympatry are found only in a very few places. In the areas between Dorrigo, New South Wales and Rockhampton, Queensland, J. Stanisic has found that up to 30 species of land snails may occur in patches of wet rainforest, but drier vegetation patches, such as vine thicket, may contain 40 to 45 species. The species diversity decreases in the less favourable country between Rockhampton and Mackay. Between Mackay and Proserpine, the diversity rises again to 30 to 35 species, but with fewer charopids,

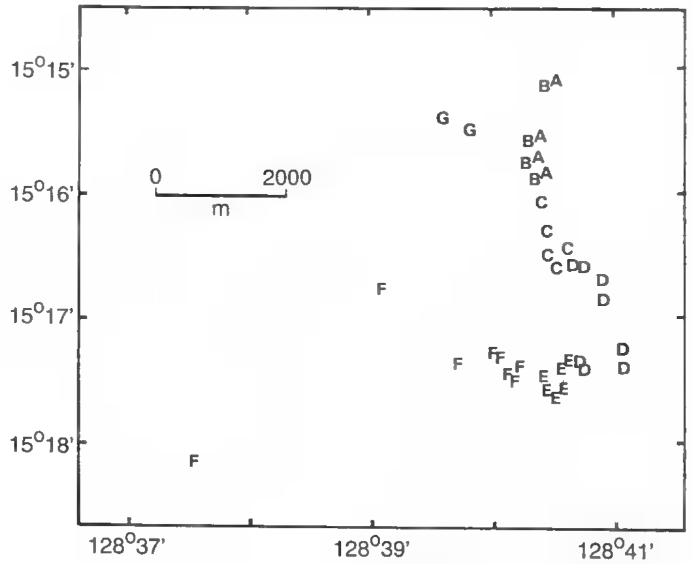


Figure 1.94 The restricted ranges of endemic camaenid species in the South Ningbing Ranges, north of Kununurra, Western Australia. **A**, *Cristilabrum simplex*. **B**, *Cristilabrum buryillum*. **C**, *Cristilabrum monodon*. **D**, *Cristilabrum primum*. **E**, *Cristilabrum grossum*. **F**, *Cristilabrum bubulum*. **G**, an undescribed *Cristilabrum* species. (After Solem 1988a) [G. Ross]

more camaenids, and the appearance of several pupininds. By Townsville, species numbers drop to 10 to 15, a level which continues north to Cape York, with the exception of some of the foothills and highlands of the Ingham-Cooktown rainforest massif, as described by Stanisic (1994).

In the Kimberley and Northern Territory north of the Roper River, rain forest patches have a mean diversity of 12.5 species/patch with a maximum of 18 to 20 species. In central Australia, species diversity rarely reaches ten. Although finding even six land snail species in one place over most of the rest of Australia is very unusual, reasonably high diversities are also found in some parts of Victoria, southern and mid-New South Wales, Lord Howe Island, Norfolk Island and Tasmania.

Thus the land snail diversity in Australia is derived from vicariance of a few groups, comprises species with very limited ranges, and shows high levels of sympatry in restricted areas of the continent.

THE FOSSIL RECORD

Because of the hard shell deposited by and housing most molluscs they have an excellent fossil record and are represented in Australia in each geological period during the 550 million years from Early Cambrian to the present day. Extensive marine transgressions through geological time over large parts of the Australian plate provided conditions suitable for deposition of fossils. Sedimentary basins so formed are shown in Figure 1.95, and timing and extent of the major transgressions are shown in Figure 1.96.

Documentation of the fauna, however, is less than adequate. Fossil molluscs which occur in all Australian States and territories, mostly represent marine species of all life habits and from most marine habitats, but only a few freshwater and terrestrial molluscs have been found. All molluscan classes are represented in the Australian fossil record, in relative proportions similar to those for the whole world (Sepkoski 1981).

Molluscan shells are commonly preserved as the original shell material, replaced by some other mineral, as extremely thin and faithful overgrowths or as a void within rock matrix. Soft tissues are preserved exceptionally rarely but muscle and ligament attachment sites and pallial lines on shells give some clues to soft anatomy. In many Tertiary limestones only calcitic molluscs such as oysters and scallops are preserved while aragonitic shells (for example, most gastropods) are not preserved.

Australian molluscs are referable to three major fossil faunas (Sepkoski & Sheehan 1983) – the Cambrian, the Palaeozoic and the 'modern' (or Mesozoic-Cainozoic). The extinction event at the close of the Permian is clearly represented while major diversifications are evident in the early Palaeozoic and at the late Cretaceous-early Tertiary.

The cratonic and intracratonic Perth, Carnarvon, Canning, Bonaparte, Daly and Georgina Basins of the Palaeozoic and Great Artesian Basin of the Mesozoic contain rich fossil faunas often dominated by molluscs. Eastern Australia including Tasmania was a geosynclinal – tectonically active – area during the Palaeozoic. Sedimentary piles on various shallow-water shelves around small land masses or volcanic arcs entombed many rich molluscan faunas. These are found in nearshore and shelf mudstones, sandstones and limestones. Rocky bottom or shoreline environments are deduced for some molluscs, such as the Permian genus *Eurydesma* (Runnegar 1979), but the only molluscs reported in deep-water environments are the few cephalopods from the graptolite shales of Victoria (Thomas & Teichert 1947; Vandenberg & Stewart 1983). The only records of freshwater molluscs are of unionid bivalves from non-marine Mesozoic basins in association with rich plant assemblages (Jack & Etheridge 1892; McMichael 1957; Ludbrook 1961; Jell & Duncan 1986).

In general, limestone faunas of the Palaeozoic have been more extensively and better studied than those of other periods because of the preservation of original shell and because latex casting techniques, facilitating study of the external moulds of many earlier fossils, only became widely used in the 1960s. Eastern Australian faunas are better known than cratonic faunas of central and western Australia, because of their proximity to centres of population.

Despite advances in many areas of specimen preparation and the high numbers of professional palaeontologists working in Australia during the last 50 years, numerous collections of undescribed and unstudied molluscs remain in museum and university collections; several postgraduate theses on fossil molluscan faunas completed during these years have yet to be published. A conservative estimate suggests that at least 50% of the fossil Mollusc fauna, particularly gastropods and bivalves, of the Palaeozoic and Mesozoic of Australia remains to be documented. The cephalopods are the best studied group because of their biostratigraphic importance from the Devonian to the Cretaceous, and probably 80–90% of species have been described. As noted below, the classes Monoplacophora, Rostroconchia, Scaphopoda and Polyplacophora are known in the fossil record but fossil forms are comparatively rare.

Most marine Tertiary rocks occur in the southern part of Australia in a series of continental basins in which shelf sediments are preserved. From west to east, these are the Bremer, Eucla, St Vincent, Otway, Bass and Gippsland Basins. There are no occurrences of deep-water deposits from the slope or ocean basins. Deposits of very shallow, subtidal origin are rare. Other factors that contribute to the absence of a fossil record are poor outcrop or lack of suitable sediments. For instance, molluscs are not found in the carbonaceous sands of shallow water origin common in the Eocene and Oligocene.

Early Tertiary sedimentation occurred in southern and western coastal basins from the Carnarvon Basin in the west to the Gippsland Basin of eastern Victoria. It continued in most of these basins up to the Pliocene, though local or basinal breaks in sedimentation are apparent in most areas.

The best preserved and most diverse faunas are known from the neritic marls and clays of the Late Oligocene to Middle Miocene. Faunas of shallow water sands and clays are more common in the Late Miocene through to Pleistocene. Fossil remains of rocky bottom dwellers such as chitons, *Haliotis* species, limpets and some trochids and turbinids are known from only a few localities and often are not well preserved. Molluscan biostratigraphy, biogeography and the nature of the Tertiary record have been summarised by Darragh (1985).

The adaptive radiation that produced the wide variety of modern molluscan forms and that allowed exploitation of the wide variety of habitats they now occupy began in or before the Early Cambrian. This has been outlined by Runnegar & Pojeta (1974, 1985) and Runnegar (1983) and is reflected in the broad range of morphologies shown in Figure 1.97. Although the unravelling of this story has relied on material from many parts of the world, a significant part was deduced from studies of Australian Palaeozoic molluscs (for example, Runnegar & Jell 1976; Pojeta, Gilbert-Tomlinson & Shergold 1977; Bengtson, Conway Morris, Cooper, Jell & Runnegar 1990). The most comprehensive account of the fossil history of the Mollusca is given in the *Treatise on Invertebrate Paleontology* Parts I–N (Moore 1957, 1960, 1964, 1969, 1971). Part J, which will describe most of the gastropods (other than 'archaeogastropods' in Part I) and Part M (Coleoidea) are still in preparation; Pojeta, Runnegar, Peel & Gordon (1987) provided a more recent account of the fossil history of the Phylum.

Palaeozoic Era

Cambrian Period. The low diversity fauna of this Period includes one of the world's earliest known bivalves, *Pojetaia runnegari* (Fig. 1.97R), which occurs in the South Australian Lower Cambrian (Jell 1980). Runnegar & Bentley (1983) interpreted it as having evolved from a laterally compressed monoplacophoran and to have given rise to the praenuculid palaeotaxodonts (Protobranchia). The bivalved *Pseudomyona* (Fig. 1.97P, Q) from the Middle Cambrian of Queensland, along with *Taurangia*, from New Zealand is considered to be a separate evolutionary offshoot from the Monoplacophora, and has no association with the Bivalvia. Development of this group of bivalved monoplacophorans is paralleled several hundred million years later by the Recent development of a bivalved group of the Gastropoda (Runnegar 1983). More than 20 genera of untorted, low to high, conical shells, including *Latouchella* (Fig. 1.97H–L), *Anabarella* (Fig. 1.97E), *Mellopegma*, *Stenotheca*, *Vallatotheca*, *Tanuella*, *Helcionella* (Fig. 1.97F, G) and *Coreospira*, are referred to the Monoplacophora (Runnegar & Jell 1976). The prominent snorkel of *Yochelcionella* (Fig. 1.97B–D) and *Eotebenna* (Fig. 1.97A) is diagnostic for the Yochelcionellidae (Runnegar & Jell 1976). Low limpet-shaped forms are thought to have given rise to the tailed forms of Helcionelloidea and coiled Bellerophontida (Runnegar & Pojeta 1985). Molluscs are common in the Lower Cambrian of the Flinders Ranges, Amadeus Basin and Gnalta Shelf and in the early Middle Cambrian of the Georgina and Daly Basins. Numerous monoplacophorans occur in the Upper Cambrian fauna of the Georgina and Amadeus Basins (Öpik 1967; Pojeta & Gilbert-Tomlinson 1977).

Runnegar & Pojeta (1985) suggested that the Gastropoda originated in the Precambrian, but the first Australian gastropod fossils appear in the Lower Cambrian, from which *Yuwenia bentleyi* (Fig. 1.97U) and *Beshtashella tortilis* (Fig. 1.97T) are recorded (Runnegar 1981; Bengtson *et al.* 1990); thereafter they are rare through the rest of the Period. *Pelagiella* (Fig. 1.97S) is a common Cambrian genus often considered to belong in the Gastropoda but it is now assigned to the Order Pelagiellida of the Monoplacophora, following Runnegar & Pojeta (1985). Similarly, the Bellerophontida have generally been considered gastropods; the alternative now suggested is that they are an

Figure 1.95 The major sedimentary basins of Australia. The boundary of the Great Artesian Basin is highlighted with dots; boundaries of most of its component basins have been omitted. **ada**, Adavale Basin; **ama**, Amadeus Basin; **bas**, Bass Basin; **bon**, Bonaparte Basin; **bow**, Bowen Basin; **brm**, Bremer Basin; **can**, Canning Basin; **cap**, Carpentaria Basin, most beneath Karumba Basin; **car**, Carnarvon Basin; **cla**, Clarence-Moreton Basin; **coo**, Cooper Basin; **dal**, Daly Basin; **ero**, Eromanga Basin; **euc**, Eucla Basin; **eyr**, Eyre Peninsula Basin; **fli**, Flinders Ranges; **gal**, Galilee Basin; **geo**, Georgina Basin; **gip**, Gippsland Basin; **gna**, Gnalta Shelf; **kar**, Karumba Basin; **lau**, Laura Basin; **mar**, Maryborough Basin; **mca**, McArthur Basin; **mur**, Murray Basin; **nga**, Ngalia Basin; **off**, Officer Basin; **ord**, Ord Basin; **otw**, Otway Basin; **per**, Perth Basin; **pir**, Pirie-Torrens Basin; **pop**, Port Phillip Basin; **stv**, St Vincent Basins; **sur**, Surat Basin; **syd**, Sydney Basin; **tas**, Tasmanian Basin; **vic**, Victoria River Basin; **wes**, Westernport Basin; **wil**, Willochra and Walloway Basins; **wis**, Wiso Basin; shading indicates hard rock formations. (After Paine 1980; AGSO 1994) [C. Eadie]

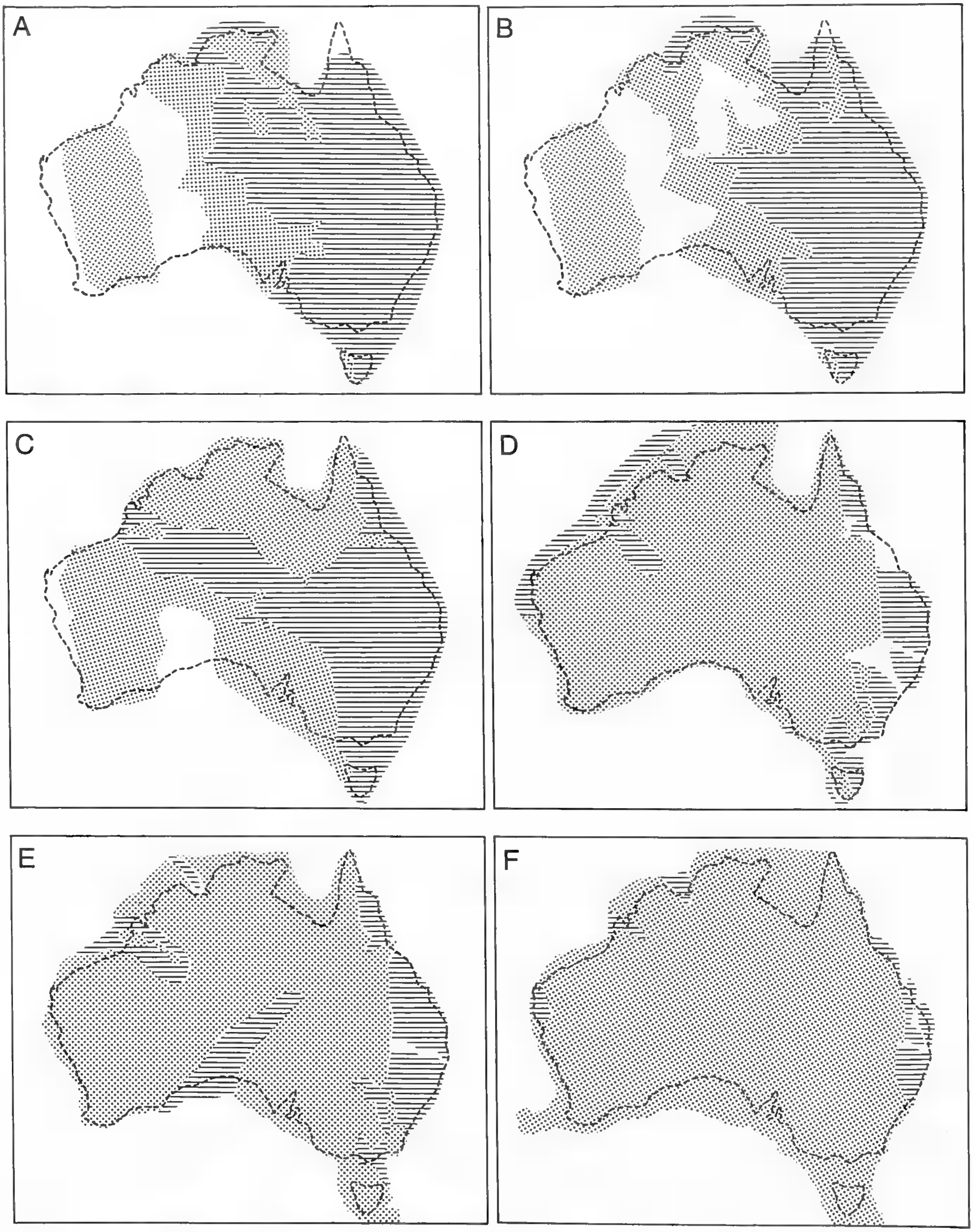


Figure 1.96 Palaeogeographic maps of Australia, showing the extent of marine transgressions and regressions in 12 'time-slices' from the Middle Cambrian to the Tertiary. Shaded areas are those for which palaeogeological information is available; marine seas are shown by horizontal lines; irregular short lines indicate ice. A, Middle Cambrian (538–532 Mya), when Cambrian seas were most extensive, and upwelling with subsequent phosphate deposition. B, Late Cambrian (518–505 Mya), when there was extensive regression with shallow seas or extensive tidal flats in central Australia. C, Ordovician (479–469 Mya), in which a major rise in sea-level re-established the shallow Larapintine Sea connecting the Great Artesian and Canning basins. D, Silurian (414–408 Mya), with limited marine intrusion in the west and limestone deposition around volcanic islands along the east coast. E, Devonian (397–388 Mya), in which a shallow sea extended from the south-west into the centre, and vulcanism continued along the inundated east coast. F, Carboniferous (346–340 Mya), when marine inundation was minimal, particularly on the west coast.

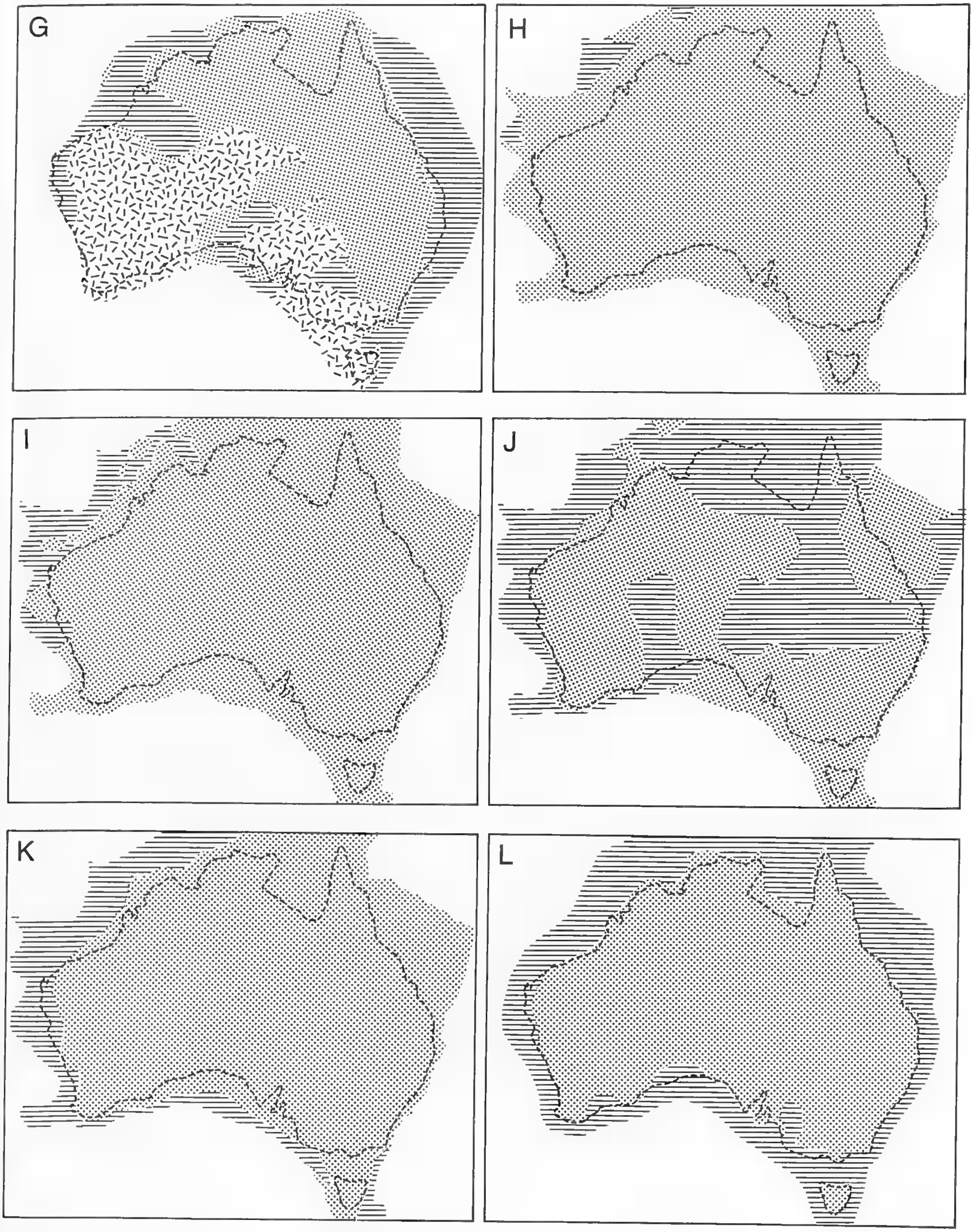


Figure 1.96 (continued) Palaeogeographic maps of Australia. **G**, Permian (286–277 Mya), in which large areas of western and southern Australia were covered by ice sheets flowing from adjacent Antarctica. **H**, Triassic (235–231 Mya), a period in which marine inundation of the continent was essentially absent. **I**, Jurassic (167–162 Mya), throughout which marine transgressions were minimal. **J**, Cretaceous (119–114 Mya), in which the most extensive marine inundation occurred since Cambrian/Ordovician times, linking all major basins in eastern Australia. **K**, Cretaceous (83–70 Mya), in which marine conditions occurred only in the Perth and Carnarvon Basins and the coast of south-western Victoria. **L**, Tertiary (30–10 Mya), when limestones were deposited in shallow seas flooding the Eucla Basin, and the Carnarvon, Murray and Gippsland basins and parts of Spencer Gulf were inundated. (After Paine 1980) [I. Hallam]

order of the Monoplacophora, with the genus *Protowenella* (Fig. 1.97M–O) from the Middle Cambrian of north-western Queensland the earliest representative (Runnegar & Jell 1976).

Cephalopoda probably evolved from a tall, septate Cambrian helcionelloid monoplacophoran, such as *Knightoconus* (Yochelson, Flower & Webers 1973), but an entirely satisfactory explanation for the origin of the siphuncle is still lacking. Alternative views on the origin of the Cephalopoda were discussed by Webers & Yochelson (1989). The first Australian nautiloids appeared near the end of the Cambrian, and nine nautiloid species are known from the Upper Cambrian fauna of the Georgina and Amadeus Basins (see Chapter 12).

The Rostroconchia is an extinct class of molluscs, confined to the Palaeozoic and rare by comparison with other classes: only 27 genera are known worldwide (Pojeta & Runnegar 1976). The class evolved from the Monoplacophora in the Lower Cambrian. Rostroconchs are bivalved with the valves permanently closed by a solid transverse strut joining the valves – the pegma. They first appear in Australia in the Upper Cambrian of the Georgina and Amadeus Basins where *Cymatopegma*, *Wanwania*, *Kimopegma*, *Oepikila*, *Pinnocaris*, *Pleuropegma* and *Ribeiria* occur (Pojeta *et al.* 1977).

Ordovician Period. The Palaeozoic fauna appeared early in the Ordovician. It is recognisable by the range of the orders, superfamilies and some families from Early Ordovician that persist well into the Permian. Nautiloid cephalopods were numerically dominant in the Ordovician and more than 70 genera (see Chapter 12) occur in carbonates of the cratonic Georgina, Amadeus, Canning, and Wiso Basins and the Gnalta and Tasmanian Shelves.

The Bivalvia diversified strongly and 23 genera have been described from the Amadeus and Georgina Basins (Table 1.6) by Pojeta & Gilbert-Tomlinson (1977). These authors also recorded *Ambonychia*, *Ctenodonta*, *Cyrtodontula*, *Deceptrix*, *Fidera*, *Zeehania*, *Inaequidens* and *Pterinea* from the Tasmanian Shelf, four of which are in common with the fauna of the Amadeus and Georgina Basins.

Although few have been described, gastropods were common and many await description. Gilbert-Tomlinson (1973) reviewed their occurrence, and recorded *Teiichispira* (Fig. 1.98F) from the Canning and Georgina Basins with *Macluritella*, *Ecculiomphalus*, *Helicotoma*, *Lesueurilla*, *Calaurops*, *Raphistomina*, *Lophospira* and *Hormotoma* in the latter basin. Gilbert-Tomlinson noted *Maclurites* in the Cleifden Caves Limestone of central New South

Table 1.6 Australian fossil bivalve faunas.

Lower Ordovician Amadeus and Georgina Basins (Pojeta & Gilbert-Tomlinson 1977)	*Alococoncha*, *Brachilyrodesma*, *Colpantyx*, *Copidens*, *Ctenodonta*, *Cyrtodonta*, *Cyrtodontula*, *Deceptrix*, *Denticelox*, *Glyptonychia*, *Inaequidens*, *Johnmartinia*, *Leconychia*, *Lophoconcha*, *Noradonta*, *Nuculites*, *Palaeoneilo*, *Phacidoconcha*, *Pteronychia*, *Runnegaria*, *Sphenosolen*, *Sthenodonta*, *Xestoconcha*.
Upper Silurian Yass Basin (Sherrard 1959)	*Actinopterella*, *Anodontopsis*, *Cardiola*, *Ctenodonta*, *Cypricardinia*, *Goniophora*, *Grammysia*, *Lunulicardium*, *Modiolopsis*, *Nuculites*, *Nuculopsis*, *Orthonota*, *Paracardium*, *Paracyclas*, *Pteronitella*, *Rhombopteria*, *Tellinopsis*.
Upper Silurian Melbourne area (Chapman 1908)	*Actinopteria*, *Ambonychia*, *Ctenodonta*, *Cypricardinia* (Fig. 1.98L) , *Edmondia*, *Grammysia*, *Leptodomus*, *Modiolopsis*, *Nucula*, *Nuculites*, *Palaeoneilo*, *Panenka*, *Paracyclas*, *Parallelodon*, *Sphenotus*.
Lower Devonian Buchan Caves Limestone (Johnston, P.A. 1993)	*Actinopteria*, *Cornellites* (Fig. 1.98M), *Glyptodesma*, *Goniophora*, *Guerangeria*, *Mytilarca*, *Paracyclas*, *Phorinoplax*, *Sanguinolites*, *Schizodus*.
Lower Devonian Cavan and Taemas Limestones, Yass (Johnson, P.A. 1993)	*Actinopteria*, *Cimitaria*, *Cornellites* (Fig. 1.98M), *Cypricardinia* (Fig. 1.98L), *Deceptrix*, *Eoschizodus* (Fig. 1.98P), *Crassatellopsis*, *Glyptodesma*, *Goniophora*, *Grammysioidea*, *Guerangeria*, *Limoptera*, *Mytilarca*, *Nargunella* (Fig. 1.98O), *Nuculites*, *Nuculopsis*, *Paracyclas*, *Phorinoplax*, *Polidevcia*, *Pseudaviculopecten*, *Sanguinolites*, *Schizodus*, *Solenomorpha*, *Tolmaia*.
Lower Devonian Wentworth and Mitchell Rivers, eastern Victoria; Heathcote, Victoria (Talent 1963, 1965)	*Actinopteria*, *Aviculopecten*, *Byssopteria*, *Ctenodonta*, *Ctenodontella*, *Cypricardella*, *Cypricardinia* (Fig. 1.98L), *Eoschizodus* (Fig. 1.98P), *Dolabra*, *Goniophora*, *Grammysia*, *Leiopteria*, *Leptodesma*, *Leptodomus*, *Modiomorpha*, *Nargunella* (Fig. 1.98O), *Nuculana*, *Nuculites*, *Palaeoneilo*, *Paracyclas*, *Parallelodon*, *Pterinea*, *Ptychopteria*, *Sphenotus*.
Lower Cretaceous Great Artesian Basin Aptian fauna (Day 1969)	*Cyrenopsis meeki*, *Fissilunula clarkei*, *Indogrammatodon robusta*, *Laevitrigonia lineata*, *Maccoyella barklyi*, *M. corbiensis*, *M. reflecta*, *M. subangularis*, *M. umbonalis*, *Maranoana etheridgei*, *Nototrigonia cinctuta*, *Pseudavicula anomala*, *Tancretella plana*, *Tatella maranoana*.
Lower Cretaceous Great Artesian Basin Albian fauna (Day 1969)	*Aucellina hughendenensis*, *Cyrenopsis hudlestoni*, several species of *Inoceramus*, *Iotrigonia*, *Maccoyella rookwoodensis*, *Myophorella*, *Nanonavis*, *Nototrigonia minima*, *Pseudavicula papyracea*, *Tancretella secunda*, *Tatella aptiana*.
Lower Cretaceous Maryborough Basin (Fleming, P. 1966a, 1966b, 1970)	*Camptochlamys*, *Camptonectes*, *Cyrenopsis*, *Ennucula*, *Eyrena*, *Fissilunula*, *Indogrammatodon*, *Limea*, *Maccoyella*, *Maranoana*, *Meleagrinella*, *Myophorella*, *Onestia*, *Opisthotrigonia*, *Panopea*, *Phaenodesmia*, *Pseudavicula*, *Tellina*, *Tancretella*.
Lower Cretaceous Canning Basin (Skwarko 1967, 1970)	*Apiotrigonia*, *Astarte*, *Cyrenopsis*, *Eyrena*, *Fissilunula*, *Maccoyella*, *Panopea*, *Pseudavicula*, *Syncyclonema*, *Tatella*, *Yoldia*.
Lower Cretaceous Carnarvon Basin (Cox, L.R. 1961)	*Glycimeris*, *Panopea*, *Pseudavicula*, *Pterotrigonia*, *Trigonia*, *Venericardia*.
Lower Cretaceous Carpentaria Basin (Skwarko 1966)	*Camptonectes*, *Cyrenopsis*, *Fissilunula*, *Grammatodon*, *Maccoyella*, *Nototrigonia*, *Panopea*, *Pseudavicula*, *Tatella*, *Trigonia*.
Upper Cretaceous Carnarvon Basin (Darragh & Kendrick 1991)	*Atreta*, *Chlamys*, *Entolium*, *Grammatodon*, *Giraliapecten*, *Limea*, *Linotrigonia*, *Neithea*, *Panopea*, *Pholadomya*, *Plagiostoma*, *Pseudolimea*, *Pycnodonte*, *Spondylus*, *Trigonia*.

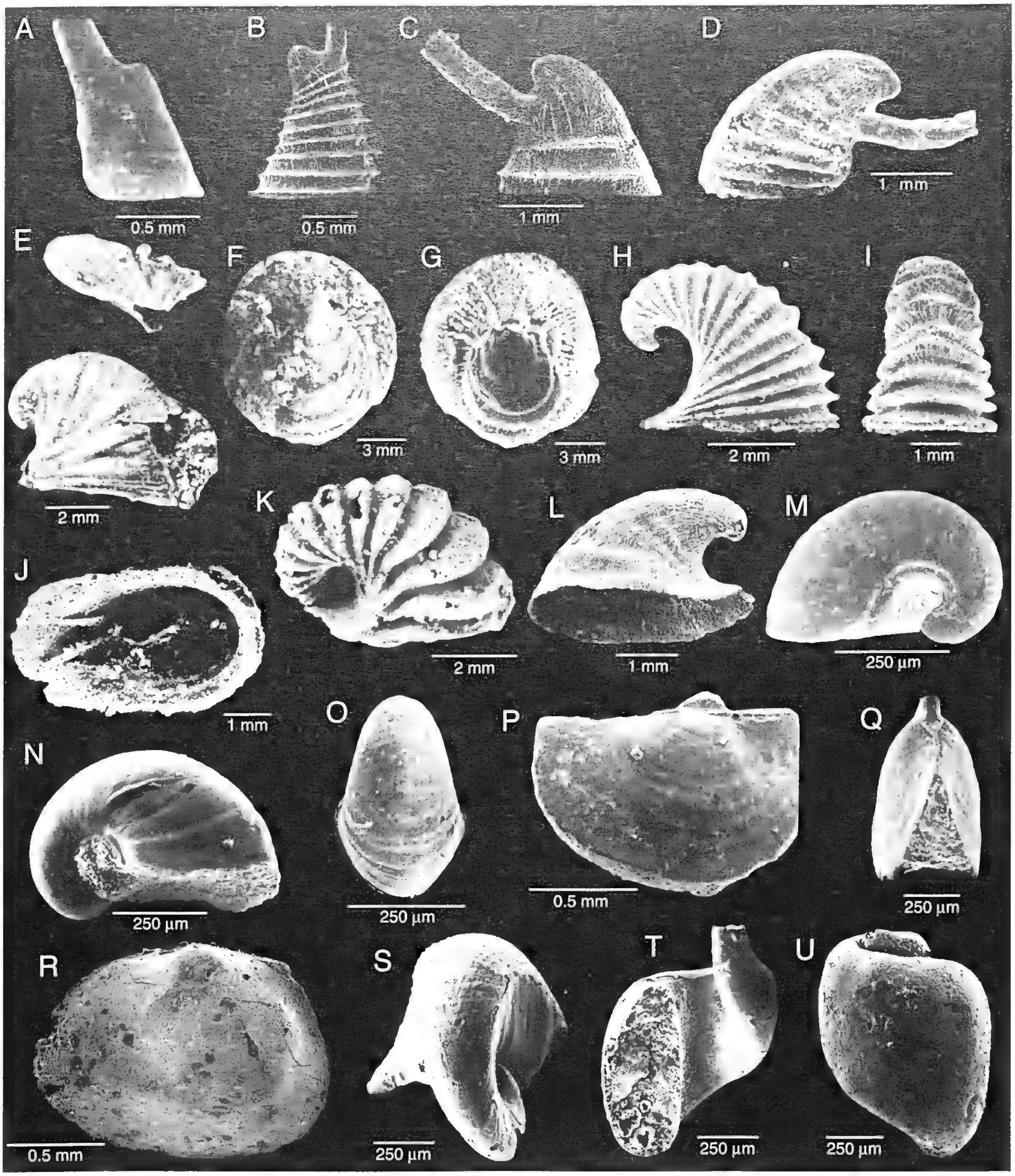


Figure 1.97. Cambrian fossil molluscs from Australia. **A**, **M–Q**, Middle Cambrian, Georgina, Queensland. **B–L**, Middle Cambrian, Gnalta, New South Wales. **R–U**, Lower Cambrian, Stansbury, South Australia. **A–Q**, Monoplacophora. **R**, Bivalvia. **S–U**, Gastropoda. **A**, *Eotebenna pontifex*. **B**, *Yochelcionella ostentata*. **C**, **D**, *Yochelcionella daleki*. **E**, *Anabarella* sp., end view (upper) and lateral view (lower). **F**,**G**, *Helcionella terraustralis*, dorsal and apertural views. **H–J**, *Latouchella accordionata*, lateral, anterior and apertural views, respectively. **K**, *Latouchella merino*. **L**, *Latouchella penecyrano*. **M–O**, *Protowenella flemingi*, lateral and end views. **P**, **Q**, *Pseudomyona queenslandica*, lateral and end views. **R**, *Pojetaia runnegari*. **S**, *Pelagiella subangulata*. **T**, *Beshtashella tortilis*. **U**, *Yuwenia bentleyi*. (A, D–M, O–Q, from Runnegar & Jell 1976; S–U, from Bengston *et al*. 1990) [B, C, N, R, P. Jell]

Wales and the Trelawney Beds of the Tamworth area, and *Lecanospira* and *Maclurites*, from Tasmania. Etheridge (1898) recorded *Trochonema* from Tasmania and Jell, Burrett, Stait & Yochelson (1984) reported on *Peelerophon* (Fig. 1.98B) in the Canning Basin and on the Tasmanian Shelf. Rostroconchs, including *Apoptopegma*, *Bransonia*, *Eopteria* (Fig. 1.98R), *Euchasma*, *Pauropegma*, *Pinnocaris* (Fig. 1.98Q), *Ptychopegma*, *Ribeiria*, *Technophorus*, *Tolmachovia* and *Wanwania* are common in the Georgina and Amadeus Basins (Pojeta *et al*. 1977) and *Bransonia* and *Tolmachovia* occur on the Tasmanian Shelf (Pojeta & Gilbert-Tomlinson 1977). The chiton, *Chelodes*, from the Tremadocian of western Queensland (Runnegar *et al*. 1979) and Arenigian of Tasmania, is the earliest polyplacophoran recorded in Australia, and follows closely the world's earliest known member of this class, *Matthevia*, from the Upper Cambrian of North America.

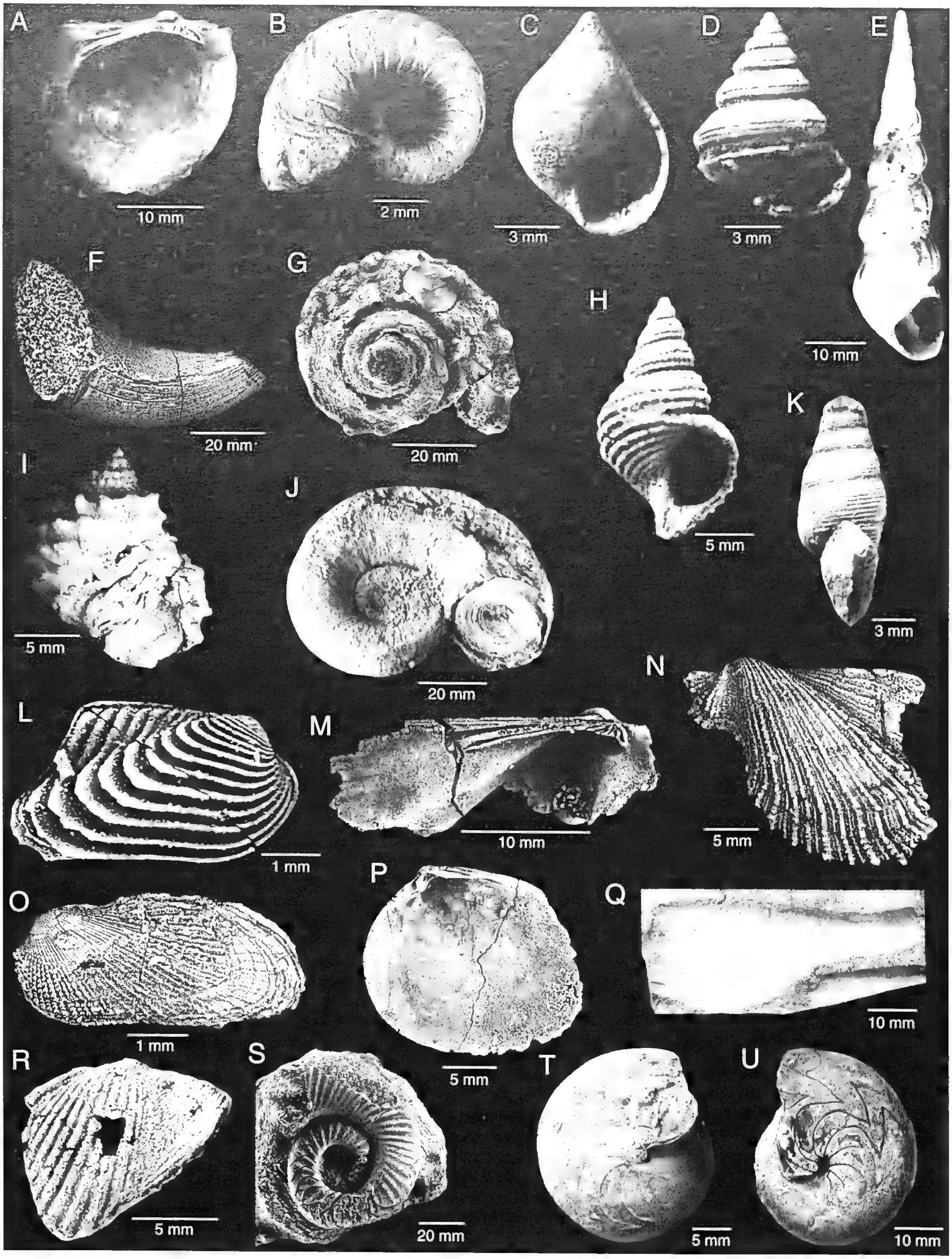


Figure 1.98. Ordovician-Devonian fossil molluscs from Australia. A, Middle Silurian, Canberra, New South Wales. **B**, Lower Ordovician, Canning, Western Australia. C–E, **H**, **K–P**, Lower Devonian, Taemas, New South Wales. **F**, **Q**, **R**, Lower Ordovician, Georgina, Queensland. **G**, Middle Devonian, Charters Towers, Queensland. **I**, Lower Devonian, Ukalunda, Queensland. **J**, Lower Devonian, Lilydale, Victoria. **S**, Lower Devonian, Buchan, Victoria. **T**, **U**, Upper Devonian, Canning, Western Australia. A, L–P, Bivalvia. **B–K**, Gastropoda. **Q**, **R**, Rostroconchia. **S**, Nautiloidea. T, U, Ammonoidea. A, *Umburra cinefacta*, left valve, internal view. **B**, *Peelerophon oehlerti*. C, *Leptoptygma australe*. **D**, *Murchisonia fermioni*. E, *Loxonema altacostatum*. **F**, *Teiichispira cornucopiae*, operculum. **G**, *Burdikinia burdekinensis*, dorsal view. **H**, *Hemizyga granifera*. **I**, *Kitikamispira ukalundensis*. **J**, *Liomphalus northi*. **K**, *Mitchellia striatula*. L, *Cypricardinia minima*. M, N, *Cornellites catellus*, left hinge line and exterior of left valve. **O**, *Nargunella comptorae*. **P**, *Eoschizodus taemasensis*, interior of right valve. **Q**, *Pinnocaris robusta*, internal mould of valve. **R**, *Eopteria struszi*. **S**, *Teicherticeras desideratus*. **T**, *Paratornoceras lentiforme*. **U**, *Sporadoceras latilobatum* (A, from Johnston, P.A. 1991; C–E, H, K, from Tassell 1982; F, from Gilbert-Tomlinson 1973; I, from Cook, A.G. 1995; J, from Linsley 1978; L–P, from Johnston, P.A. 1993; Q, R, from Pojeta *et al*. 1977; T, U, from Petersen 1975)

[B, G, S, P. Jell]

Silurian Period. Upper Silurian molluscs are common in the Yass Basin north of Canberra. The fauna includes 18 bivalve genera (Table 1.6; Sherrard 1959), the gastropods *Bellerophon*, *Murchisonia* (Fig. 1.98D), *Euomphalus*, *Loxonema* (Fig. 1.98E) and *Platyceras* (Brown I.A. 1941) and the chiton *Chelodes* (Etheridge 1897). Present also are the nautiloids *Endoceras*, *Orthoceras*, *Actinoceras*, *Ophidioceras*, *Protobactrites*, *Spiroceras* and *Cyclolituites* (Brown, I.A. 1941). Sherrard (1959) described similar Upper Silurian bivalve faunas from several other parts of New South Wales. The bivalve *Umburra cinefacta* (Fig. 1.98A), from just north of Canberra, is fundamentally significant as the possible stem of the Subclass Pteriomorphia (Johnston, P.A. 1991).

The clastic sedimentary pile in the Melbourne Trough of central Victoria contains a rich but largely unstudied molluscan fauna. Öpik (1953) described an Early Silurian fauna from the Heathcote district with the bivalve *Ctenodonta* and the gastropods *Sinuitina*, *Phragmolites*, *Tropidodiscus*, *Bellerophon*, *Kokenospira* and *Halopea*. Chapman (1908) recorded 15 genera of Upper Silurian bivalves in the Melbourne area (Table 1.6). Talent (1965) identified a large molluscan fauna from the Heathcote district in the Dargile and McIvor Formations, listing more than 30 bivalve and 20 gastropod taxa, including Öpik's fauna, to which he added the nautiloid genus *Anaspyroceras*. Nautiloids are common but generally unidentifiable or unstudied.

Devonian Period. Lower and Middle Devonian molluscs occur in eastern Australia and form a minor component of the many diverse marine fossil faunas in both limestone and clastic environments. The fauna is incompletely studied although almost 100 genera have been described. The gastropod fauna of the Lochkovian-Pragian Lilydale Limestone near Melbourne has been studied comprehensively by Tassell (1976, 1980) and Linsley (1978). It includes 21 genera – *Tremanotus*, *Bellerophon*, *Straparollus*, *Phanerotrema*, *Stenoloron*, *Oriostoma*, *Naticopsis*, *Murchisonia* (Fig. 1.98D), *Michelia*, *Gyrodoma*, *Scalaetrochus*, *Siluriphorus*, *Loxonema* (Fig. 1.98E), *Liomphalus* (Fig. 1.98J), *Tropidodiscus*, *Palaeoscurria*, *Australonema*, *Anomphalus*, *Littorinides*, *Ostioma* and *Subulites*.

The gastropod fauna of the Bell Point Limestone, southern Victoria, differs from others in south-eastern Australia as it is dominated by medium-sized rotelliform and trochiform genera, notably *Orecopia* and *Bassotrochus* but also includes *Tropidodiscus*, *Straparollus* (*Euomphalus*), *Micromphalus*, *Mourlonia*, *Gyronema*, *Murchisonia* and *Hormotomina* (Tassell 1978).

The Buchan Caves Limestone in East Gippsland contains an Emsian bivalve fauna comprising species of 10 genera (Table 1.6; Johnston, P.A. 1993). All of these genera are known also from the very similar and rich molluscan faunas in the contemporary *Receptaculites* and Warroo Limestones south of Yass, New South Wales, from which Johnston, P.A. (1993) recorded 20 bivalve genera. There were also 29 gastropods genera – *Ptychosphaera*, *Coelocyclus*, *Tropidodiscus*, *Retispira*, *Euomphalus*, *Serpulospira*, *Arizonella*, *Mourlonia*, *Oehlertia*, *Bembexia*, *Hesperiella*, *Umbotropis*, *Coelozone*, *Trochonema*, *Halopea*, *Platyceras*, *Naticopsis*, *Murchisonia*, *Mesocoelia*, *Michelia*, *Stegocoelia*, *Taemasotrochus*, *Mitchellia* (Fig. 1.98K), *Loxonema* (Fig. 1.98E), *Palaeozygopleura*, *Hemizyga* (Fig. 1.98H), *Leptoptygma* (Fig. 1.98C), *Subulites* and *Ianthinopsis* (Tassell 1982).

Diverse molluscan faunas have been described from the Heathcote district in central Victoria (Talent 1965) and the Wentworth and Mitchell River areas in eastern Victoria (Talent 1963). Some 24 bivalve genera have been recorded (Table 1.6) with the gastropods *Bucanopsis*, *Tropidodiscus*, *Temnodiscus*, *Ulrichospira*, *Bembexia*, *Straparollus* and *Loxonema* (Fig. 1.98E). The only rostroconch is *Conocardium* and some poorly preserved straight nautiloids are known. Equally diverse and similar faunas occur in the mudstones and fine siltstones of the Melbourne, Lilydale, Kinglake and Kilmore districts but have not yet been described comprehensively. The only monoplacophoran described is a species of *Vallatotheca* (Tryblidiida) which occurs in the Lower Devonian of Victoria (Talent 1959; Tassell 1980). Large Lower and Middle Devonian molluscan faunas are known from northern Queensland but few have been described. Heidecker (1959) described the Middle Devonian gastropods *Labrocuspis*, *Austerum* and *Burdikinia* (Fig. 1.98G) and the bivalve *Tanaodon* from near Charters Towers. The high-spired septate gastropod *Fletcherviewia* is known from the same area (Cook, A.G. 1993). Cook, A.G. (1995) also described a fauna from Ukalunda including *Tropidodiscus*, *Trochonema*, *Kitikamispira* (Fig. 1.98I) and *Hornyzyga*. Middle Devonian bivalves – *Modiomorpha*, *Actinopteria*, *Pterinopecten* and *Sphenotus* – were found in cores from the subsurface Adavale Basin in western Queensland (McKellar 1966a, 1966b), and large undescribed molluscan faunas occur in the Broken River Embayment north of Charters Towers.

Upper Devonian sediments in eastern Australia are largely of non-marine origin and molluscan remains are rare. However, Upper Devonian faunas in the Canning Basin of Western Australia associated with extensive reef development are rich in molluscs, principally gastropods, such as *Straparollus* (Fig. 1.99A), *Turbonellina*, *Cyrtogomphus*, *Lophospira*, *Loxonema* (Fig. 1.98E), *Euomphalus*, *Macrochilina*, *Cyclonema*, *Naticopsis*, *Bellerophon*, *Murchisonia* (Fig. 1.98D) and *Philoxene*, and the bivalves *Palaeoneilo*, *Paracyclas* and *Praecardium*; these have been reported (Teichert 1949) but never described.

These sediments also contain many cephalopods, including both nautiloids and goniatite ammonoids. The goniatite succession has been correlated at species level with that of Europe mainly using *Cheiloceras*, *Sporadoceras* (Fig. 1.98U), *Manticoceras*, *Clymenia*, *Platyclymenia*, *Timanites*, *Mesobeloceras*, *Maenoceras*, *Beloceras*, *Ponticeras*, *Paratornoceras* (Fig. 1.98T), *Prototornoceras*, *Protactylocylmenia*, *Pernoceras*, *Praemeroceras* and *Cycloclymenia* (Teichert 1941; Glenister 1958; Petersen 1975; Becker, House & Kirchgasser 1993).

Carboniferous Period. Lower Carboniferous shallow marine shelf calcarenites and calcisiltites in the intracratonic basins of Western Australia contain molluscan faunas but formal taxonomy is not available and it is uncertain in which intervals of the Period some of the sediments were deposited. Straparollid gastropods and bellerophont monoplacophorans are common (Runnegar & Campbell 1976).

Throughout the Period, sediments were deposited on the Tamworth and/or Yarrol Shelves in eastern Australia (Campbell & McKellar 1969) and fossil molluscs are common at many horizons. Only parts of the molluscan faunas have been studied thoroughly. For example, the Tournaisian Tulcumba Sandstone in central New South Wales contains the bivalves *Euchondria*, *Polidevcia*, *Nuculopsis*, *Palaeoneilo*, *Cypricardinia*, *Panenka* and *Chaenocardiola* and the gastropods *Ruedemannia*, *Worthenia*, *Angyomphalus*, *Straparollus* (Fig. 1.99A) and *Loxonema* (Fig. 1.99D). Also present are the bellerophont monoplacophorans *Retispira*, *Sinuitina* and *Euphemites* and the ammonoids *Protocanites*, *Imitoceras* and *Muensteroceras* (Campbell & Engel 1963).

Numerous long-ranging and/or cosmopolitan genera occurred in eastern Australia, among them the monoplacophorans *Retispira*, *Sinuitina* and *Euphemites* (Fig. 1.99G, H), the gastropods *Straparollus*, *Loxonema* (Fig. 1.99D) and *Worthenia* and the bivalves *Euchondria*, *Polidevcia*, *Nuculopsis*, *Palaeoneilo*, *Cypricardinia* (Fig. 1.98L), *Chaenocardiola* and *Panenka*.

Most remarkable among the gastropods is the miniature fauna, all < 10 mm, from the Tournaisian of the Tamworth shelf (Yoo 1994) in which more than 50 genera are represented by specimens replaced by chlorite and etched free from the limestone with weak acid. Bivalves and scaphopods also occur but have not been studied as extensively. Molluscs of this size have not been studied from anywhere else in the Palaeozoic of Australia, except the Cambrian, and highly diverse assemblages may be expected to be discovered elsewhere and in other geological periods.

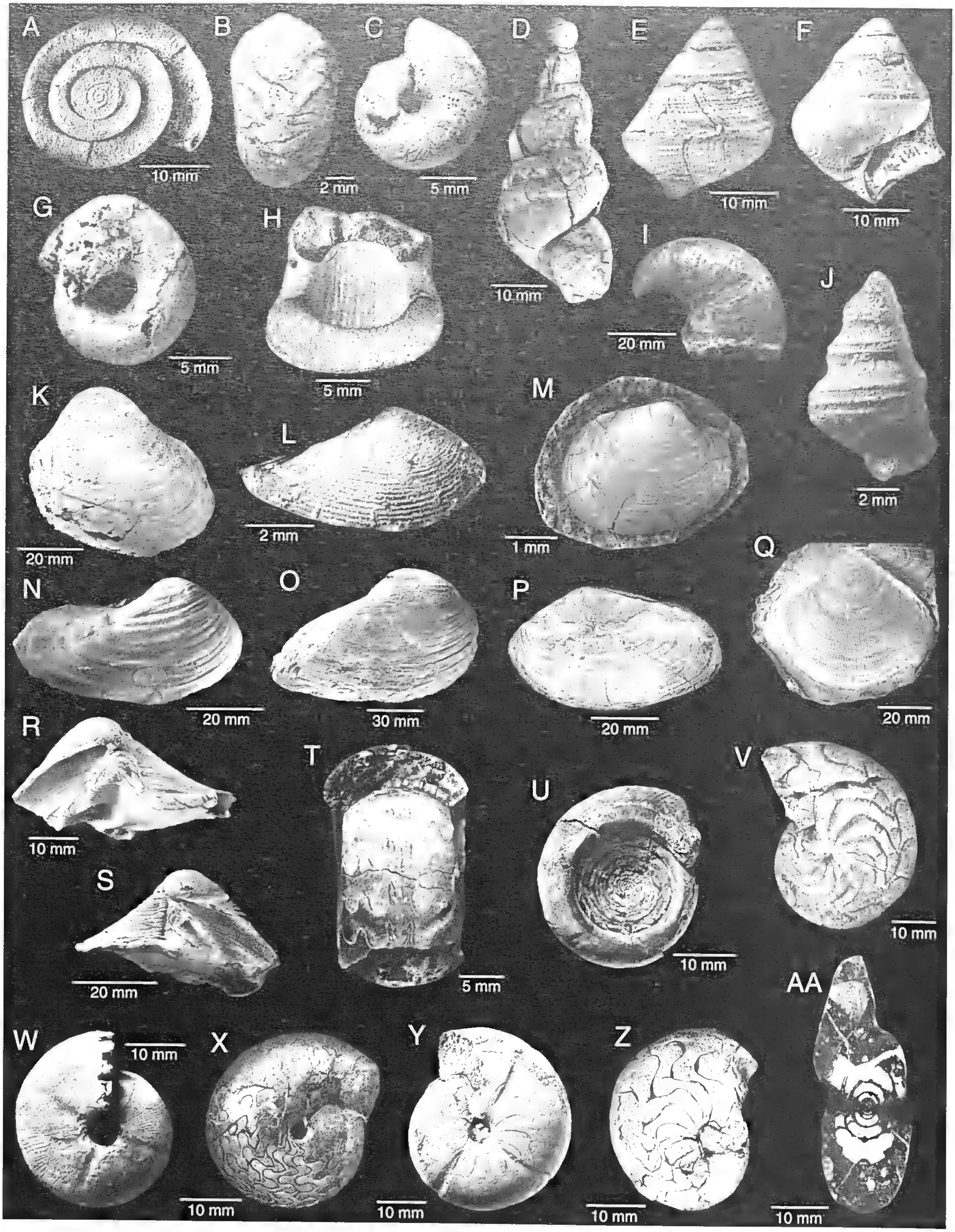


Figure 1.99. Carboniferous-Permian fossil molluscs from Australia. A, Lower Carboniferous, New England, New South Wales. **D**, **V**, **Y–AA**, Lower Carboniferous, Yarrol, Queensland. **B**, **C**, **G**, **H**, Lower Permian, Canning, Western Australia. **Q**, Lower Permian, New England, New South Wales. **E**, **F**, **O**, **P**, **R**, **S**, **W**, Lower Permian, Bowen, Queensland. **I**, **K**, **M**, **N**, **X**, Lower Permian, Sydney, New South Wales. **J**, **L**, Lower Permian, Carnarvon, Western Australia. **T**, **U**, Lower Permian, Perth, Western Australia. **A**, **D–F**, **I**, **J**, Gastropoda. **B**, **C**, **G**, **H**, Bellerophontida. **K–S**, Bivalvia. **T–AA**, Ammonoidea. **A**, *Straparollus davidi*, dorsal view. **B**, **C**, *Warthia intermedia*, sectional and lateral views. **D**, *Loxonema lamellosa*. **E**, **F**, *Platyteichum costatum*, lateral and apertural views. **G**, **H**, *Euphemites wynnensis*, lateral and sectional views. **I**, *Rhabdocanthus altum*. **J**, *Peruvispira umariensis*. **K**, *Megadesmus grandis*. **L**, *Phestia darwini*. **M**, *Astartila intrepida*. **N**, *Vacunella waterhousei*. **O**, *Myonia carinata*. **P**, *Oriocrassatella queenslandica*. **Q**, *Deltopecten farleyensis*. **R**, **S**, *Eurydesma cordatum*, umbonal fragment. **T**, **U**, *Metalegoceras kayi*, apertural and lateral views. **V**, *Irinoceras tuba*. **W**, **X**, *Neocrimites meridionalis*, lateral views with and without shell preserved. **Y**, *Goniatites granosus*. **Z**, **AA**, *Beyrichoceras mackellari*, lateral view and median sections. (A, from Campbell & Engel 1963; B, C, G, H, from Dickins 1963; E, F, from Dickins 1961a; I, from Fletcher 1958; J, L, from Dickins 1957; P, from Dickins 1961b; T, U, from Glenister *et al*. 1973; V, Y–AA, from Campbell *et al*. 1983; W, from Teichert & Fletcher 1943; X, from Armstrong *et al*. 1967)

[D, K, M–O, Q, R, S, P. Jell]

Goniatites form a minor component of the molluscan fauna at any horizon on the Tamworth or Yarrol Shelves. Rarely more than one or two specimens occur at any site and at no more than three horizons in any one section (Campbell, Brown & Coleman 1983). However, occurrences of some key taxa of established biostratigraphic schemes in Europe and North America enable global correlation making these fossils extremely important geological tools. Genera described are *Imitoceras*, *Amonellipsites*, *Irinoceras* (Fig. 1.99V), *Muensteroceras*, *Beyrichoceras* (Fig. 1.99Z, AA), *Bollandites*, *Nomismoceras*, *Karagandites*, *Girtyoceras*, *Goniatites* (Fig. 1.99Y), *Protocanites*, *Erdbachites*, *Cantabricanites* and *Pseudarietites* (Campbell *et al.* 1983).

Permian Period. Permian faunas of Western Australia have been reviewed comprehensively by Skwarko (1993a). Diverse molluscan faunas occur in the Bonaparte Gulf, Canning, Carnarvon and Perth Basins. The bivalves, bellerophontids and gastropods are mainly in littoral and sublittoral sediments, whereas the cephalopods occur in deeper water sediments. Among the bivalves, *Edmondia*, *Glyptoleda*, *Praeundulomya*, *Undulomya*, *Oriocrassatella*, *Parallelodon*, *Pseudomyalina*, *Cosmomya*, *Euchondria*, *Acanthopecten* and *Girtypecten* are more common in Western Australia than in eastern Australia (Dickins & Skwarko 1993a).

Gastropods are common in Western Australia but large faunas await description (Dickins & Skwarko 1993b). In lowest Permian sediments associated with glacials the temperature-tolerant *Keenia*, *Peruvispira* (Fig. 1.99J) and *Mourlonia* are prominent, probably because of the lack of other forms. This fauna was succeeded by a warmer water – probably cool temperate – fauna, which included the bellerophontids *Bellerophon*, *Euphemites*, *Retispira* and *Stachella*, pleurotomariids *Ptychomphalina*, *Pseudobaylea*, *Woolnoughia*, *Platyteichum* (Fig. 1.99E, F) and *Baylea*. High-spired species and forms resembling *Straparollus* (Fig. 1.99A) were absent.

Cephalopods are relatively rare but include the ammonoids *Agathiceras*, *Juresanites*, *Svetlanoceras*, *Pseudoschistoceras*, *Metalegoceras* (Fig. 1.99T, U), *Neocrimites* (Fig. 1.99W, X), *Paragastrioceras*, *Propopinoceras*, *Thalassoceras*, *Bamyaniceras*, *Dauchites*, *Cyclolobus*, *Popanoceras* and *Mescalites* (Glenister, Rogers & Skwarko 1993) and a few nautiloids (see Chapter 12). The ammonoids have provided the major tool for correlation of the international and Australian Permian. They show a provincial affinity with the Boreal Realm in the Lower Permian but are cosmopolitan in the Upper Permian (Glenister *et al.* 1993). Rare scaphopods have been reported from the Lower Permian of the Canning and Carnarvon Basins (Skwarko 1993b).

In eastern Australia, a number of different environments have been identified (Runnegar & Campbell 1976) in some of which molluscs are dominant, and in others are absent. In the sublittoral of the rocky shore environment, the large shallow infaunal and epifaunal bivalves *Eurydesma* (Fig. 1.99R, S), *Megadesmus* (Fig. 1.99K), *Deltopecten* (Fig. 1.99Q), *Schizodus*, *Pyramus*, *Australomya* and *Merismoptera* and the gastropod *Keenia* are dominant.

Sands in slightly deeper water are dominated by burrowing bivalves (Runnegar 1967) of the genera *Myonia* (Fig. 1.99O), *Megadesmus*, *Pyramus*, *Astartila* (Fig. 1.99M), *Australomya*, *Schizodus* and *Stutchburia*, and the bellerophont *Warthia* (Fig. 1.99B, C).

The shallow shelf environment supports the most diverse faunas with many bivalves, such as *Aviculopecten*, *Deltopecten* (Fig. 1.99Q), *Eurydesma*, *Megadesmus* (Fig. 1.99K), *Myonia*, *Merismopteria*, *Parallelodon* and *Stutchburia*. Shelf carbonates on the Gympie Shelf and New England region contain the bivalves *Atomodesma* and *Eurydesma*, respectively.

Among more than 50 Australian Permian bivalve species, representatives of the large distinctive monomyarian *Eurydesma* (Fig. 1.99R, S) were endemic to Gondwanaland and are notable for their upright life position resembling living *Tridacna*, for their apparently gregarious nature and their massive, thickened shells. Gastropods are also well represented in the Permian acme of the Palaeozoic fauna with at least 40 genera in Australia, including members of the Pleurotomariida and Macluritida (Fletcher, H.O. 1958; Dickins 1963; and others). *Conocardium* was the only rostroconch to persist to the Permian in Australia (Fletcher, H.O. 1943). Cephalopods are less evident than in earlier periods, although ammonoids were significant in Western Australia; the latter were rare in eastern Australia (only *Neocrimites* (Fig. 1.99W, X) and *Uraloceras* (Armstrong, Dear & Runnegar 1967). Seven Permian nautiloid genera are known from Australia (see Chapter 12), and Iredale & Hull (1927b) recorded a single Permian chiton, *Permochiton australianus*, from the Berry Formation in the Sydney Basin.

Mesozoic Era

Triassic Period. Very little is known of Australian mollusc faunas of this first period in the Mesozoic, because of a major regression of the sea from virtually all the continent. Only three isolated, marine Triassic faunas are known. In borehole BMR 10, in the Perth Basin (Dickins & McTavish 1963) the bivalves *Claraia*, *Trigonucula*, *Bakevellia* and *Anodontophora* occur with the ammonites *Ophiceras*, *Subinyoites* and *Glyptophiceras* in the very lowest Triassic (Otoceran) Kockatea Shale.

The other two faunas are slightly younger (not older than Flemingitan) and probably represent a single marine incursion into the Maryborough Basin, Queensland. P. Fleming (1966c) reported the bivalves *Nuculopsis*, *Nuculanella*, *Bakevellia*, *Myalina*, *Neoschizodus*, *Ctenodonta* and an indeterminate astartid with a poorly preserved otoceratoid ceratite from the Brooweena Formation west of Maryborough, Queensland. Runnegar (1969) described *Latisageceras*, *Dieneroceras*, *Flemingites*, *Paranorites*, *Anaflemingites*, *Pseudohedenstroemia* and *Arctoceras* in the Traveston Formation exposed in a railway cutting near Woondum south of Gympie, Queensland. The freshwater mussels *Protovirgus*, *Prohyria*, *Unionella* and *Mesohyridella* are recorded from eastern Australia (McMichael 1957) and *Tihkia*, *Unio* and *Protovirgus* from central Australia (Ludbrook 1961).

Jurassic Period. Australian marine Jurassic faunas are known only from Western Australia. In the western part of the Canning Basin, around the Edgar Ranges east of Broome, diverse molluscan faunas have been reported (Teichert 1940; Brunnschweiler 1954), and include bivalves *Meleagrinella*, *Buchia* and *Inoceramus*, ammonites *Virgatosphinctes* and *Kossmatia* and the belemnite *Belemnopsis*, among more extensive undescribed faunas.

In the northern Carnarvon Basin, molluscan faunas in Cape Range Bores 1 and 2 are of Middle and Late Jurassic age (McWhae, Playford, Lindner, Glenister & Balme 1958) and include the ammonites *Perisphinctes*, *Kossmatia*, *Macrocephalites*, *Otoites* and *Pseudotoites*, and the belemnites *Belemnopsis*, and the bivalves *Inoceramus* (Fig. 1.100L), *Meleagrinella*, *Posidonia* and *Quenstedtia*.

In the northern Perth Basin, east of Geraldton, the Middle Jurassic (Bajocian) Newmarracarra Limestone contains a rich molluscan fauna; represented are ammonites *Newmarracarroceras*, *Sonninia*, *Witchellia*, *Otoites*, *Pseudotoites*, *Zemistephanus* and *Stephanoceras*, bivalves *Astarte*, *Cucullaea*, *Meleagrinella*, *Modiola*, *Lopha*, *Ctenostreon*, *Ostrea* (Fig. 1.100C), *Oxytoma*, *Pecten* and *Trigonia*, gastropods, *Cerithium*, *Pleurotomaria*, *Rissoina* and *Turbo* and the nautiloid *Nautilus peronatus* (Moore 1870; Crick 1894; Arkell & Playford 1954; Hall 1989). One freshwater unionid bivalve is recorded from eastern Australia (McMichael 1957).

Cretaceous Period. The Great Artesian Basin of eastern Australia contains rich Lower Cretaceous (Aptian-Albian) marine faunas dominated by molluscs (Day 1969) which were widespread in Queensland, New South Wales and South Australia. These have been described in large monographs (Moore 1870; Etheridge 1892,

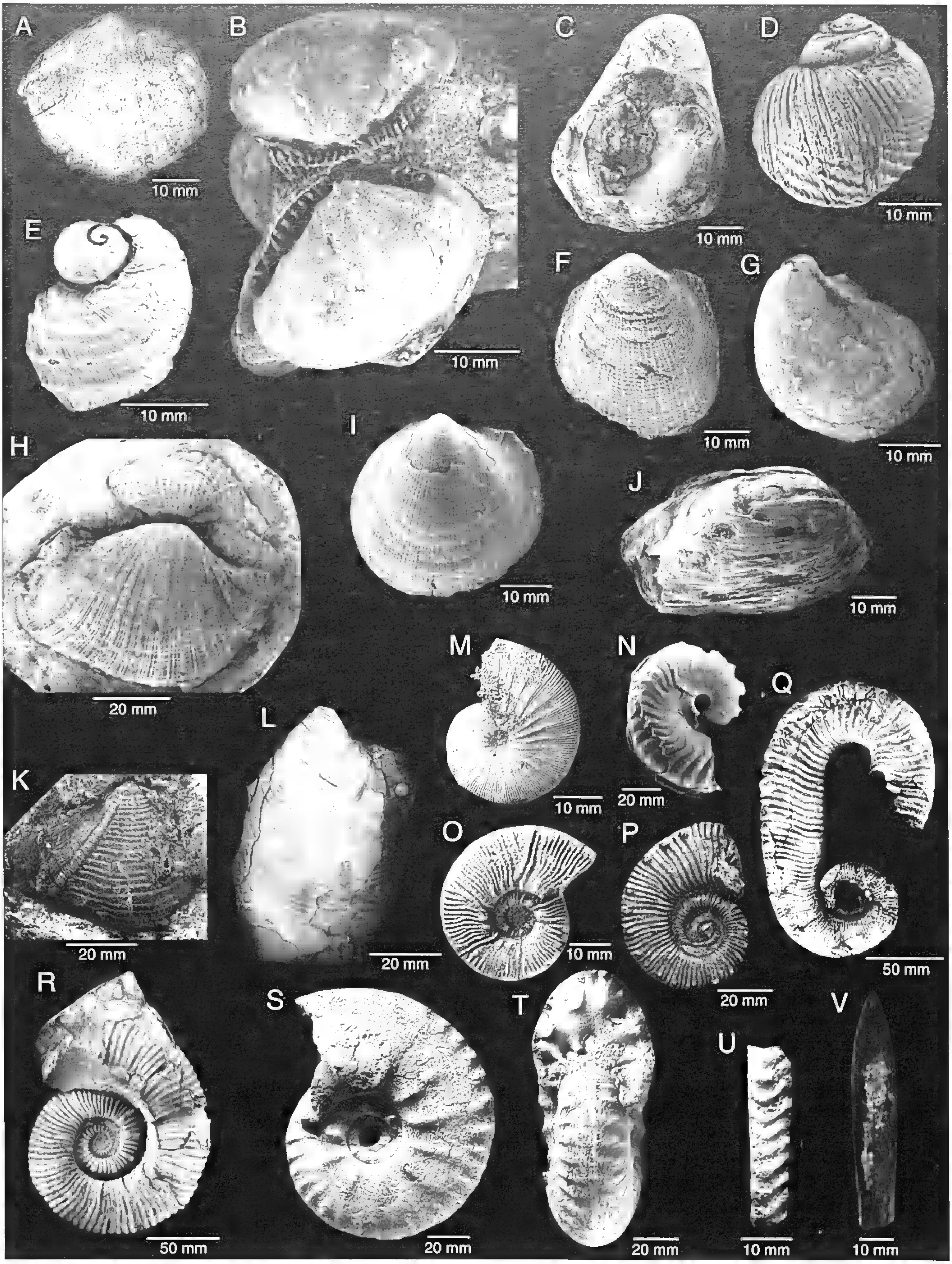


Figure 1.100. Mesozoic fossil molluscs from Australia. **A–G**, **I**, **K**, **L**, **N**, **P–R**, **V**, Lower Cretaceous, Great Artesian Basin, Queensland. **H**, Maryborough, Queensland. **J**, Lower Triassic, Ipswich, Queensland. **M**, **O**, **S–U**, Upper Cretaceous, Carnarvon, Western Australia. **A–C**, **F–L**, Bivalvia. **D**, **E**, Gastropoda. **M–U**, Ammonoidea. **V**, Belemnoida. **A**, *Maccoyella barklyi*. **B**, *Leionucula quadrata* (internal moulds). **C**, *Ostrea vesiculosa*. **D**, *Vanikoropsis jacki*. **E**, *Neritopsis minmiensis*. **F**, *Meleagrinella woodsi*. **G**, *Aucellina hughendenensis*. **H**, *Grammatodon robusta*. **I**, *Pseudavicula australis*. **J**, *Mesohydrilla ipsvichensis*. **K**, *Opisthotrigonia nasuta*. **L**, *Inoceramus carsoni*. **M**, *Phylloceras (Neophylloceras) surya*. **N**, *Sanmartinoceras fontinale*. **O**, *Kossmaticeras (Natalites) brunnschweileri*. **P**, *Crioceras ammonoides*. **Q**, *Myloceras auritulum*. **R**, *Australiceras jacki*. **S**, **T**, *Pachydiscus (Pachydiscus) jacquoti australis* (lateral and apertural views). **U**, *Baculites lechitides*. **V**, *Dimitobelus diptychus*. (A, L, from Jack & Etheridge 1892; M, O, S, T, from Henderson & McNamara 1985; Q, from McNamara 1978; U, from Henderson R.A. *et al*. 1992; V, from Ludbrook 1966) [B–K, N, P, R, P. Jell]

1902a, 1902b, 1907, 1909, 1920; Whitehouse 1926; Ludbrook 1966; Day 1974) and many other papers. Aptian faunas are distinguished by the ammonites *Sanmartinoceras* (Fig. 1.100N), *Aioloceras*, *Australiceras* (Fig. 1.100R), *Toxoceratoides*, *Tropaeum* and *Lithancylus*, and the belemnite *Peratobelus*. Characteristic bivalves include several species of *Maccoyella* and representatives of 10 other genera (Table 1.6; Day 1969).

The succeeding Albian fauna is characterised by the ammonites *Prohysteroceras*, *Falciferella*, *Labeceras*, *Appurdiceras*, *Myloceras*, *Beudanticeras*, *Brewericeras*, and *Boliteceras* (Fig. 1.100Q), and the belemnite genus *Dimitobelus* (Fig. 1.100V). The fauna also includes 11 bivalve taxa referred to 10 genera (Table 1.6) together with several species of *Inoceramus* (Day 1969).

Gastropods form a minor component of the fauna, and include *Euspira*, *Ampullina*, *Vanikoropsis* (Fig. 1.100D), *Anchura* and *Avellana* (Ludbrook 1966), the scaphopod *Dentalium (Fustiaria)*, the nautiloids *Kummelonautilus hendersoni* and *Cimomia* (see Chapter 12) and the squids *Muensterella*, *Boreopeltis* and *Trachyteuthis* (Wade 1993).

East of the Great Artesian Basin a comparable Lower Cretaceous molluscan fauna is found in the Maryborough Basin of south-eastern Queensland, with 19 bivalve genera (Table 1.6) along with the gastropod *Euspira*, the ammonite *Australiceras jacki* (Fig. 1.100R), a belemnite, *Peratobelus*, and the scaphopod *Dentalium* (Fleming, P. 1966a, 1966b, 1970).

In Western Australia, the Canning, Carnarvon and Perth Basins contain Lower Cretaceous faunas with molluscan elements similar to those of eastern Australia. The Gin Gin Chalk of the Perth Basin contains abundant *Inoceramus*, oysters, *Anomia* and other bivalves (Feldtman 1963) together with ammonites resembling *Pachydiscus* (Fig. 1.100S, T). Six bivalve genera (Table 1.6; Cox, L.R. 1961) are found in the Carnarvon Basin with the ammonites *Tropeum*, *Paracanthoplites* and *Aconeceras* (Brunnschweiler 1959), and representatives of 11 bivalves occur in the Canning Basin (Table 1.6; Skwarko 1967, 1970). Collectively these taxa indicate close similarity with Great Artesian Basin molluscan faunas of eastern Australia, the implications of which are discussed by Skwarko (1967).

Rich Lower and mid Cretaceous molluscan faunas have been reported from the northern part of the Northern Territory (Skwarko 1966; Henderson 1990). The Early (Neocomian and Aptian) faunas in the coastal belt on the western side of the Gulf of Carpentaria are fairly typical of the Great Artesian Basin fauna. They include 11 bivalves (Table 1.6), gastropods (*Diodora*, *Cellana*, *Pleurotomaria*), belemnites (*Peratobelus*, *Dimitobelus*) and the ammonite *Australiceras* (Skwarko 1966).

The Albian fauna of the Point Charles-Darwin area contains 18 ammonites – *Desmoceras*, *Beudanticeras*, *Naramoceras*, *Hysteroceras*, *Myloceras* (Fig. 1.100Q), *Labeceras*, *Ptychoceras*, *Scaphites*, *Worthoceras*, *Lechites*, *Sciponoceras*, *Hamites*, *Lytohamites*, *Mariella*, *Pseudhelicoceras*, *Notostreptites*, *Idiohamites* and *Anisoceras* – along with undescribed bivalves, gastropods and belemnites (Henderson 1990). On adjacent Bathurst Island a late Albian to Cenomanian fauna contains representatives of the ammonites *Stomohamites*, *Sciponoceras*, *Hypoturrilites*, *Turrilites*, *Borissiakoceras*, *Acanthoceras*, *Scaphites*, *Chimbuites* and *Euomphaloceras* (Wright 1963).

The Upper Cretaceous (Maastrichtian) molluscan fauna of the Miria Marl near Exmouth Gulf in the Carnarvon Basin is as diverse as many Tertiary faunas. The bivalves are mainly endemic species of 15 cosmopolitan or wide ranging genera with a few endemic genera, such as *Giraliapecten* (Table 1.6; Darragh & Kendrick 1991). All the gastropod genera identified were widespread at the time and no endemic genera have been recognised. Herbivores, detrital feeders, grazers and predatory and ectoparasitic carnivores are represented. Gastropods included *Conotomaria*, *Nododelphinula*, *Eovolutilithes*, *Gyrodes*, *Euthriofusus*, *Xenophora*, *Leptomaria*, *Avellana*, *Fusinus*, *Confusiscala*, *Cirsocerithium*, *Graphidula*, *Hainaspira*, *Amaea*, *Striaticostatum*, *Boutillieria*, *Cimolithium*, *Dolicholatirus*, *Woodsella* and *Bathraspira*, together with the scaphopod *Dentalium* (Darragh & Kendrick 1994).

The ammonite fauna is the most abundant known from the Maastrichtian with over 1500 specimens available so it is highly relevant to any assessment of their abundance and diversity immediately before their extinction at the end of the Cretaceous. The fauna includes the non-heteromorph ammonites *Neophylloceras*, *Phyllopachyceras*, *Anagaudryceras*, *Gaudryceras*, *Gunnarites*, *Pseudophyllites*, *Desmophyllites*, *Kitchinites*, *Kossmaticeras* (Fig. 1.100O), *Neograhamites*, *Maorites*, *Grossouvrites*, *Pachydiscus* (Fig. 1.100S, T) and *Brahmaites* (Henderson & McNamara 1985). Also present are the heteromorph ammonites *Nostoceras*, *Eubaculites*, *Diplomoceras*, *Glyptozoceras* and *Baculites* (Fig. 1.100U) (Henderson, Kennedy & McNamara 1992) and the nautiloid *Cimomia tenuicostata* (Glenister, Miller & Furnish 1956). Maastrichtian molluscs were also recorded from a borehole in the Perth Basin where fragments of an *Inoceramus* (Fig. 1.100L) and the ammonite *Grossouvrites* were found (McNamara, Rexilius, Marshall & Henderson 1988).

Freshwater Cretaceous molluscs are rare but Ludbrook (1961) recorded the freshwater unionid *Protovirgus* in the Lower Cretaceous of northern South Australia.

Cainozoic Era

Tertiary Period. Most families of shell-bearing molluscs have left some form of record in the Tertiary sediments of Australia. Often it is possible to trace the origin of Recent marine species and genera well back into the Tertiary period. This fossil record is very patchy and dependent on the nature and distribution of the Tertiary rocks (Darragh 1985). Tertiary non-marine molluscs are not common and have been little studied. The most recent contributions are those of McMichael (1968) and Ludbrook (1980, 1984).

Apart from a few records from the Carnarvon Basin in north-western Western Australia, Tertiary tropical molluscs are not very well represented, owing to lack of suitable marine tertiary rocks outcropping in the northern half of Australia. This is not such a problem for phylogeny as it might seem, because the northern tropical molluscan fauna is a part of the Indo-Pacific molluscan fauna for which there is a reasonable fossil record in the Tertiary rocks of Burma, India, the Philippines, Indonesia and New Guinea. Shuto (1969) and van der Vlerk (1931) presented extensive bibliographies relating to this fossil fauna.

The oldest known Tertiary fauna is from the late Palaeocene shallow water sands and gravels of the Otway Basin. Molluscs are not common and the fauna is limited. The earliest records of the genera *Dentalium*, *Columbarium* (Fig. 1.101F), *Polinices*, *Cucullaea* (Fig. 1.101T), *Limopsis*, *Pinna*, *Caryocorbula*, *Anomia* and *Panopea* are found here. Other genera – *Lahillia* (Fig. 1.101Q, R) and *Australoneilo* – known only from the Tertiary of New Zealand, Antarctica and South America are not found higher in the stratigraphic column.

Late Eocene faunas are widespread across southern Australia, though outcrop is limited or the sediments are not very fossiliferous. Most of the common molluscan families and some genera first appear at this time and persist through to the present (listed in Darragh 1985). Examples are *Bolma*, *Sassia*, *Ellatrivia*, *Murexsul*, *Pteropurpura*, *Pterynotus*, *Athleta* (1.101D, E), *Notopeplum*, *Ennucula*, *Sacella* (Fig. 1.101AC), *Glycymeris*, *Arca*, *Lima*, *Chama* (Fig. 1.101U), *Salaputium*, *Dosina* and *Myodora*. Some, such as *Cypraedia* and *Orthochetus* found only at this horizon are representative of the Old World Eocene. The principal localities are Walpole and Esperance in Western Australia, Aldinga and Adelaide (Kent Town) Bore in South Australia, and Browns Creek, Victoria.

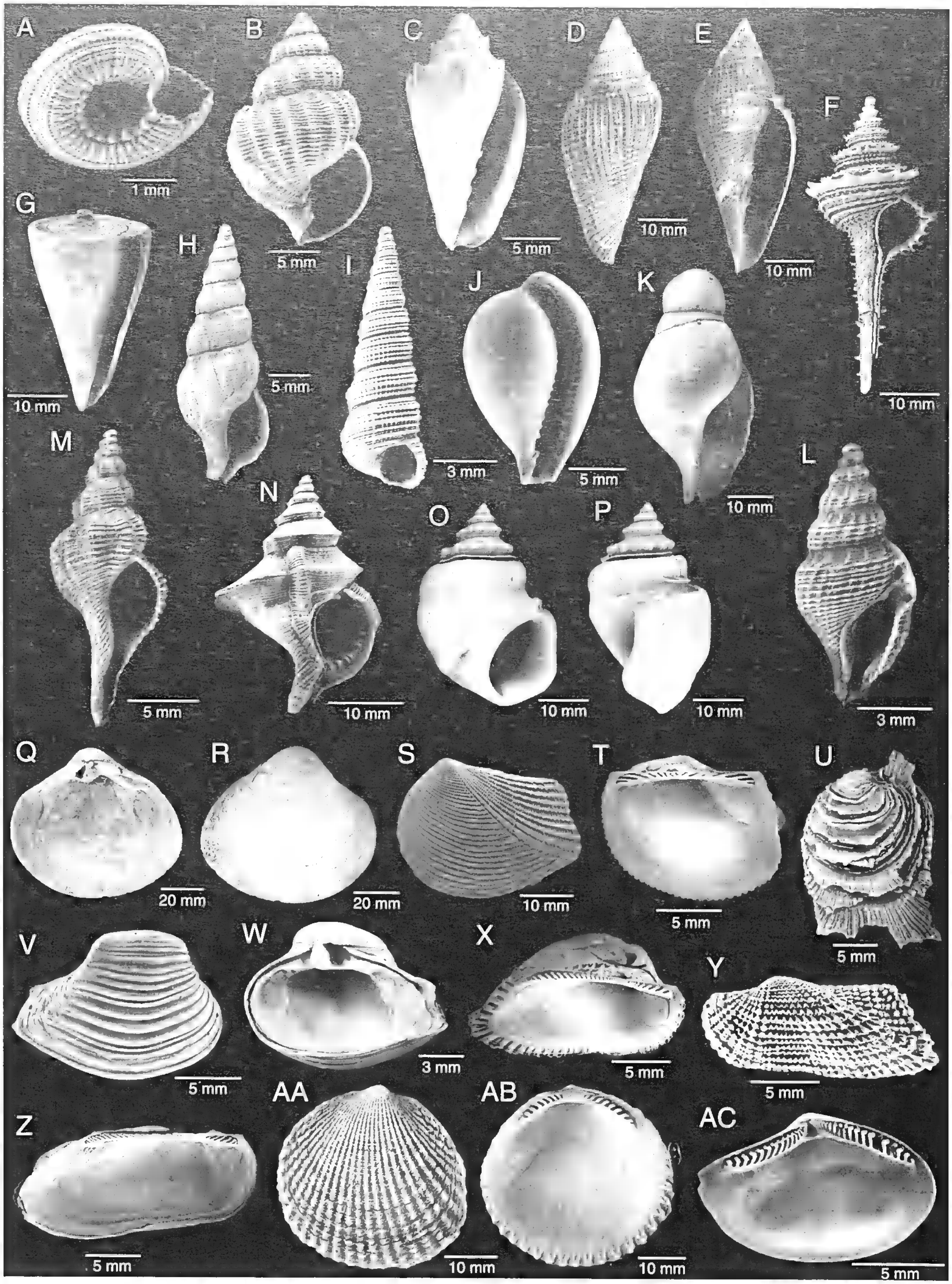


Figure 1.101. Tertiary fossil molluscs from Australia. **Q**, **R**, Palaeocene, Victoria. **S**, **T**, Oligocene, Victoria. **B**, **U**, Miocene, Tasmania. **A**, **C–N**, **V–AC**, Miocene, Victoria. **O**, **P**, Pliocene, Victoria. **A–P**, Gastropoda. **Q–AC**, Bivalvia. **A**, *Discotectonica wannonensis*, apertural view. **B**, *Bonellitia varicifera*. **C**, *Nanamoria strophon*. **D**, **E**, *Athleta (Ternivoluta) subcrenulifera*, lateral and apertural views. **F**, *Columbarium acanthostephes echinatum*. **G**, *Lithoconus dennanti*. **H**, *Dennantia ino*. **I**, *Cirsotrema transenna*. **J**, *Notoluponia pyrulata*. **K**, *Ericusa hamiltonensis*. **L**, *Etrema obdita*. **M**, *Penion longirostris*. **N**, *Austrotriton gibbus*. **O**, **P**, *Tylospira coronata* (apertural and lateral views). **Q**, **R**, *Lahillia australica* (internal and external views). **S**, *Eotrigonia subundulata*. **T**, *Cucullaea corioensis*. **U**, *Chama lamellifera*. **V**, **W**, *Notocorbula ephamilla*, (external and internal views). **X**, **Y**, *Acar celleporacea*, internal and external views. **Z**, *Notogrammatodon cainozoicus*. **AA**, **AB**, *Tucetona gunyoungensis*, external and internal views. **AC**, *Saccella vagans* (S, from Darragh 1986) [A–N, T–AC, P. Jell; O–R, T. Darragh]

The time span from Late Oligocene through to Middle Miocene is represented by abundant outcrops of a diverse range of sediments from the Eucla Basin in the west to the Gippsland Basin in the east. During this period the transgression of the Tertiary sea reached its maximum, and older deposits were blanketed. It was also the period of maximum sea temperatures which allowed many warm water Indo-Pacific taxa to penetrate southwards; examples are the genera *Crassatella*, *Pratulum*, *Solecurtus*, *Cassidaria*, *Ranella*, *Biplex*, *Eudolium*, *Concholepas*, *Tudicla*, *Eocithera* and *Baryspira*. Sediments are relatively fossiliferous and the fossils readily accessible, so that the faunas from this part of the column are very well known and form the basis of many of the papers by well-known nineteenth century palaeontologists such as Frederick McCoy, Ralph Tate, J.E. Tenison Woods, R.M. Johnson and G.B. Pritchard.

During this time two provinces developed in southern Australia – the Austral Indo-Pacific Province and the South-East Australian Province. The former is an extension of the Indo-Pacific Province in the northern half of the continent into the Eucla and St Vincent Basins of Western Australia and South Australia. This area contained warmer water than in the Otway, Bass and Gippsland Basins to the south-east. As a result, genera such as *Diastoma*, *Campanile*, *Anodontia* and *Veremolpa* are found in these basins and no further east. Such provincial differences persisted into the Pliocene.

Representative localities for the Late Oligocene occur at Bird Rock cliffs, Victoria, and for the Early Miocene at Fossil Bluff, Tasmania. Middle Miocene deposits occur at Muddy Creek and Fossil Beach, Victoria, and at Morgan, South Australia.

Late Miocene to Pliocene deposits represent a regressive phase of the Tertiary sea and sediments consisting of sands, shell beds and oyster banks were deposited in water shallower than in the Late Oligocene and Middle Miocene. Many genera, particularly gastropods such as *Xenophora*, *Notopeplum*, *Notovoluta*, *Columbarium* and *Austroharpa*, which are common in earlier periods, are rare or absent in these sediments, but still live on the shelf. Conversely, genera of shallower waters such as *Placamen*, *Bassina*, *Leiopyrga*, *Bankivia*, *Sydaphera* and *Tylospira* (Fig. 1.101O, P) appear for the first time. By late Pliocene times the fossil fauna is almost entirely composed of genera and species still living in nearby areas.

Representative localities for the Late Miocene occur at Beaumaris and Bairnsdale, Victoria, and for the Early Pliocene at Lakes Entrance, Muddy Creek and Grange Burn, Victoria. Late Pliocene fossils are found on the Glenelg River in Victoria, on Flinders Island, Bass Strait, and on Roe Plain, Western Australia. Pleistocene and Holocene deposits are confined to coastal fringes, mostly in Western Australia, South Australia and Victoria. On the east coast such deposits are uncommon. The faunas of the Pleistocene and Holocene deposits consist principally of very shallow water species. With one or two important exceptions, such as *Anadara*, all of these are still extant in adjacent areas. Valentine (1965), Ludbrook (1984) and Kendrick, Wyrwoll & Szabo (1991) have described or listed molluscs from some of these deposits.

Tertiary fossil chitons are listed by Cotton & Godfrey (1940) and Cotton (1964). All other Tertiary molluscs are listed by Darragh (1970) with a bibliography. Subsequent contributions have been made by Cernohorsky (1970), Darragh (1971, 1986, 1989, 1991), Ludbrook (1971, 1978, 1983), Smith, B.J. (1971) Garrard (1972, 1977), Ponder (1973, 1983, 1984, 1985), Vokes (1974a, 1974b, 1985a, 1985b), Ponder & Darragh (1975), Buonaiuto (1977), Fleming, C. (1978), Beu & Ponder (1979), Darragh & Kendrick (1980), Long (1981) and Janssen (1990). Ludbrook (1973) and Darragh (1985) have provided stratigraphic and biogeographic information about the Tertiary Period relating to molluscs. General references to Tertiary stratigraphy are given in the volumes on the geology of the various states and those produced by the Bureau of Mineral Resources, Canberra (now the Australian Geological Survey Organisation).

METHODS OF STUDY

Methods and Techniques in Malacology

Methods used in the study of molluscan biology, taxonomy and ecology are similar to those employed in other groups of animals. An overview of some of those that have been successfully employed is offered and certain approaches are highlighted. Space does not permit detailed description of these methodologies, and there are many other methods in molluscan research that could be added to those mentioned below.

Apart from a brief general introduction covering collecting methods, preservation and storage of molluscs, three main areas of study are described: the study of morphology, phylogeny and systematics and quantitative sampling methods employed in ecology. Methodologies for investigating embryology, development, and physiology, and the techniques associated with photography are not covered, and the reader should consult an appropriate text book dealing with those very extensive subject areas.

Collection. Molluscs occur in most habitats capable of supporting life, from alpine areas to the deep sea, from artesian springs to hydrothermal vents and from beneath the pack ice of Antarctica to the arid heart of Australia. Methods employed in collecting can therefore be very diverse, though generally they fall into two main categories – collecting by hand and the use of remote devices.

Hand collecting involves picking specimens up directly or with a hand-held sieve, scoop or rake, or sampling substrata such as mud or weed for later examination, usually under magnification. SCUBA diving, for example, is one obvious method that employs hand collecting but divers can also use an airlift pump to suck up material from the substratum for later sorting.

Remote collecting devices – for example, a dredge, benthic sledge, grab, trap/cage, trawl or a plankton net – are all attached to a rope or wire and towed or dropped, usually from a boat. These methods of sampling are characterised by the investigator 'working blind'. A remote-controlled submersible is also a remote sampling device but the catch can be selected using video cameras.

The nature of the sampling device depends upon the type of habitat to be sampled. In addition different kinds of molluscs require different collecting techniques. Whereas many macroscopic species can easily be collected by picking directly from the substratum, small-sized species are most effectively obtained by collecting the substratum in or on which they live, such as leaflitter, soil, mud, washings from weed, algae or rocks. Very few adult molluscs will pass through a 0.5 mm mesh and none through a 0.2 mm mesh. Thus sieving the fine fraction will speed the sorting process. Sorting should be done using a low-powered stereoscopic microscope or at least a strong hand lens.

Planktonic species can be obtained by means of a plankton net towed behind a boat. Midwater and benthic cephalopods are much more difficult to collect without resorting to larger gear of the type used in commercial fishing operations or in major oceanographic research programs.

When collecting, take only the material that is needed, and do this with care and consideration for the environment. Simple measures such as returning a log or rock to its original position will assist the survival of attached organisms.

Permits are required before collecting can be undertaken in some locations. In terms of the Constitution, control of the collection of components of the Australian fauna is the responsibility of the six States and two mainland Territories which comprise The Commonwealth of Australia. There are a number of administering authorities in each State or Territory and it is essential to obtain the permission of each relevant authority before collecting begins. Permission to enter any land is a separate issue which collectors should clarify with landowners before collecting. This applies especially to Aboriginal lands and heritage areas.

To assist researchers, a detailed guide to requirements for collecting Australian plants and animals is available (ABRS 1993). The guide provides the contact personnel and addresses of State and Commonwealth authorities responsible for issuing collection permits and licenses. Copies of this guide may be obtained from the Australian Biological Resources Study, GPO Box 636, CANBERRA ACT 2601; telephone (06) 2250 9430 or 2250 9443, facsimile (06) 2250 9448.

Import and export of legally collected material from Australia requires strict observance of international conventions, such as the Convention on International Trade in Endangered Species (CITES). Further information may be obtained from the Chief Executive Officer, Biodiversity Group, Environment Australia, GPO Box 636, CANBERRA ACT 2601; telephone (06) 2250 0200 within Australia, or +61 6 2250 0200 from overseas.

Preservation. It is very difficult to preserve the soft body of most molluscs adequately in a state resembling that in life, because the muscles contract and distort the body shape. Relaxation before killing and preservation can help to maintain some semblance of the shape of the living animal. Many chemical and other techniques can be used (see Van der Schalie 1953; Carriker & Blake 1959; Rosewater 1963; Runham, Isarankura & Smith 1965; Meier-Brook 1976a; Lincoln & Sheals 1985; Aranjo *et al.* 1995) but some common methods include an isotonic solution of magnesium chloride which works well on some marine gastropods and bivalves, tobacco or menthol crystals for freshwater molluscs and drowning (in a container of water with air excluded) for pulmonate terrestrial snails. Propylene phenoxetol also relaxes marine bivalves (Turner, R.D. 1960a; Rosewater 1963). Usually the animals die in an expanded state after 6 – 12 hours and should be fixed as soon after death as possible before tissue deterioration occurs. By slowly freezing live animals in water, extended preparations can be obtained, but material fixed after this form of relaxation is of little use for histology, because of tissue damage. Flash freezing can also be used (Bowler, P.A., Johnson & Mautz 1996).

Commonly used preservatives include 70% ethanol or 5% formalin seawater after fixation in 10% formalin; 90% alcohol is recommended for fixation of terrestrial pulmonates by A. Solem (personal communication). Formalin should be handled with care as it is known to be carcinogenic. It must also be neutralised or it will attack any shell material. Sodium bicarbonate to excess has proven to be a reliable, inexpensive neutralising agent. Chitons can be prevented from curling up by tying them to a flat object with cotton tape before fixation. Special fixation will be required for material to be used for purposes such as histology, critical point drying or transmission electron microscope (TEM) examination, although formalin is a reasonably good all-round fixative, and even proves adequate for TEM studies (Healy 1986c). Microwave fixation is successful with some marine invertebrates, including molluscs (Berg & Adams 1984). Material required for electrophoretic or DNA studies should be sorted alive and frozen at < -88°C as soon as possible. Fixation in 95% ethanol will also suffice for DNA studies.

Prior to fixation, the colour of the external body should be noted if this information is likely to be needed, because loss of colour will probably occur when the material is preserved. Photographs or sketches can be made to record the colour, shape and other details of the living animal before the specimens are fixed.

Shells that are to be dried should be washed in freshwater first to remove the salt and dirt. Small animals can simply be dried inside the shells, especially if they have previously been stored in alcohol or formalin. Larger animals need to be removed from the shell; this may be done by simply pulling out the body if it has been fixed previously, allowing the body to rot or by heating the animal in a microwave oven (Ryser 1985).

Storage. Shells should be stored in an acid free, dry environment. Wet material is most conveniently stored in watertight glass jars, ideally with lids constructed of a non-corroding material. Unfortunately the ideal jar has not yet been invented; metal tops corrode, plastic tops become brittle and crack and rubber seals break down, so regular maintenance is generally required.

Wet and dry material should be labelled in such a way that all essential information is readily retrieved and visible without the need to open the container, especially in the case of wet material. Labels should be on durable paper. Basic information for each specimen lot should include the locality, date of collection, the collector and habitat details. Cross referencing to a database or card catalogue is a useful way to provide access to the information in the collection in ways other than the arrangement of the material on the shelf or in cabinets – for example, retrieval of information on species found in a particular locality or habitat when the material is arranged taxonomically.

If dry specimens are stored in open boxes with loose labels, some way of tying the label to the specimens is required to prevent accidental mixing. One way to do this is to write a number or some other identification code on the specimen using Indian ink and on the label. Another way is to place the label and specimens in a clip-top plastic bag. Smaller dry specimens can be stored in glass vials stopped with cotton wool or plastic stoppers. Very small shells can be stored in cardboard slides used by micropalaeontologists, gelatin capsules, glass micro-vials or small lengths of acid-free glass tubing with cotton wool in both ends. Labels can be attached to these specimens by placing the label with the micro-container in a larger vial or small clip-top plastic bag.

Observing living molluscs. An enormous amount of biological information can be obtained from patient observations of living animals. This is one of the most neglected areas of research, and one in which amateur naturalists can make a very useful contribution. Useful data can be obtained from field observations, or by keeping living aquatic (marine and freshwater) molluscs in aquaria and terrestrial species in terraria. Photographs and videos can be taken or sketches made to record the observations in these artificial habitats or in the field.

Information on movement, shape and colour of the living animal, food preferences and feeding strategies, time of feeding – for example, night or day, or the height of the tide – reproductive behaviour, spawn, hatching of eggs, and type and behaviour of larvae can all be obtained by direct observation. Such data are available for only a very small number of Australian molluscs. Important new data can be obtained on most species, including most of the common intertidal, terrestrial and freshwater species. However, to be useful to the broader community this information must be published. Many such useful observations are published as notes or articles in shell club newsletters by amateur observers.

Investigating morphology. Shells are the most accessible part of most molluscs and consequently are very important in taxonomy, especially in distinguishing species. Examples of important aspects of shell morphology include size (for example, maximum length or width), the kind of sculpture (including its development and position), and details of the hinge in bivalves, the aperture in gastropods and the insertion plates in chitons. Most bivalves and gastropods are unusual in the animal kingdom in that they retain their larval shells – the protoconch and prodissoconch in gastropods and bivalves, respectively. These are usually clearly delineated from the adult shell and are often differently sculptured, providing an important set of additional taxonomic characters. Measurements on shells can be made accurately and in a repeatable way, but less readily on the soft bodies of molluscs which are prone to distortion. Shell measurements are thus more amenable to statistical procedures.

The study of shell morphology can often be enhanced by using a scanning electron microscope (SEM) to study microsculptural details not properly visible using a light microscope. Using scanning electron micrographs is also an ideal way to illustrate small shells.

The form of the external parts of the molluscan body can provide important morphological characters. Ideally these should be examined in living specimens, but if these are not available, well-relaxed, preserved specimens can often provide reliable information. Important characters of the living animal such as colour are often lost following preservation, as are details such as tentacle length and shape, mantle reflexion, detailed shape of the foot, and siphonal length in bivalves. Such details are extremely important in shell-less molluscs like nudibranch gastropods. Permanent records of living animals can be kept as colour photographs or sketches.

With the exception of bivalves, most molluscs have a radula. These structures are very important in classification and are readily accessible for study. The radula can be removed intact from the surrounding soft tissues by gently heating the animal, or the head only for large species, using a strong potassium hydroxide or sodium hydroxide solution, a bleach, or 0.5N quaternary ammonium hydroxide (Bleakney 1982). The radula can then be removed and cleaned of any remaining tissue in water, using fine needles or fine watchmaker's forceps. The radula should then be washed in clean distilled water.

The standard modern method of radular examination is to use a scanning electron microscope. If the radula is to be mounted on an SEM stub, it can be placed in a small drop of distilled water on double-sided tape or a thin smear of rubber cement. If the outer teeth of the radula are bent inwards, these should be spread outwards before the radula is dried in place. Breaking the radula into two or more pieces can also help to reveal details otherwise obscured by overlapping teeth. Very minute radulae can be mounted on a small piece of coverslip in water and allowed to dry directly onto the glass. The piece of coverslip can be placed under a compound microscope before drying to check that the radula is orientated correctly. The coverslip can be fixed to the SEM stub using double-sided tape. Once dry, the radula can then be coated and scanned.

Radulae for examination with a compound microscope can be dehydrated using a graded series of alcohol, then stained and mounted; various mountants are available (Turner, R.D. 1960b; Mikkelsen 1985). Temporary mounts directly from water can be made using polyvinyl lactophenol (Salmon 1949), and staining with an acid stain such as picric acid usually gives good results. Hickman (1977) recommended using both light microscope and SEM methods.

Serial section, dissection and whole body mounts are the three main methods used to investigate the anatomy of molluscs. Dissection is the most easily employed method for most molluscs. Snails are the most difficult to work with because of their coiled bodies. Black wax melted into a shallow dish or tray makes a convenient dissecting dish and enables flaps of tissue to be pinned back to expose underlying structures. The equipment needed is also simple; pins, mounted needles, fine forceps, iris scissors and a steady hand are all that is necessary. Dissection guides are available for a few common, larger taxa. Distortion of internal, as well as external, structures occurs during fixation, which hinders detailed comparisons of specimens fixed in different ways (Meier-Brook 1976b; Emberton 1989).

Material to be examined by sectioning should be properly fixed using a standard histological fixative such as Bouin's solution. Formalin fixation is also suitable but does not give the best results. Serial sections can be obtained by embedding properly fixed specimens or parts of specimens in paraffin blocks after dehydration in a graded series of ethanol and then clearing in a clearing agent. Traditionally xylene, benzine or toluene were used but non-toxic alternatives are now available. The material is then placed in paraffin heated to slightly above its melting point and the paraffin changed once or twice; if it is too hot it will harden the material making it difficult to cut. The specimen can then be orientated in the liquid paraffin and allowed to cool and set as a block. A microtome is used for cutting the block in thin sections which form a ribbon as they come off the knife. These ribbons are then floated on warm water to smooth out wrinkles and then placed onto slides. The wax is dissolved using an organic solvent and the tissue is stained before being dehydrated again, covered with a special mounting medium and protected with a coverslip. Successful histology requires considerable skill and expensive equipment. The literature is extensive but Kiernan's (1990) text provides a good introduction.

Whole mounts are sometimes useful to obtain gross details of internal structures of small molluscs, although this method is not as useful as it is with some other phyla. Basic methods can be obtained from many text books, of which Kiernan (1990) is an excellent starting reference.

Extremely detailed histology and cytology (ultrastructure) can be studied by transmission electron microscopy (TEM) to examine very thin sections. Fine surface details of soft tissue can also be obtained by critical-point drying of the soft parts of an animal or parts thereof, followed by examination of the specimen using SEM.

Chromosome number, structure and shape have been employed in molluscan taxonomy with some success. Molluscan chromosomes are typically small, however, and difficult to study. A somewhat dated summary of molluscan chromosome studies can be found in Patterson (1969) and Nakamura (1985) and detailed methods are given in MacGregor & Varley (1983). Usually chromosomes are examined by fixing tissue in which cells are actively dividing, such as the testis, in a special fixative such as Carnoy's fluid. The tissue is squashed and stained and then examined using a compound microscope. A general review of chromosomes and their study is given by Baverstock (1987).

Molecular methods. Baverstock (1987) provided a succinct overview of molecular methods, to which the reader is referred for more detail. Allozyme electrophoresis is, however, discussed below as it has had wide usage in studies on molluscan taxonomy and genetics. More recently, studies on molluscan DNA and RNA are becoming commonplace (see Hillis & Moritz 1990 for details of these techniques).

Allozyme electrophoresis has been used widely in taxonomy (reviewed by Buth 1984) and in population genetics as a method of obtaining genetic data directly and efficiently. In all life forms, enzymes are, like all proteins, genetically determined. The primary structure of each protein is of a particular sequence of amino acids joined by carboxyl bonds. Each amino acid has a different side chain, which varies in size and shape and electrical charge (positive, neutral or negative). Enzymes are used in electrophoresis because they have specific reactions with other chemicals that can be used to identify them precisely.

The electrical charge of a protein depends on the pH of the buffer in which it is dissolved. The protein is put on a substrate (referred to as a gel) which is then placed in a buffer solution. An electrical charge is applied, causing the protein to migrate at a speed determined in part by its own charge and its size. Because several samples can be run on the same gel, the comparative speeds of the same enzyme can be examined from different species or individuals.

Some enzymes are produced by more than one gene – in other words more than one protein that catalyses the same reaction in a particular animal. These different types (alleles) of a single enzyme assist geneticists in determining the genetic structure of populations. A detailed account of the methods and the analyses used in protein electrophoresis can be found in Richardson, Baverstock & Adams (1986).

Methods employed in systematics. The classification of organisms and the study of their relationships is fundamental to all biological sciences. A good general introduction is given by Cogger (1987) and this subject is outlined here only briefly. Classifying molluscs, like any other organisms, requires several processes. Typically, after collecting the animals are sorted into what appear to be different groups. This is usually done on the basis of the overall similarity of the specimens within each group and some common differences of all members of the group from members of any other group.

These similarities and differences can be loosely referred to as characters that distinguish groups (taxa). Taxa can be species, genera (groups of species), families (groups of genera) or higher groups (superfamilies, orders, classes, phyla). The species is the unit at which most taxonomy is practised – the recognition of previously named species (identification) and the naming of new species (description).

To carry out either of these tasks, the taxonomist must have access to a comprehensive library because species descriptions are scattered widely through the literature and valid descriptions date back to 1758. There is no general agreement on how much information is needed to describe a species properly. To a large extent this depends on the group but generally the more information provided the better others are able to make use of it. Sometimes information given, that may seem at the time to be of marginal interest, is vital to another research worker.

Aspiring taxonomists should note that it is undesirable for new names to be published in small circulation journals or newsletters. Publication in a widely circulated refereed journal will enable present and future workers to access the description more readily. The name for a species is usually based on a single specimen (holotype) associated with other type material (paratypes), often, although not necessarily so, from the same locality. Commonly in the past no particular single specimen was chosen, and several specimens were designated as syntypes. Subsequent workers may designate one of the syntypes as lectotype which then effectively has the status of a holotype, and the remaining syntypes become paralectotypes.

Type material should be placed in a public natural history museum so that future workers can have access to it. Unfortunately the practice of lodging types in private collections, although uncommon, still occurs and causes considerable problems if workers need access to the material. Such type material is often lost once the collector dies or loses interest. New species should generally not be described on the basis of a single specimen because it may be an abnormal animal.

The study of the relationships of organisms depends ideally on data obtained from a variety of sources. Gross morphological data are still very important and new data on the fine structure of cells and tissues obtained by using TEM and SEM are also being used to good effect. Molecular data (RNA and DNA) are extremely important and will be used increasingly to estimate the relationships of organisms at all levels. Other techniques such as chromosome morphology and immunology are also used to a lesser extent in molluscan systematics.

Two main approaches are taken to analyse data to determine relationships. One method involves looking at overall similarities or differences and is called phenetics, a branch of which is numerical taxonomy (Sokal & Sneath 1963). In the other method, cladistics, character states that define two or more taxa (synapomorphies), are found and phylogenies are estimated on the strength of the synapomorphies defining different groupings (clades); see Wiley (1981) for a detailed coverage of phylogenetic methods and theory, and Baverstock (1987) and Cogger (1987) for succinct overviews of both methods. Although both schools have firm adherents who insist that theirs is the only true way, both methodologies have their strengths, and neither, as currently practised, is ideal. However, cladistics is now generally agreed to be sounder conceptually for estimating phylogenies than using phenetic methods. Computer programs are readily available to assist the research worker to analyse data within both of these conceptual frameworks.

Quantitative Ecological Sampling of Molluscs

This section provides only a very cursory introduction to quantitative methods for studying molluscs. Most research programs require estimates of abundances for populations in natural habitats. Some studies require quantitative determination of spatial patterns (dispersion) or knowledge of size-frequency distributions.

Representative samples. The absolute abundance of a population of molluscs is rarely required. Consequently, molluscs are counted in samples of the area to provide an estimate of the density of the population, that is, as number per unit area, per volume sampled or per quadrat, core or dredge.

The choice of sampling units to sample out of the large number possible (that is, where to put the dredges, quadrats, cores, etc.) is crucial. Sample-units must be placed to provide a representative sample of the entire area. By definition, the numbers of organisms per unit in a representative sample must have the same properties – the same range, mean and frequency distribution – as the whole population. To obtain a representative sample, it is customary to take a *random* sample of the population. This may be achieved by dividing the whole area into a grid of the size of the quadrats to be used in the study and random squares in the grid are sampled. The random sample can be obtained objectively by choosing coordinates in the grid from a table of random numbers (for example, Fisher & Yates 1963). Randomly chosen transects can be sampled with a trawl, or random coordinates within the study area can be chosen to take a grab or core sample.

Choosing a random sample does not guarantee a representative sample; it only ensures that unconscious bias on the part of the sampler does not influence the sample taken. In general, the more units that are sampled the more likely the overall sample is to be representative (for example, see Snedecor & Cochran 1980).

Accuracy of a sample. Ideally, the accuracy of a sample must be known, that is, how closely the number per unit estimated from the sampled units actually represents the true number per unit for the population as a whole. Unfortunately, the only way to determine the accuracy of a given method of sampling is to count an entire population and compare the numbers with those estimated from a sample. Considerations of accuracy are, however, important, as discussed by Andrew & Mapstone (1987).

Inaccuracy is caused by biases in sampling. Such biases are the result of any process that causes a sample to misrepresent the true numbers in a population. For example, if a beam-trawl is used to sample benthic molluscs in soft-sediments, individuals smaller than the mesh of the trawl will not be retained. The estimated density per trawl will inevitably be less than the true magnitude for the population. Here, the population must be redefined to identify the subset of animals that can actually be counted. Failure to define the population properly with regard to the sampling procedure will lead to bias in the samples and confusion in other workers' attempts to compare data.

Accuracy is also affected by the way animals are caught in, extracted from and counted in the samples. Fortunately, most molluscs other than cephalopods are relatively slow-moving and cannot avoid sampling units.

Often, absolute accuracy is not required. Most studies require comparisons from time to time in a site and/or comparisons among sites at a single time. Even though the actual numbers are not known very accurately at any one time or place, if the methods of sampling used are equally accurate, or equally biased, in all sites or at all times, spatial differences or temporal changes in the population can still be detected reliably.

Independence of samples. Independence of sample-units is the most important consideration of sampling (Cochran 1947; Eisenhart 1947), yet is apparently the least understood requirement of simple sampling (Underwood 1981b; Hurlbert

1984). For all statistical estimation from samples, the individual sample-units must be independent of one another; each sample-unit must be taken without any relationship to the numbers found in other sample-units.

Consider what happens when counting numbers of animals in quadrats (as sample-units) if the quadrats are placed non-independently. This would happen if, for example, quadrats were placed in pairs in the study area. Only the first of each pair is placed in a random position and the second of each pair is placed immediately adjacent to it. If the animals being counted are clumped, as they often are, such non-independently placed pairs of quadrats will seriously underestimate the spatial variance of the animals, and will thus overestimate the precision of the sample. Whenever one quadrat happens to be in or out of a clump, its partner has a greater chance of also being in, or out of, the clump than would be expected for an independently placed second quadrat. Half of the quadrats in the sample have more similar numbers in them than would be expected from independent units sampled properly. Random sampling ensures independence of the samples and is recommended as the best strategy to solve the potential problems of non-independence. Where non-independent samples are taken, statistical procedures for comparing samples from time to time and place to place, and the calculation of precision of the sample are unreliable (for example, see Eisenhart 1947; Winer 1971).

Precision. The other important attribute of a sample is its precision, that is, how repeatable is the density estimate gained from the sample. If the sample provides a precise estimate, similar samples would provide similar estimates of the mean density of the molluscs. Conversely, if a sample provides an imprecise estimate of the mean density, it must be considered more doubtful. A similar sample would furnish a quite different estimate of the mean density.

Unlike accuracy, precision can be determined from the sample. In any area to be sampled, there is variation from place to place for all sorts of reasons, such as selection of microhabitats by the animals, or chance variation during recruitment from the plankton. As a result, the numbers of animals found in randomly placed sampling units vary, reflecting the variance in spatial distribution of molluscs in the region sampled. When the variance of a population is large, a small random sample may be quite different from the whole population. A second such sample would be somewhat different from the first, and a single sample can only provide a rather imprecise estimate of the density of the molluscs. In contrast, where the variance from place to place in a study area is small, repeated random samples would all be rather similar and any one would provide a reasonably precise estimate of average density.

Any sample provides an estimate of the variance of the population and this can be used to estimate the precision of the estimated density. Methods for estimating precision involve calculating the sample standard error or confidence limits around the estimated mean (see any good textbook such as Winer 1971; Snedecor & Cochran 1980).

Size of sample. The aim of most sampling programs is to produce the most precise estimate of abundance possible within a particular set of logistical constraints imposed by the environment, time and the level of funding available. Clearly, a large sample – one with more sample-units – taken from any population must be more representative of the whole population than is a small sample. A large sample therefore provides a more precise estimate of the numbers per sample-unit.

It is very important to determine in advance of any sampling program the appropriate number of sample-units to achieve the required precision. Details of the various methods available, including pilot studies, cost-benefit analyses, sequential sampling and so forth, can be found in Cochran (1963), Green (1979), Underwood (1981b) and Andrew & Mapstone (1987).

The precision achieved must be sufficient for the aims of the research program. Suppose, for example, the number of molluscs in some area is to be monitored to detect pollutants in the system. Serious pollution would cause at least one third of the animals to die. The mean number per square metre might be estimated as, for example, 60 ± 30, but the true mean might be as small as 30 or as large as 90. With such imprecise sampling, a change in numbers from 60 to 40 could not be detected, because the original numbers estimated from the first sample might have been as small as 40, making it impossible to conclude that any change has taken place. In this case, precision of sampling must be increased; larger samples would decrease the error with which the mean is estimated and make it possible to detect smaller changes. Sampling programs should be discussed with competent statistical advisers before beginning the work, clarifying why the numbers need to be known, and what the consequences would be if samples were imprecise.

Stratified sampling. Molluscs are not usually scattered equally throughout all parts of a habitat. On rocky shores, in beaches and mangrove swamps, many species show quite marked differences in density from the top to the bottom of the shore. Animals often show considerable selection for microhabitats (Meadows & Campbell 1972). As a result, estimates of numbers in the entire area sampled are usually much less precise than estimates in each level on the shore or in each microhabitat.

Stratified sampling involves subdivision of an area to be sampled, allowing random sampling to be done in smaller or more homogeneous areas called strata. Sample-units within each stratum will contain similar numbers of animals and a sample of units in any stratum will have a smaller sampling variance and therefore greater precision than will a single large sample taken from the whole area.

Stratification is a major tool for increasing the precision of sampling. It also allows information to be gathered about the spatial variation in numbers of a population and provides some insight into the sorts of habitats that contain large or small numbers of a given species of mollusc. Stratification is discussed in detail by Cochran (1963) and a good example is available in Green & Hobson (1970).

Dispersion. When the actual spatial pattern, or dispersion, of the molluscs must be known, some types of sampling are unsuitable. For example, samples from beam trawls or any moving dredges or nets may not be appropriate because they slurry together the specimens from the entire distance covered, whereas box-cores will preserve the small-scale spatial structure of assemblages in soft sediments (see Warwick, Gee, Berge & Ambrose 1986). Photographic transects or quadrats of organisms on hard substrata will preserve their spatial patterns (see Underwood 1976b). Analyses of spatial pattern are discussed in Pielou (1969), Underwood (1976b, 1976c) and Andrew & Mapstone (1987).

Sizes of molluscs. Sizes and growth rates of molluscs are often determined in field samples. Most molluscs have conspicuous hard parts making them easy to tag and recover to measure growth. Apart from obvious comments that random samples are necessary for estimating growth and that statistical analysis of sets of samples is quite complex, one technique has considerable virtue for molluscs that are easy to handle. Instead of using callipers to measure each individual, Cassie (1954) invented a simple device to minimise the time required to measure large samples. Every research program that involves measurement of shells of molluscs should consider this method. Analyses of growth are discussed by Cassie (1954), and a useful computer package has been developed by Pauly & David (1981).

CONSERVATION

Molluscs are one of several invertebrate phyla which together comprise 95–99% of animal life. However, the agendas of conservation organisations worldwide are largely dominated by vertebrates, especially mammals and birds, and by forests. The

1994 edition of the IUCN Red Data Book (Groombridge 1994) showed that of all major groups, the largest number of documented extinctions occurred among non-marine molluscs; in addition, non-marine molluscs were second only to arthropods for the largest number of threatened species. Despite this, there has been very little research into non-marine molluscan conservation, partly because most malacologists work on marine molluscs. Also, in common with the situation for other invertebrate groups, there has been a lack of funding because of minimal political and public interest, often no legislative framework, and the bias of most government and non-government conservation organisations towards vertebrates and higher plants (for example, Ehrlich 1992; Ponder 1992b, 1995b; Wells, S.M. 1995).

Australia's environmental record is poor; it has, for example, one of the highest clearance rates of native vegetation in the developed world (see Graetz, Wilson & Campbell 1995) and high extinction rates for vertebrates. Some 60% of the forest cover in all categories has disappeared since European settlement (Graetz *et al.* 1995). Eastern Australian rainforests have been reduced to about half of their former extent (AUSLIG 1990).

Even the less populous states have suffered major impacts as a result of land clearing and pastoral activities. Many of these changes to terrestrial environments have had an adverse impact on the habitats of land and freshwater molluscs which, typically, have very specific habitat requirements and, often, restricted distributions.

Two main approaches can be identified in the considerable and healthy debate about the most appropriate conservation strategies to maintain biodiversity: a species-based approach and a habitat or community approach (for example, Franklin 1993). The present discussion cannot do justice to the many complex general issues relating to conservation and the reader is referred to New (1995) for an excellent summary of invertebrate conservation biology.

Within an ecological framework, the following groups of species are thought to deserve special conservation consideration (for example, Noss 1990; New 1995): *indicator species* – those which could provide an early indication of environmental changes, although the term can have several distinct meanings (Spellerberg 1993); *keystone species* – those upon which the functionality and diversity of a large component of the ecosystem depends; *umbrella species* – those that require large areas for their protection, thus assisting the survival of other taxa living in the area; *flagship species* – popular species. A fifth category of *vulnerable species* – those prone to extinction – can also be recognised.

Whereas molluscs readily fall into the first and last of these categories, most species lack general popular appeal and none can be compared with, say, a large mammal or a tree as a keystone or umbrella species. There is also a danger that by adopting a primarily 'keystone species' approach, as advocated by some (Mills, Soulé & Doak 1993; Jones, G.P. & Kaly 1995), most attention will continue to be focused on a very tiny, but obvious, fraction of biodiversity. Conservation strategies which are based primarily on ensuring that representative portions of main habitat types are protected are also inappropriate for the conservation of endemics with limited, or narrow, ranges. Not all species are equal and, given a choice, a higher priority might be given to those taxa representing distinct lineages rather than putting resources into saving a taxon very closely related to several others (for example, Vane-Wright, Humphries & Williams 1991). However, such choices require a well-constructed phylogeny of the group concerned, a luxury not available for many Australian vertebrates, let alone molluscs and other invertebrates. Clearly, a range of approaches will be necessary for the conservation of biodiversity to be successful.

Australian Non-Marine Molluscan Fauna

In order that the reader may realise its conservation value, the nature of the Australian land and freshwater molluscan fauna is summarised briefly.

Excluding species from Lord Howe and Norfolk Islands, which are treated separately below, the native land and freshwater molluscan fauna of Australia consists of 1020 described species (244 freshwater, 796 terrestrial; Smith, B.J. 1992, and subsequent papers to June 1995; Table 1.7). A further 55 taxa are introduced (Smith, B.J. 1992, and subsequent papers). Of the native species, only 14 (1.4%) occur naturally outside Australia. Thus land and freshwater molluscs have a very high endemicity, even by Australian standards (98.6%, compared with: mammals, 82%; birds, 45%; reptiles, 89%; vascular plants, 85%).

Table 1.7 Species-group taxa of freshwater and terrestrial molluscs listed by B.J. Smith in 1992, with the number of species-group taxa named since his compilation in parentheses. The number of species-group taxa restricted to the State or Territory are in square brackets. Numbers of threatened species follow Groombridge (1994).

	New South Wales	Queensland	Victoria	South Australia	Western Australia	Northern Territory	Tasmania	Total
Freshwater taxa								
Total	42	56(58)	37(45)	34	31	27	42(98)	178(244)
Endemic	[11]	[24]	[16]	[11]	[20]	[8]	[86]	[176]
Threatened	1	13	5	9	1	0	60	88
Terrestrial taxa								
Total	140	234(236)	50	72(99)	226(230)	71(94)	44	743(796)
Endemic	[79]	[172]	[20]	[83]	[201]	[52]	[35]	[642]
Threatened	18	26	13	19	63	21	7	167
Total taxa	182	290(294)	87(95)	106(133)	258(262)	98(121)	86(141)	901(1020)
Endemic	[90]	[196]	[36]	[94]	[221]	[60]	[121]	[818]
Threatened	19	39	18	28	64	21	67	255

The Australian non-marine molluscan fauna is reasonably well known in comparison with most other non-marine invertebrate groups, although 30–40% of taxa, particularly small land snails, remain undescribed, according to B.J. Smith (1992). A more likely estimate is about 50%, with the total non-marine fauna comprising around 2000 species. Most of the named freshwater fauna (72% of 176 species-group taxa) and the named terrestrial fauna (81% of 642 species group taxa) are restricted to a single State or Territory.

The terrestrial molluscan fauna. The terrestrial fauna is diverse and includes some spectacular species. Of the described fauna, the Camaenidae, a family of large-sized species, is by far the largest. The 406 valid, named species-group taxa comprise 51% of the named terrestrial land snails. Many of these species have very small distributions. The second-largest family, the Charopidae, includes 128 small-sized, named, valid species-group taxa, forming 16% of the named native fauna. Together these groups total about half the unnamed land molluscs of eastern Australia (Stanisic 1994). Of the 23 Australian terrestrial mollusc families, the Helicarionidae (60 taxa), Pupillidae (40 taxa), Bulimulidae (31 taxa), Punctidae (23 taxa) and Pupinidae (19 taxa) are important. Of particular concern is the need for modern comprehensive reviews and revisions which will result in new information on the current status of many species.

The freshwater molluscan fauna. The large-sized freshwater molluscs are not particularly diverse, including only 17 species of freshwater mussels (Unionoidea: Hyriidae) and, according to our current classifications, very few large gastropod species. Apart from the hyriids, corbiculid species (two), viviparids (six) and thiariids (nine), small-sized forms make up most of the fauna (nine families). The hydrobiids are by far the most diverse family (117 named species-group taxa comprising about half the actual number of species), and many species have very restricted distributions (Ponder 1994).

Most families of freshwater molluscs are in urgent need of species-level revision: Planorbidae (about 40 valid species), Corbiculidae, Viviparidae, Bithyniidae, Pomatiopsidae, Thiaridae, Assimineidae, Glacidorbidae and Lymnaeidae. More undescribed freshwater taxa are known in Assimineidae, Bithyniidae, Viviparidae and Glacidorbidae than are currently described in those families.

Threatened taxa. The great majority of threatened and virtually all of the extinct mollusc species are from terrestrial or freshwater habitats.

The 255 threatened Australian taxa (see Table 1.7) listed in the IUCN 1994 Red List represent only some of the Australian non-marine species that meet the IUCN criteria for listing as threatened. Many more will be added as more details on their distributions and status become available. Other species belong in groups which require taxonomic revision but the largest group of unlisted taxa are species which await description.

Many undescribed narrow-range camaenids are known, especially from Western Australia, the Northern Territory and Queensland. Charopids are speciose in eastern Australia and many undescribed species have very narrow ranges, especially those on limestone outcrops. Many narrow-range hydrobiids are also unnamed, especially from Tasmania and mainland south-eastern Australia.

Extinctions. About 80% of the 284 documented extinctions of molluscs (Groombridge 1994) are on oceanic islands. There are no published records of confirmed extinctions of non-marine molluscs on the Australian mainland to date, although the extinction of at least four Tasmanian hydrobiids is suspected (W.F. Ponder personal observations). However, this lack of confirmation probably reflects the general lack of systematic and/or well-documented early collecting in many areas which are now entirely rural and urban, as well as the poor taxonomic state of many groups.

Undoubtedly many hydrobiids have become extinct in the last 200+ years, especially along the north coast of Tasmania, as a result of their considerable localisation and high vulnerability in permanent, mainly lowland streams. However, apart from a few observations such as those noted above, there is no direct evidence to support this claim because of the general lack of early systematic collection and documentation.

Drawdown from extraction of artesian water since the turn of the century has destroyed many of the artesian (mound) springs associated with the Great Artesian Basin (Habermehl 1982; Ponder 1986b), including almost all those in north-western New South Wales. Considerable endemic aquatic invertebrate faunas are associated with many of these springs, including 24 hydrobiid species (Ponder 1986b). None of these invertebrate faunas (with one exception) was recorded until the 1980s, and they are still poorly known. Thus, it is probable that extinctions of significant undocumented faunas have occurred.

Near extinctions of viviparids have been reported in the Murray River – the only known surviving population of one of these species lives in a few irrigation pipelines (Sheldon & Walker 1993a, 1993b; see also Molluscs of Inland Waters, this Chapter). Another species, extinct in the Murray, is known from a few populations elsewhere. At the time of writing the vivipariids in the pipelines are in imminent danger of being exterminated because they pose a nuisance through clogging the spray nozzles (K. Walker personal communication).

Similarly, there is very poor information about the molluscan fauna in most of the extensive tracts of forests that were cleared for agriculture in south-eastern Australia and Tasmania before the middle of last century. The few molluscs collected at that time were largely picked up as objects of curiosity, or by/for private collectors, and data associated with the extant specimens is generally very poor.

In northern New South Wales and Queensland much of the lowland coastal rainforest was cleared for growing sugar, commencing in the latter half of last century with marked expansion through most of the 1900s. The first detailed survey for molluscs in east coast rainforests was undertaken by the Australian Museum in mid-eastern Queensland in 1975. At 10 surveyed sites, 42% of the 92 species collected were undescribed (Colman & Burch 1977).

Modification of vegetation and other aspects of the habitat by rural activities has occurred over more than half of Australia, but in the absence of systematic collecting prior to the most of the habitat modification, the level of impact, including extinction, on molluscan and other invertebrate faunas, will never be known.

Genetic studies. Conserving genetic diversity is a stated aim in the conservation of biodiversity (for example, DEST 1993). As a minimum, an understanding of the genetics of at least a subset of taxa is required to understand the population structure, dispersal capabilities and distinctive nature of particular groups of taxa (for example, Daniell 1994) in order to formulate management strategies. To date, the amount of genetic information available for Australian non-marine taxa is very limited. Studies include those of Stoddart (1983, 1985; thiarids), Ponder and colleagues (Ponder, Colgan, Clark, Miller & Terzis 1994; Ponder, Eggler & Colgan 1995; Ponder, Colgan, Terzis, Clark & Miller 1996; hydrobiids), Woodruff & Solem (1990; a camaenid), Hill, Johnson & Merrifield (1983; *Bothriembryon* species) and Daniell (1994; cystopeltid slugs).

Threatening Processes

Effects on habitat. About 50% of Australia's rainforests have been cleared in the last 200 years (AUSLIG 1990), especially in north-eastern Queensland, the southern half of Queensland and northern New South Wales. About 33% of the existing forest lies between Cooktown and Ingham in northern Queensland. Most of these forests occur in areas with more than 1200 mm annual rainfall. Rainforests rarely occur more than 150 km from the coast and most of the lowland rainforest has been cleared for agriculture.

High levels of land clearing still occur in Australia (Alexandra 1995), although much of this is probably in areas that are not important molluscan habitats. Generally, the remaining wet forests, particularly rainforests, are being protected, although forestry activities still have a significant impact in some areas. Although forestry activities currently affect only about 2% of the total land area of Australia (AUSLIG 1990), forested areas are amongst the most important habitats, from the point of view of mollusc conservation.

State forests, and some National Parks, carry out regular 'control burning'. Some work on the impacts of this management strategy on litter and soil invertebrates in dry forests has been done, but there are no data on its impact on molluscs, although it is probably considerable.

Urban development affects little more than 0.1% of the land area but it is often concentrated in areas of importance as mollusc habitats, as with forests.

The impact of rural activities is far more significant. In total, pastoral activities affect about 60% of the land area. Although much of this occurs in dry country of little significance to molluscs, it also includes some of the pockets of high endemism. Pastoral activities can have a strong impact on vegetation and otherwise disturb and pollute habitats. Overgrazing is not uncommon and can have serious long-term effects on vegetation and soil. Although intensive cropping and animal production occupy only about 10% of the land area, these activities are focused in the wetter parts of Australia and destroy the habitats that are of importance to native molluscs.

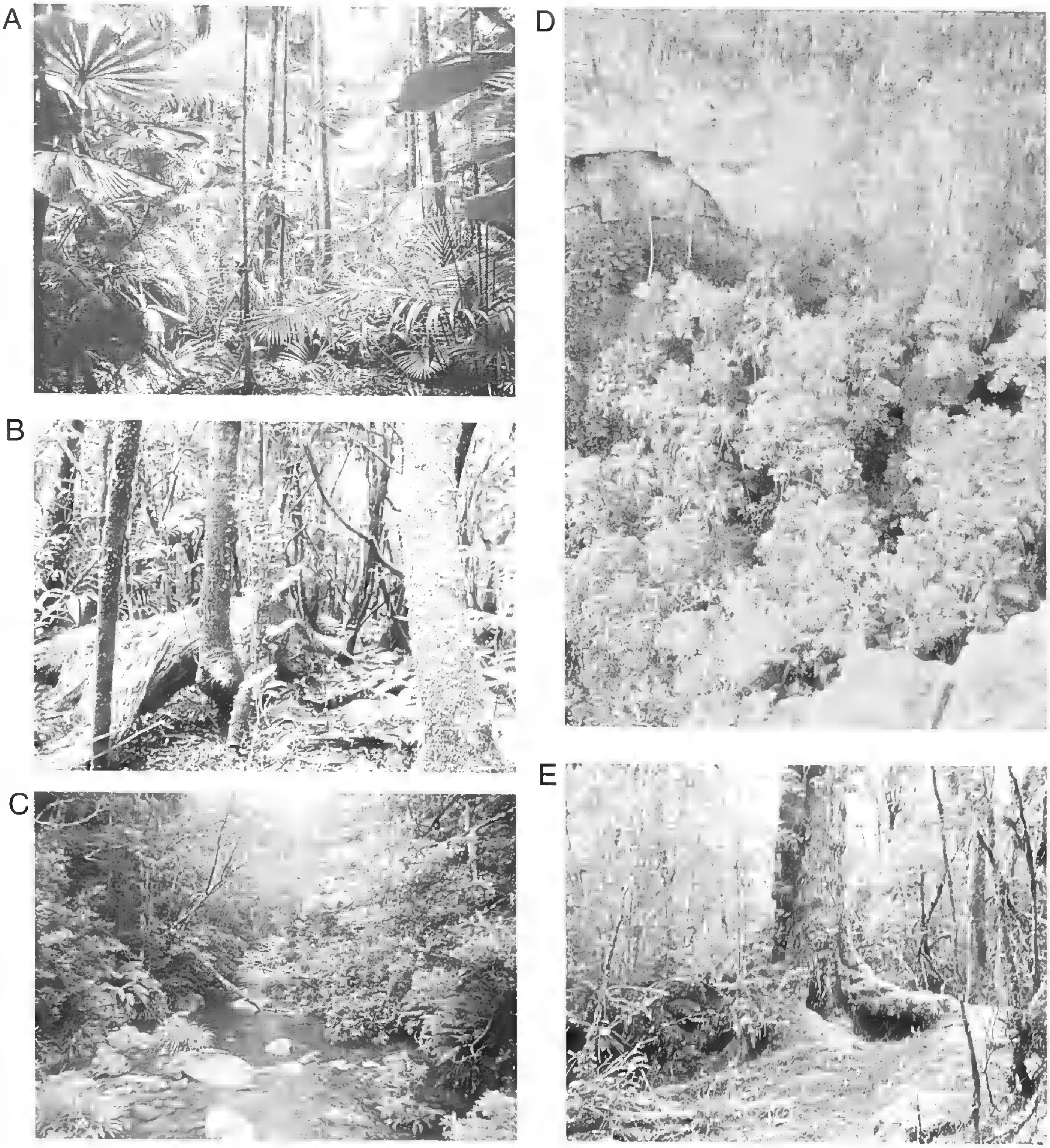


Figure 1.102 Examples of Australian rainforest habitats. **A**, tropical coastal forest at Mission Beach, near Tully, northern Queensland. **B**, tropical montane forest at the summit of Mt Bellenden Ker (1600 m ASL), northern Queensland. **C**, a subtropical forest stream, Gibralter Range National Park, northern New South Wales. **D**, a pocket of tropical rainforest in the gorge of Tolmer Falls, Tabletop Range, Northern Territory. **E**, temperate *Nothofagus* forest in Tasmania. [M. Fagg]

Mining, particularly of limestone, could have serious impacts on locally endemic taxa, although it affects only a very small proportion of the total Australian landscape. Limestone areas are particularly vulnerable, because their cave and surface faunas are often highly localised. In the main, systematic collection in these habitats has only begun in the last 10 years. Clearing of trees from limestone areas for rural activities has probably had a serious effect in some areas.

Salinisation is a common problem in Australia, particularly in the irrigation areas along the River Murray. Although there are very few data on the effects of this phenomenon on mollusc populations, it is undoubtedly having an impact.

Land clearance, particularly from mining, rural and forestry activities also affects aquatic faunas through its effect on streams and rivers, such as siltation and changes in water quality (for example, Michaelis 1984b; Campbell & Doeg 1989). Dams and other forms of water regulation seriously affect molluscs and other animal groups (Walker, K.F. 1985). However, there are few data on these effects for most areas. Pollution from urban, agricultural and mining activities are presumably affecting animal species and some data support this (Ridge 1995). Mining effluent also affects stream and river faunas, including molluscs (for example, Norris, Lake & Swain 1982).

Introduced species. Introduced species are recognised as one of the most serious threats to populations of native species (Clout 1995).

There are no data on the impact of introduced animals, such as rats, on native land molluscs, although casual observation suggests this may be important locally. Stock and feral animals, such as rabbits, pigs, goats, horses, camels and water buffalo, all have a heavy impact on native vegetation and water courses and increase erosion. Clearly they have a significant effect on molluscan habitats, especially in drier areas. Litter-dwelling molluscs would also be susceptible to trampling by stock and large feral animals.

Introduced fishes (Tilzey 1980; Pollard & Burchmore 1986) pose a threat to native fishes, aquatic molluscs and other aquatic invertebrates. Amongst the most important of these are brown and rainbow trout (for example, Jackson 1981) which feed on a wide variety of invertebrates, including molluscs (Evans, J.W. 1942; Wilson, J.H. 1966). The introduction of European carp and grass carp has also had a serious impact on the Murray-Darling system (Pollard & Burchmore 1986) and these fish are likely to spread to other systems in the next few decades.

In Australia, 55 introduced mollusc species have been recorded, of which 10 live in freshwater and the rest are terrestrial (Smith, B.J. 1992, and subsequent papers). Most of these are found in rural and urban areas, mainly in the southern, south-eastern and south-western coastal areas and Tasmania (Smith, B.J. 1981, 1992; Kershaw 1991). Some helicids (see Smith, B.J. & Kershaw 1979; Baker 1989) and limacid slugs (see Altena & Smith 1975) are significant economic pests (see Molluscs as Plant Pests, this Chapter). Little, if anything, is known about the interactions between native and introduced taxa but this, in some areas at least, could have an impact on native species. For example, *Potamopyrgus antipodarum* from New Zealand is now abundant in many south-eastern Australian freshwater systems and may be competing with native species (Ponder 1988).

Ill-informed biological control measures have directly resulted in the extinction of large numbers of terrestrial mollusc endemics on Indian Ocean and Pacific Islands (Clarke, B., Murray & Johnson 1984; Murray, Johnson & Clarke 1988; Kinzie 1992; Griffiths, Cook & Wells 1993). The voracious predatory snail *Euglandina rosea* was introduced to many islands to reduce the numbers of the giant African snail, *Achatina fulica*, and instead has decimated native species. On Moorea the native species of *Partula*, intensively studied as an evolutionary model (Murray & Clark 1980), were wiped out only five years after the introduction of *Euglandina rosea*, an action undertaken there and elsewhere despite considerable protest from the malacological community.

The New Guinea flatworm, *Platydemus manokwari*, is the most recent factor in the snail devastation biological control saga. Originally introduced to Guam in the late 1970s, it rapidly spread and is a serious threat to native snails (Eldredge 1994). Now this species is also having a very serious impact on native molluscs in other parts of the Pacific. Although in Australia much more consideration is given to the introduction of such pests, the New Guinea flatworm is now present in some suburban areas of North Queensland. There are also plans to attempt to control the introduced pest helicid snails in southern Australia using supposedly host specific flies, beetles or flies (Eldredge 1994).

Conservation Strategies and Priorities

The belief that conservation of habitats for targeted organisms (namely vertebrates and higher plants), or on a representative ecosystem basis, will provide effective conservation for invertebrates is well entrenched. Whereas this may be effective for many widely distributed species (which are typically at low risk), it is generally inappropriate for many of the taxa of high conservation significance such as narrow-range endemics, including many relict taxa. However, general conservation interests and those of molluscan conservation coincide in some areas, either because of general conservation concerns for important habitats such as rainforests, or because of happy accidents, where areas set aside for conservation include important areas for narrow-range endemic invertebrate taxa, often inadvertently (for example, limestone cave reserves).

Terrestrial habitats. The conservation of rainforests is critical for molluscan conservation; such areas form only about 4.5% of Australian forests but contain a large proportion of the terrestrial molluscan taxa. Existing rainforests occupy only about 20 000 sq km (0.26% of Australia, including Tasmania), mainly along Australia's east coast (Webb & Tracey 1981; Walker, J. & Hopkins 1984) with a few small areas of monsoonal rainforest patches from Cape York Peninsula in the north-east to the Kimberley in the north-west.

The tropical rainforests of north-eastern Queensland have a rich endemic fauna and flora and are identified as having a particularly high conservation significance (DEST 1994). They extend over some 921 000 ha from sea level to the summit of Mt Bartle Frere (1622 m) and are very important habitats for land molluscs (Fig. 1.102; A, B Stanisic 1994). Dry rainforest (vine thickets) inland from the coast in Queensland have lower diversity, averaging about 10 species, although inland areas of moist refugia or limestone have higher diversities (Stanisic 1994).

Figure 1.103 Limestone outcrops, such as these at Ningbing Ranges, Western Australia, are often important centres of high molluscan diversity.
[W.F. Ponder]

Figure 1.104 Endemism in terrestrial molluscan faunas occurs in refugia found in arid regions, for example, Stokes Creek Canyon, Watarrka National Park, Northern Territory. [W.F. Ponder]

The subtropical rainforests of south-eastern Queensland and New South Wales (Fig. 1.102C) also contain diverse molluscan faunas (Colman & Burch 1977; Stanisic 1994). A total of about 447 000 ha remains, mostly in state forests or national parks. They generally support a lower diversity of land snails than their tropical counterparts (Stanisic 1994). Land snail diversity in these habitats appears to decline southwards, and is relatively low in Victorian and Tasmanian rainforests. Areas associated with limestones in the Macleay Valley peak in species diversity at 36 but in most sites in northern New South Wales 10–20 species are usual (Stanisic 1994). There are few areas in the world in which the land mollusc diversity exceeds 30 species (Solem 1984b) so mid-eastern and north-eastern Australia are of world significance in this regard.

Monsoonal rainforests are found in small isolated patches across northern Australia (Fig. 1.102D). Molluscs of most of those in northern Australia are poorly documented but the Kimberley rainforest patches have been surveyed (McKenzie, Johnston & Kendrick 1991). These contain a rich molluscan fauna (Solem 1991; Solem & McKenzie 1991) with 115 species recorded, all but 22 of these being camaenids. On average, there are 12.5 species per rainforest patch, including 3.7 camaenid species, in patches varying from less than 1 ha to more than 20 ha. The mean species range for camaenids was about 20 km in diameter and about 64% of camaenids were recorded from only one or two patches.

Temperate rainforests, typically dominated by *Nothofagus*, are found in Victoria and Tasmania, although the greatest area (456 000 ha) is in Tasmania (Fig. 1.102E). These forests contain a distinctive, but less diverse, molluscan fauna.

The relict nature of many of the areas of Australian rainforests emphasise the point made above about local endemism. Although the conservation significance of these habitats seems obvious, either because of their relict status or because their area is now restricted, such rainforest remnants are still being cleared and are considered of little or no conservation value unless they are large enough to maintain large vertebrates. However, such areas can be vital for the continued existence of locally endemic invertebrates, small plants and even small vertebrates.

The remaining 95.5% of Australian forests are mostly dry forests of which about 67% are dominated by eucalypts. Such forests are generally poor habitats for terrestrial molluscs, although wet sclerophyll forest (mixed eucalypt and rainforest species) can contain diverse faunas. Rainfall can be high in some areas with eucalypt forests but even in these areas molluscan faunas typically appear to be sparse, probably because of low water retention in soils in general and regular fires. However, dry forests can be important habitats when local topography or geology establishes suitable conditions for refugia.

Other terrestrial areas of high conservation value are largely circumscribed by geological and/or geomorphological features which make them suitable as very long-term habitats. Limestone outcrops are of particular importance (Fig. 1.103), as endemicity of terrestrial species in these habitats is usually high. This is especially true in eastern Queensland and New South Wales (Stanisic 1994), and in north-western Western Australia as shown in the numerous studies by Alan Solem. Where limestones occur in rainforests, diversity is particularly high (Stanisic 1994). Limestone habitats are often protected, at least in part, if they are associated with caves. However, many other outcrops are not protected and are often mined.

Arid zone refugia, particularly deep gorges and canyons (Fig. 1.104), can be very important, especially if associated with limestone. There are rich camaenid faunas in the Kimberley (Solem 1979, 1981a, 1981b, 1984a, 1985, 1988a, 1988b, 1988c, 1991), Flinders Ranges (Solem 1992a, 1992b) and the gorges of central Australia (Solem 1993), and a few endemic species occur in coastal areas along the Great Australian Bight (Solem 1992a, 1992b). In an important review of arid zone refugia (Morton, S.R., Short & Barker 1995), terrestrial and aquatic molluscs were taken into account. However, when assessing the relative conservation importance of particular habitats only threatened vertebrates (ANZECC listed species) were considered.

Aquatic habitats. W.D. Williams (1980b) gave an overview of the distinctive features of Australian inland waters, and the conservation of Australian aquatic habitats in general was reviewed by Lake (1980) and McComb & Lake (1988). The only national review of the conservation of the Australian inland aquatic fauna is that of Michaelis (1986), who also discussed the Tasmanian freshwater fauna (Michaelis 1984a). Only a few molluscs were noted in these accounts.

The few large rivers in Australia have a rather low diversity of freshwater molluscs and other freshwater animals compared with North America. Most of the hyriids are widely distributed, although *Hyridella glenelgensis* (south-western Victoria) and *H. moretonicus* (Tasmania; McMichael & Hiscock 1958) are exceptions. Viviparids are typically widespread but two species which were once widespread in the Murray-Darling river system are now severely restricted due to river control (Sheldon & Walker 1993a, 1993b). The river control measures in the Murray River also appear likely to affect other mollusc species (Walker, K.F., Thoms & Sheldon 1992).

Coastal rivers in northern Australia contain a molluscan fauna of reasonable diversity, although generally diversity is low compared with South-East Asia and Papua New Guinea. Thiaridae, the most diverse family, are low in diversity in most areas and Neritidae, a conspicuous family in rivers in many nearby tropical areas, are absent in many northern Australian rivers.

Figure 1.105 Many rivers and streams in Tasmania, such as this one in the south-western region, harbour endemic hydrobiid species. [J. Waterhouse]

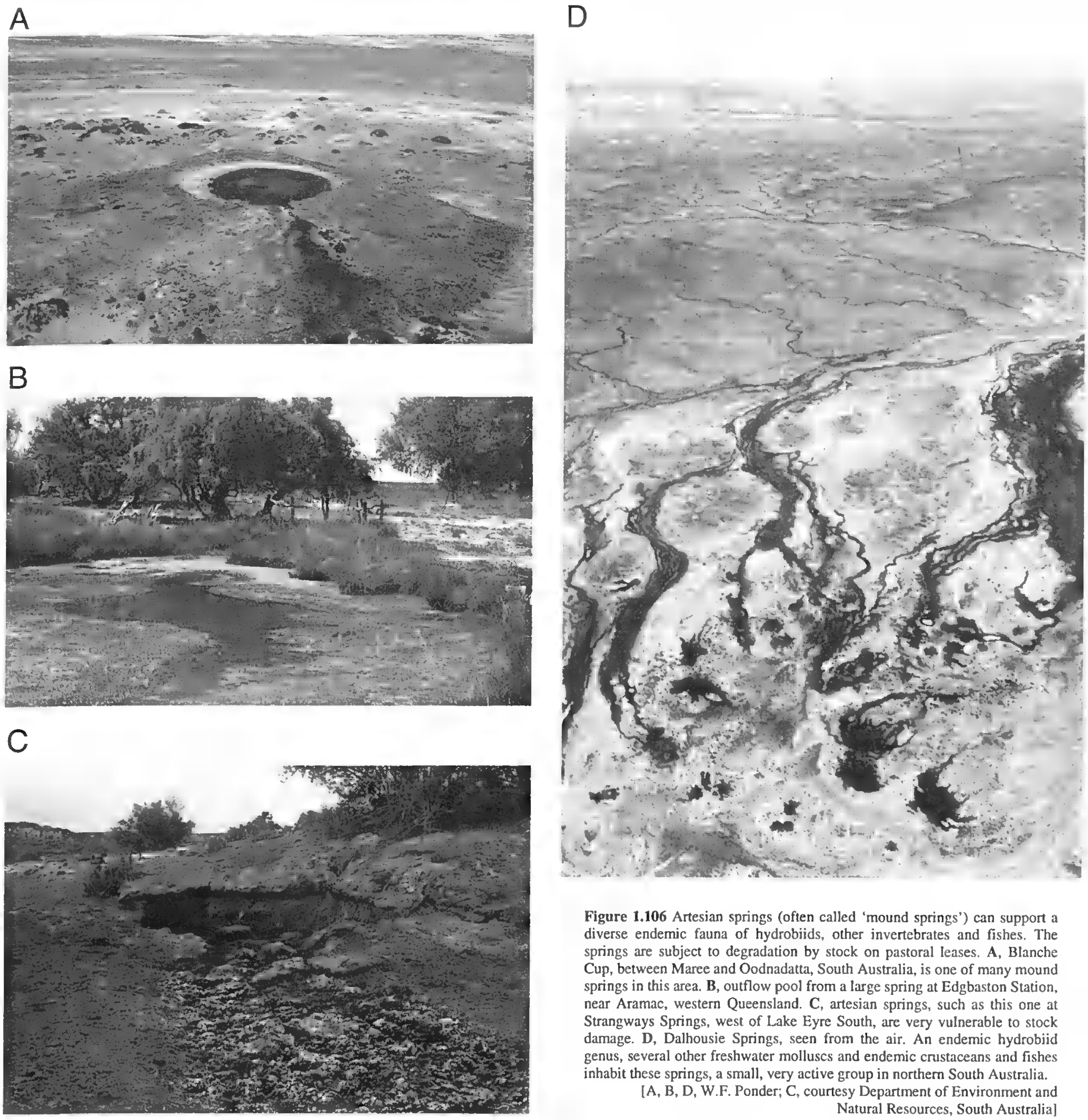


Figure 1.106 Artesian springs (often called 'mound springs') can support a diverse endemic fauna of hydrobiids, other invertebrates and fishes. The springs are subject to degradation by stock on pastoral leases. **A**, Blanche Cup, between Maree and Oodnadatta, South Australia, is one of many mound springs in this area. **B**, outflow pool from a large spring at Edgbaston Station, near Aramac, western Queensland. **C**, artesian springs, such as this one at Strangways Springs, west of Lake Eyre South, are very vulnerable to stock damage. **D**, Dalhousie Springs, seen from the air. An endemic hydrobiid genus, several other freshwater molluscs and endemic crustaceans and fishes inhabit these springs, a small, very active group in northern South Australia.
[A, B, D, W.F. Ponder; C, courtesy Department of Environment and Natural Resources, South Australia]

In geological terms, most Australian lakes are very recent and do not contain endemic molluscan faunas (for review see Timms 1980). A few Tasmanian lakes, particularly Lake Sorrel, Lake Crescent and Great Lake, are older and contain a few endemics (Fulton 1983), including some molluscan taxa. At least one hydrobiid species appears to have become extinct in Great Lake following its damming and the resultant rise in water level in 1922.

Small streams and, to a lesser extent, local ground-water seepages and springs are the major habitats of most hydrobiid species in south-eastern and south-western Western Australia. Ponder (1994) has argued that these taxa have very poor powers of dispersal, on grounds of their restricted distributions and local genetic differentiation (Ponder *et al.* 1994), and are good indicators of long term permanent water. The areas containing these stream-associated molluscan faunas are (in order of decreasing diversity) Tasmania (Fig. 1.105; Ponder, Clark, Miller & Toluzzi 1993), Victoria, eastern South Australia (and the Flinders Ranges), southern New South Wales, northern coastal New South Wales, southern coastal Queensland, Northern Territory and south-western Western Australia. Several undescribed and highly localised assimineids are now known from springs in north-western Western Australia (Pilbara and Kimberley) and in the Northern Territory.

The artesian springs associated with the Great Artesian Basin (Ponder 1986b) are almost all located in arid areas and are very important habitats for a large number of indigenous aquatic invertebrates and fishes (Fig. 1.106; Ponder 1986b; Morton, S.R. *et al.* 1995). Now recognised as a significant component of Australia's biodiversity (DEST 1994; Morton, S.R. *et al.* 1995), most of these springs are still on pastoral leases, where they continue to be threatened directly by stock (Fig. 1.106C) and the sinking of bores resulting in local and general drawdown. Nevertheless, about 24 endemic hydrobiid species are known from the remaining springs associated with the Great Artesian Basin (Ponder, Hershler & Jenkins 1989; Ponder & Clark 1990; Ponder, Eggler & Colgan 1995).

Locally endemic aquatic molluscan faunas do not appear to occur in non-artesian springs, billabongs and other water bodies in the arid areas of Australia, including those in areas such as Palm Valley and other gorges in central Australia (see Davis, J.A., Harrington & Friend 1993 for general account of aquatic invertebrates) that contain land snails, and other endemic and relict plants and animals (W.F. Ponder personal observations). Wetlands such as freshwater swamps and marshes in non-arid areas are not known to contain very localised faunas but have the same faunas seen in other water bodies such as billabongs.

An indigenous genus and species (*Pseudotricula eberhardi*) described from Precipitous Bluff caves in south-western Tasmania (Fig. 1.107; Ponder 1992c), is one of at least 13 hydrobiid species (the rest are unnamed) now known to inhabit these caves. A few unnamed hydrobiid species occur in other cave systems in Tasmania, some New South Wales caves and sink holes in South Australia, and two unnamed species were collected from a cave in the Northern Territory. Eberhard (in manuscript) has shown that siltation caused by limestone mining operations resulted in a significant reduction in the population of a cave-living snail in south-eastern Tasmania. At least one unnamed hyporheic hydrobiid is known from the Flinders Ranges (Cooling & Boulton 1993).

Salt lakes (Williams, W.D. 1986, 1993, 1995) are common in Australia and are the habitat of the endemic pomatiopsid genus *Coxiella*. Although the taxonomy of *Coxiella* is in need of revision, currently nine species are recognised (Smith, B.J. 1992). These animals are often inconspicuous but in some localities their empty shells are extremely abundant (Fig. 1.73). Tasmanian populations of *C. striata* are considered to be threatened. Some biological information on one species is available (Williams, W.D. & Mellor 1991).

Habitat protection. Non-marine molluscs are absent or have a very low diversity in many Australian habitats but, by world standards, they are diverse in some habitats. Although the details of important areas need to be identified, in general, rainforests, wet sclerophyll forests, damp gorges (especially in some arid areas) and limestone areas are of special importance. Freshwater systems generally have low to moderate diversity, with endemism low or absent in many areas. Notable exceptions are the artesian springs associated with the Great Artesian Basin, and rivers and streams in parts of Tasmania and south-eastern Australia. Many of these localities and habitats of great importance to mollusc conservation are not afforded any protection.

Frequent fires, especially 'control' burning for 'fuel reduction', is probably a significant contributor to the low molluscan diversity in many dry forests. Virtually no studies have been carried out on how various fire management practices impact on mollusc faunas. The few studies that have been carried out on invertebrates have concentrated on the more actively mobile members of the ecosystem.

Current Measures. At present, four Australian States recognise invertebrates as fauna – Victoria (*Fauna and Flora Guarantee Act 1988*; see Butcher, Clunie & Yen 1994); Tasmania (see Invertebrate Advisory Committee 1994); Western Australia (*Wildlife Conservation Act*); New South Wales (*Threatened Species Conservation Act 1995*). Until this situation is redressed in Queensland and both Territories, a serious attempt to conserve the molluscan fauna (and other invertebrates) of Australia will not be possible. The Commonwealth *Endangered Species Protection Act 1992* presently lists only two invertebrate species – the freshwater crustacean, *Astocopsis gouldi*, and the giant earthworm, *Megascolides australis*. Tasmania has listed all the threatened species identified in that state in the IUCN list (Groombridge 1994), but Victoria has yet to list any molluscan species (for example, Butcher & Doeg 1995).

National strategies for improvement of land management practices include reserve systems encompassing representative habitats, total catchment management (for example, Williams, W.D. 1980c; Martin, P. & Lockie 1993) and the beginnings of a national approach to river management (for example, Hart 1993). Many of these strategies concentrate on the main river systems but much of the molluscan (and probably other invertebrate) diversity is focused in small permanent or semi-permanent headwater streams.

At present, among invertebrate zoologists, entomologists, are pressing hardest for invertebrate conservation and mollusc conservation generally has a low profile. For example, non-marine molluscs were barely mentioned in a recent issue of the *Victorian Naturalist* (volume 112, 1995) devoted to invertebrate conservation. However, three papers on molluscs were published in the proceedings of the first meeting on Australian invertebrate biodiversity and conservation (Ingram, Raven & Davie 1994) and at the second meeting in Melbourne (1995) 10% of 70 papers dealt exclusively with molluscs. On an international level, the Mollusc Specialist Group of IUCN is preparing an Action Plan for non-marine mollusc conservation with a brief coverage of all countries. To date, the only published IUCN invertebrate action plan is for swallow-tailed butterflies (New & Collins 1991).

Figure 1.107 Caves at Precipitous Bluff, south-western Tasmania, are home to at least 13 endemic hydrobiid snail species. These caves are located in the South-Western World Heritage area, but elsewhere such habitats are vulnerable to human activities including tourism and mining. [S. Eberhard]

Captive breeding. This approach must be seen as a last resort and will never be appropriate or practical for the great majority of severely threatened species. However, several European zoos are successfully breeding species of *Partula*, some of which are extinct in their native habitats (Tudge 1992; Gerlach 1994), and breeding of endangered species of the Hawaiian genus *Achatinella* is also in progress (Hadfield 1995).

What needs to be done? Before much progress can be made it is of critical importance that Queensland and the Territories amend legislation to enable invertebrates to be recognised as fauna and to enable them to be listed as endangered taxa. This will facilitate the conservation of habitats of great importance to molluscs, such as limestone areas and mound springs, as well as remnant rainforest

Figure 1.108 Lord Howe Island, viewed here northwards over low montane rainforest (foreground) from Mt Gower past Mt Lidgbird, is the home of many endemic gastropods. [I. Hutton]

and other important forest patches too small to be considered significant for vertebrate conservation. Such action could be aided by a requirement for state government agencies to consider the presence of narrow-range molluscan (and other invertebrate) endemics in assessment procedures such as Environmental Impact Statements. In the short term, as a general rule it is important that remaining rainforests and other wet forests be afforded high conservation priority.

Much of the damage to aquatic habitats could be avoided if land owners and other land management agencies conserved adequate strips of riparian vegetation, paying particular attention to the heads of streams. These strips are also important refuges for terrestrial taxa. High priority should be given to the protection of streams known to contain narrow-range endemics.

No additional data are needed for many of the above actions to be implemented. However, prioritisation of, for example, wet forest remnants, limestone outcrops, streams, and arid zone refugia requires better data than we have at present. An efficient way of determining areas of high conservation significance is the identification of 'hot-spots' (for example, Myers 1988; Eisner, Lubchenco, Wilson, Wilcove & Bean 1995). An important step forward in this process would be the databasing of existing state museum collections of non-marine molluscs. Such data could greatly facilitate assessment of diversity as well as identification of areas in need of further survey work.

Additionally, encouragement and support for the production of field guides, identification keys and interactive CD-ROM-based keys will greatly facilitate the use of molluscs (and other invertebrates) in survey work. In parallel with this, monographic studies on problematic groups of Australian non-marine molluscs are needed urgently.

Apart from taxonomic and distributional data, there is virtually no information on the biology and ecology of Australian non-marine molluscs. Such basic data gathering is vital to our understanding of how we might best facilitate the long term survival of many taxa. Coupled with this, work on impacts on molluscs needs to be encouraged and facilitated. For example, there are virtually no data on the long term affects of fire, damming, salinisation, pollution or exotic taxa, including other molluscs, on Australian molluscs.

Lord Howe Island and Norfolk Island

These two small oceanic islands are dealt with separately because their faunas are almost entirely endemic and have special conservation significance.

Lord Howe Island. Lying 700 km NE of Sydney at 31° 30'S, 159° 05'E, this small island is volcanic in origin and is about 7 million years old (McDougall, Embleton & Stone 1981). Its 15 km^2 area is dominated by Mt Gower (866 m) and Mt Lidgbird (765 m) (Fig. 1.108). The rural areas, settlement and airstrip are in the middle part of the island, and the northern end is hilly (up to 218 m). The island was proclaimed a World Heritage site in 1982.

The whole island was originally covered in dense rainforest and since 1981 nearly 70% has been protected as a Permanent Park Reserve. Such natural areas are located mainly on the southern and northern ends of the island. The only aquatic habitats are many, often permanent, streams and seepages which are especially numerous on the southern end of the island (see Ponder 1982 for details).

The biota of the island is highly endemic, with 105 of the 459 species of vascular plants being endemic. Eight of the 15 indigenous bird species are now extinct. Introduced cats, dogs, pigs, goats and rats, along with humans, have all had a major impact (Recher & Clark 1974).

The size of the terrestrial molluscan fauna was last reviewed by Iredale (1944b) who listed 79 species and nine subspecies in 30 genera, although Solem (1974b) estimated 51 species and B.J. Smith (1992) lists 69 native terrestrial species. Of the 10 families present, the most diverse are the Helicarionidae

(18 species-group taxa), Charopidae (17 species-group taxa), Diplommatinidae (14 species-group taxa) and Punctidae (11 species, with several undescribed, Climo 1981). The lowland form of *Placostylus bivaricosus* and another large snail *Gudeoconcha sophiae* are still extant in wooded areas in the northern and middle parts of the island. No recent review of the fauna has been undertaken although collecting in the last couple of decades has provided a very useful source of additional material. Many of the small species are still extant.

The freshwater molluscan fauna comprises an ancylid (Ponder 1981a) and a remarkable hydrobiid fauna (Ponder 1982) with 15 named endemic species-group taxa in three genera.

Only 12 species are listed in the 1994 IUCN Red List (Groombridge 1994) – eight hydrobiids, three assimineids and one hydrocenid. This listing does not reflect the true nature of the situation. For example *Placostylus bivaricosus* is certainly threatened, being restricted to a few very small colonies which suffer from rat predation. Some of the small land snails restricted to lowland parts of the island are also potentially threatened through habitat loss. Data are needed urgently on these taxa and their current distributions.

There have been some extinctions of large land snails on Lord Howe Island. Rats were introduced in 1918 from a grounded ship and rapidly became abundant. They played a major role in the loss of five of the bird species (Recher 1977) and evidence from dead shells suggests that they were probably largely responsible for the extinction of at least two large land snail species (Smithers, McAlpine, Colman & Gray 1977). A large mountain-dwelling species, *Epiglypta howinsulae*, is almost certainly extinct (Stanisic 1981), as is a local 'form' of *Placostylus bivaricosus*, *P. b. etheridgei.* Both of these taxa occurred in the well-forested southern part of the island. A 'form' of *Placostylus*, *P. cuniculinsulae*, from Rabbit Island is now extinct (Smithers *et al.* 1977; Hutton, I. 1986), as apparently are the other supposed endemics (see Iredale 1944b) from that island.

Pigs and goats, once serious pests, have now been eradicated. Various programs to control rats have been implemented since the 1920s but have had little real success. Thus, even taxa with their distributions inside reserves are still at serious risk from rat predation. Most of the hydrobiids are within reserves, but two highly threatened species outside the protected areas will need special action if they are to survive.

The terrestrial molluscan fauna needs to be reassessed and revised, using the extensive collections now available (mainly in the Australian Museum) and supplementary field studies. Recovery plans for the immediately threatened taxa need to be developed as a matter of urgency.

Norfolk Island. Of volcanic origin, the island was formed on the Norfolk Ridge about 3 million years ago. It lies at 29° 02'S 167° 56'E, 1675 km ENE of Sydney and 1065 km N of Auckland. It is about 8 km long and 5 km wide with a total area of 3455 ha. The average elevation is about 100 m with two hills (Mt Pitt and Mt Bates) rising to about 316 m. The climate is mild and subtropical with a winter minimum of 7°C and a summer maximum of 29°C; rain falls throughout the year and totals an average of some 1350 mm annually. When discovered in 1774 by James Cook, Norfolk Island was uninhabited, although, unlike Lord Howe Island, there is evidence of previous occupation. The island has been settled since 1788. A large island, Phillip Island, 258 ha in area, is little more than 6 km from Norfolk and rises to 280 m. Nepean Island is just off the coast and is only 4 ha in area. Terrestrial molluscs have been described from all three islands.

In contrast to Lord Howe, Norfolk Island has been much modified by human activity. Since 1788 much of the original vegetation has been cleared. There is a large resident population (about 1800), a substantial tourist population (3000 beds, with around 20 000 visitors per year), a very high car ownership and a total of 80 km of roads. Much of the island has been cleared for farming – mostly cattle of which there are up to 2000 – housing and roads. The only substantial reserve is the Mount Pitt Reserve (410 ha; 11.9% of the land area in contrast to 70% on Lord Howe Island), which was not fenced until the early 1980s and consequently suffered much damage from stock.

The native forests are rainforests, dominated by the Norfolk Pine (*Araucaria heterophylla*). These are now largely reduced to small remnants, and the Mt Pitt Reserve. The vegetation on the steep seacliffs (primarily the 'flax' *Phormium tenax*) also provides a relict habitat for land snails. Much of the vegetation is now dominated by introduced weeds such as *Lantana* and guava.

Iredale (1945) reviewed and catalogued the terrestrial molluscs. These were also catalogued by B.J. Smith (1992) who recognised 66 native species in nine families. Of these the Helicarionidae are by far the most diverse (35 species-group taxa), with the Charopidae (14 species-group taxa) the other major family. There are also five species-group taxa in the Diplomatinidae and Punctidae.

The environmental degradation of the island and the introduction of feral animals have resulted in the extinction of five of the 14 endemic land birds and several plants. A recent survey of the terrestrial molluscan fauna of Norfolk Island has been undertaken by R. Varman and he found (communication) that at least five species are now extinct. However, the current status of many species is uncertain. Iredale (1945) recorded three endemic taxa on Phillip Island which was completely stripped of vegetation by feral animals by the time of his review, and these species are now almost certainly extinct, along with an endemic parrot. Eradication of the few remaining rabbits began in the early 1980s and the island is now becoming revegetated, perhaps providing a refuge for some of the endangered taxa on the main island.

The only recorded freshwater mollusc, the hydrobiid *Posticobia norfolkensis*, is extinct (Ponder 1981b).

An assessment of the current status and distribution of the terrestrial molluscan fauna is required urgently so that detailed management plans can be recommended. In the short term, all habitats with native vegetation should be considered potentially important for molluscan faunas.

The Australian Marine Molluscan Fauna

There are perhaps more than 15 000 species of marine molluscs in Australian waters. However, compared with non-marine faunas, there are few immediately obvious problems with the conservation of marine molluscs. In fact there are very few documented extinctions of marine invertebrates in the last 200–300 years (Carlton, Vermeij, Lindberg, Carlton & Dudley 1991; Carlton 1993). Many marine species have large ranges and planktonic larvae and are unlikely to become threatened, although local extinction through habitat destruction, or possibly over-collecting, may be possible. Massive and indiscriminate shell gathering by local people in areas such as the Philippines has resulted in local denudation of shores (Wells, S.M. 1982; Gomez, Aliño, Yap & Licuanan 1994) and this can be exacerbated by concurrent habitat destruction in many areas from, for example, use of explosives for fishing, as well as from pollution, runoff from land clearance, and development.

Massive over-collecting is generally not a problem in Australia where local regulations usually prohibit such activities and the commercial return would be inadequate for the effort that would have to be expended. Illegal fishing for giant clams (Tridacnidae) and *Trochus* shell can be a problem in some areas, and fishing operations for these taxa in the past have reportedly depleted numbers severely in many areas. In more general terms, considerable concern has been expressed about the state of the marine environment in Australia (Phillips, Hutchings & Walker 1993; Jones, G.P. & Kaly 1995) and elsewhere (Norse 1993). As with the terrestrial environment, most attention has been focused on vertebrates, although coral reefs (as habitats) have also attracted considerable attention and resources.

The mollusc species listed by IUCN (Groombridge 1994) include all species of Tridacnidae, which are also listed by CITES. Whereas the large *Tridacna* species are certainly very vulnerable, it is probably not the case with the smaller species, namely *Tridacna maxima* and *T. crocea*, both of which can be extremely common, are not exploited in many areas (including Australia) and have very wide geographic ranges. Local extinctions of some tridacnid species have been reported in parts of their range (Wells, S.M., Pyle & Collins 1983; Heslinga, Perron & Orak 1984; Munro 1989). Some other marine molluscs are sometimes regarded as commercially threatened, for example, the pearl oysters (*Pinctada maxima* and *P. margaritifera*) and the green snail (*Turbo marmoratus*) which all occur in tropical Australian waters. *Concholepas concholepas* from western South America and the Caribbean Queen Conch (*Strombus gigas*) are other species that have been considered to be commercially threatened. Commercially exploited molluscan species occurring in tropical Australian waters almost all have wide Indo-West Pacific distributions (for example, *Trochus niloticus*; Nash 1985; Goldman 1994). Species of abalone (Haliotidae) are very intensively fished, particularly in Australia, California and Japan and, without careful management, can be severely depleted locally (see Fisheries and Mariculture, this Chapter).

Starmülhner (1988) reviewed information on rare and threatened marine molluscs worldwide but to date there is no reliable list of potentially threatened Australian marine molluscs. In one attempt, Fry & Robinson (1986) listed many species as vulnerable, with no supporting evidence. Many of the taxa they listed are widely distributed and in no way threatened, although their list has been cited as authoritative (for example, Jones, G.P. & Kaly 1995).

Normally collecting for commercial specimen shells in Australia targets species of particular interest to shell collectors, especially species with a high commercial value (Willan 1986). A few large predatory species, such as *Charonia tritonis* and *Cassis cornuta* are so conspicuous, and their shells so desirable as ornaments, that they are potentially vulnerable locally to human collecting activities, both commercial and recreational. However, these species are relatively common and of little commercial value. In contrast, species desired by serious shell collectors are typically more difficult to obtain, usually reasonably large, often colourful, and normally found in inaccessible areas, putting them beyond the reach of the average collector. Prized taxa are found in a few families, such as the Cypraeidae (cowries), Volutidae (volutes), Conidae (cones) and Muricidae (muricids) (see Shell Collecting, this Chapter). Many of these species are found mainly by SCUBA divers, as bycatch from trawling operations or by dredging. A few of these, with direct development and low fecundity, are restricted to small geographic areas and are in reach of SCUBA divers or even intertidal collectors. Some of these latter species may be potentially threatened.

Criteria for assessing the conservation status of marine species are largely based on terrestrial situations and are generally not appropriate for marine taxa (Jones, G.P. & Kaly 1995). They suggest that species potentially at threat in the marine environment have one or more of the following characteristics: unusually restricted in range (applies to some molluscs); unusually restricted breeding sites (unlikely to apply to most molluscs); very large, long-lived and/or have low fecundity (applies to some molluscs); subject to large-scale mass mortality; subject to prolonged periods of recruitment failure; highly susceptible to environmental stress; extreme habitat specialists; live exclusively in supratidal, intertidal, estuarine and coastal embayment habitats (especially those restricted to the most populated areas); and are subject to over-exploitation.

Although many taxa have large ranges (see Marine Distributions, this Chapter), some are restricted in distribution. Perhaps the most notable example is *Smeagol*, a genus of small interstitial slugs restricted to pebble beaches, a rare habitat in Australia. Several species of this genus occur in Australia, where they are known only from single locations (Tillier & Ponder 1992).

Habitat destruction and environmental pollution or modification are probably the most serious threat to local molluscan communities. While reclamation, mangrove clearing, and marina developments are very visibly destructive to the natural environment, other less obvious activities are also having a serious impact. The major destructive activity over large areas of the sea floor is bottom trawling by commercial fishermen. This activity destroys epibenthic organisms which provide food and shelter to whole communities of animals (Hutchings 1990). More serious local impacts are caused by scallop dredging, sand mining and other similar activities which affect the infauna as well as the epibenthic organisms. Although marine protected areas have become established in Australia in recent years, most of these encompass only the intertidal and shallow sublittoral regions. In 1992, 267 such areas covered about 400 000 sq km (McNeill 1994).

Introduced exotic species can at least partially displace native species, even within protected areas. During an attempt to establish oysters (*Ostrea lutaria*) from New Zealand in Tasmania late last century, several other species may have been accidentally introduced (Dartnall 1969; Hutchings *et al.* 1987; Pollard & Hutchings 1990). These included *Maoricolpus roseus*, a turritellid which is now dominant on the sea floor in parts of Tasmania and has also spread to the mainland, and some bivalve species which have also become established. An Asian oyster, *Crassostrea gigas*, was introduced to Tasmania in the late 1940s (Thompson, J.M. 1952) and has now spread into New South Wales where it competes with the native rock oyster in some areas. A large Asian starfish, *Asterias amurensis*, is now common in the Tamar Estuary and feeds on small molluscs (Buttermore, Turner & Morrice 1994). This is one species, among others, that is thought to have been introduced on the hulls of ships and in ballast water (see reviews by Hutchings *et al.* 1987; Pollard & Hutchings 1990; Hutchings 1993).

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CLASS APLACOPHORA

CHAPTER 2

DEFINITION AND GENERAL DESCRIPTION

The Aplacophora are worm-shaped marine molluscs covered by a cuticle invested with innumerable calcareous spicules (Fig. 2.1; Pl. 7.1). Most species are small, often less than 5 mm in length, but some attain 300 mm. The head is poorly differentiated. There is a small posterior mantle cavity. Although the aplacophoran shape is specialised, the organ systems such as the radula, integument, gonad-pericardium, muscles and nervous system reflect a primitive molluscan condition.

The class comprises two distinct subclasses, the Neomeniomorpha and Chaetodermomorpha. Neomenioids have a ventral groove within which there is a narrow foot. Chaetoderms lack a groove or foot, and have a cuticular shield around the mouth.

Aplacophorans are mostly continental shelf and deep-sea forms. Eleven families, 17 genera, and 33 species from the continental shelf of Australia and Macquarie Island are considered in this chapter. These are based on the author's identifications of material collected recently, much of it unpublished. Most of the large collection from the upper continental slope off south-eastern Australia requires identification and has been excluded. Salvini-Plawen (1978a) has described Aplacophora from off the Australian Antarctic Territories, which are not treated here. No aplacophorans have been reported from the islands of Lord Howe, Cocos (Keeling), Christmas or Norfolk, although a few species are known in the region of Heard Island (Salvini-Plawen 1978a).

Because of their general inaccessibility, the study of aplacophorans has been based primarily on fixed material from depths exceeding 30 m. Observations on living neomenioids have been made on only 24 species (Scheltema & Jebb 1994, Table 1). One neomenioid genus, however, affords a unique opportunity for experimental and observational research – *Epimenia* in the monotypic family Epimeniidae. *Epimenia* species are large (> 100 mm) and occur throughout the Indo-Pacific at depths accessible to divers and are easily kept in aquaria at ambient temperatures. Details of collection and habitat appear under the Family Epimeniidae below. Observations on living chaetoderms are more restricted and have depended on dredged material (Salvini-Plawen 1968a). However, if kept cool and provided with sediment, *Chaetoderma* and *Limifossor* species can be maintained in the laboratory (Wirén 1892a; Heath 1904a; A.H. Scheltema personal experience).

HISTORY OF DISCOVERY

Chaetodermomorphans and neomeniomorphans were first discovered in Scandinavian waters in 1844 and 1875, respectively. Subsequently, aplacophorans were recognised in collections dredged by early oceanographic expeditions before 1915, and from inshore dredgings, especially in the vicinities of European marine research stations. It was not until the early 1960s that improved equipment, sieving techniques and systematic sampling provided adequate representation of continental shelf and deep-sea macro-infaunal populations (Sanders, Hessler & Hampson 1965). Aplacophorans are now known to form a numerically small but consistent element of the deep-sea fauna (Gage & Tyler 1991), but particular species are sometimes numerically dominant in quantitative samples (Scheltema 1985, 1997). Recent studies on the inshore meiofauna have shown that aplacophorans often occur as part of the sand meiofauna (Morse 1979; Salvini-Plawen 1985a).

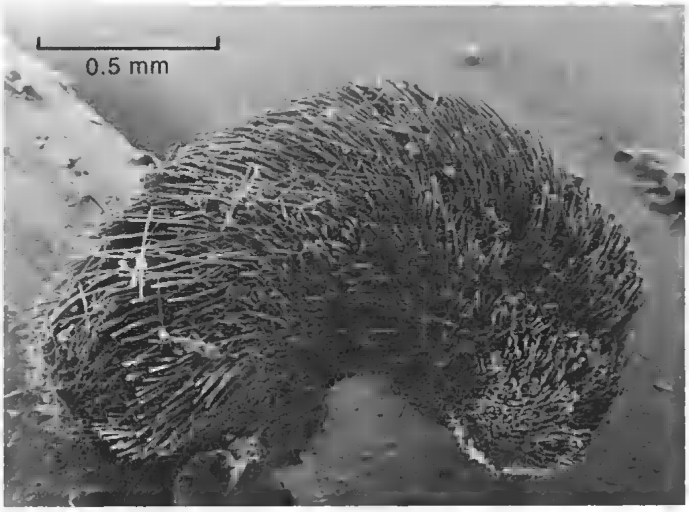

Figure 2.1 A neomenioid aplacophoran *Eleutheromenia* sp. (Pruvotinidae) from Bass Strait. Normally upright, the spicules have been depressed by the preparation for the scanning electron micrograph.
[A.H. Scheltema & A.M. Kuzirian]

Five late 19th and early 20th century expeditions dredged in Australian waters, or collected Pacific and Indian Ocean aplacophoran species or members of genera that may also occur off Australia – those of the *Challenger*, *Gazelle*, *Valdivia*, *Siboga* and *Albatross* (Selenka 1885; Thiele 1897, 1902a, 1902b, 1906; Nierstrasz 1902; Heath 1911; Stork 1941). Other aplacophorans have been described from off Japan, the Red Sea, Bass Strait, Macquarie Island and the Chatham Islands (Baba 1940a; Salvini-Plawen 1969, 1978a, 1988a; Ponder 1970; Ivanov 1984).

Nearly a century has elapsed since Thiele (1897, 1902c) described the first neomenioids *Epimenia australis* and *Notomenia clavigera* from off northern Australia. The next collections were made only recently, when surveys were conducted from 1975 onwards on the shelf of the Great Barrier Reef, Macquarie Island and Bass Strait, and the continental slope off south-eastern Australia. They include five chaetoderm species from the slope and shelf (Scheltema 1989), the first of this subclass to be reported from Australia. A sixth chaetoderm has been collected at Rottnest Island, Western Australia (Scheltema 1995).

MORPHOLOGY AND PHYSIOLOGY

A general description of aplacophorans was provided by Salvini-Plawen (1985b), and Scheltema, Tscherkassky & Kuzirian (1994) described their microscopic anatomy.

External Features and Spicules

The shape of aplacophorans varies considerably, from nearly spherical to elongate and slender, but is usually consistent within families and genera. In cross-section, chaetoderms are round, whereas neomenioids may be round, depressed, compressed or triangular, and may have one, two or three carinae or keels dorsally. The spicular covering varies from smooth to very spiny, and imparts a silvery appearance to the animal. Only *Epimenia* species are brightly coloured with green, blue, red and yellow spots or stripes (Baba 1939; Scheltema & Jebb 1994). The undifferentiated head has a terminal or subterminal mouth opening. The opening of the small posterior mantle cavity is defined by a terminal circular ridge or brush of spicules in chaetoderms and often by a brush of subterminal spicules in neomenioids. The neomenioid foot is a simple, non-muscular, ciliated fold or folds, hidden within the ventral, longitudinal groove in preserved specimens.

The epidermis produces the cuticle and spicules. The cuticle of *Rhopalomenia* is considered to be an early mucoid stage in the evolution of the molluscan shell (Beedham & Trueman 1968). The cuticle in chaetoderms is fibrous (Scheltema 1985; Scheltema *et al.* 1994).

Each spicule is secreted extracellularly (Haas 1981), as in the Polyplacophora. It starts within an invagination of an individual cell and grows out through the cuticle. A collar of neighbouring cells seals off the crystallisation chamber. Spicules are aragonitic except in *Notomenia* species, which lack calcium carbonate. Spicule morphology varies greatly (Figs 2.5–2.15) from flattened and leaflike in chaetoderms and some neomenioids to paddle-shaped, hooked or needle-like in other neomenioids. There may be slight to elaborate ornamentation on the spicules of chaetoderms, and in many neomenioids the spicules are hollow. A specimen usually has several forms of spicules, which are species-specific and may be restricted to particular regions of the body.

Musculature

Four muscle layers, not always fully expressed, lie beneath the epidermis. Two oblique layers at right angles to each other lie between an outer circular layer and an inner longitudinal layer. Neomeniomorpha also have two ventral bands of thickened longitudinal muscles, giving many species a typical flexed new-moon shape. In chaetoderms (except *Limifossor*), the longitudinal muscles separate into four distinct bands which either run throughout the body length or are restricted to anterior or posterior regions. Posteriorly, muscles or bands from the longitudinal muscles extend to and retract the ctenidia or gills (in chaetoderms) or respiratory folds (in neomenioids) of the mantle cavity, and, anteriorly, move the head. Internal organs are attached by fine strands to the body wall. In most neomenioids, series of latero-ventral muscles produce sacs of the midgut.

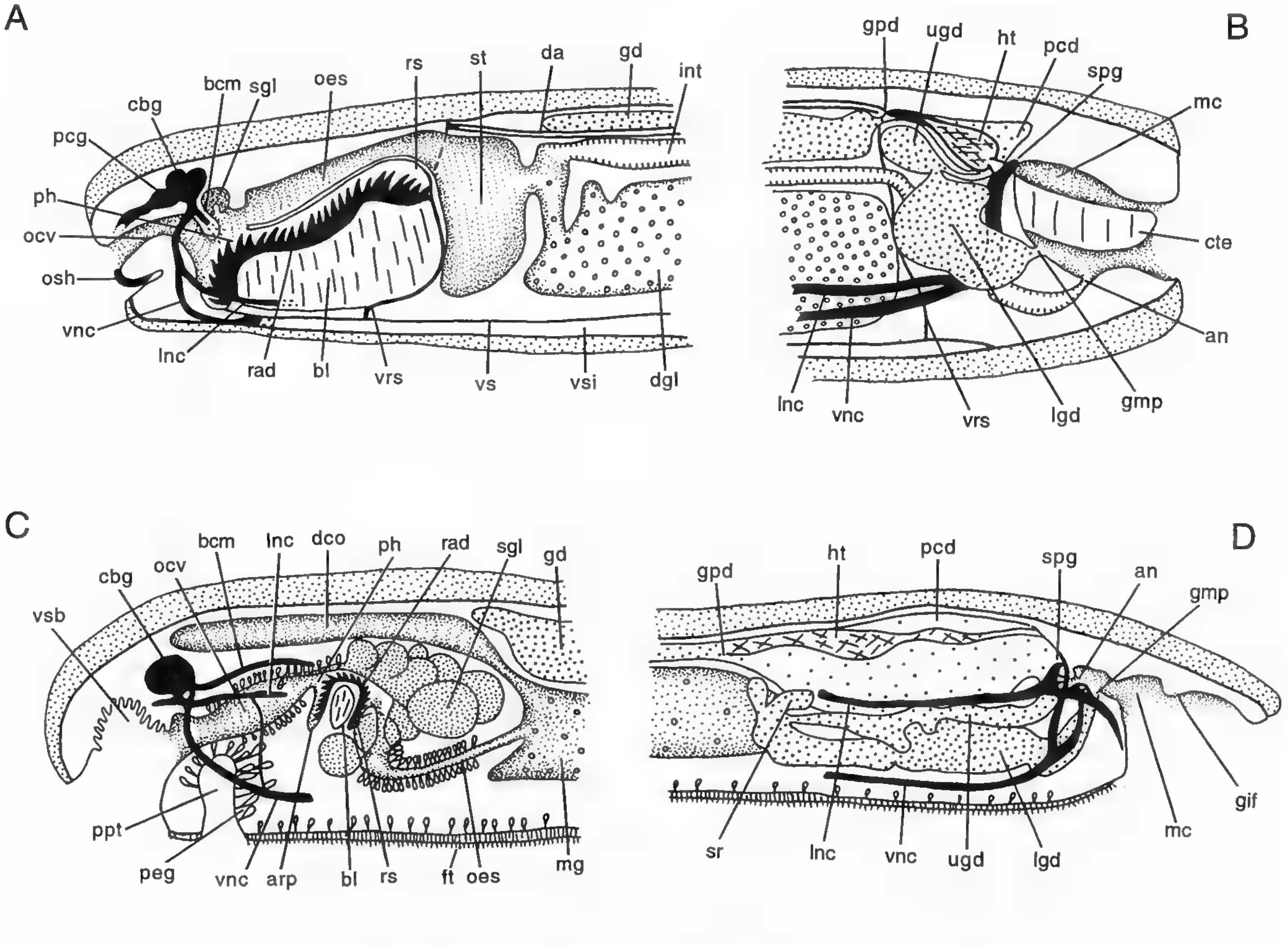

Figure 2.2 Semischematic sagittal sections of aplacophorans. **A**, **C**, anterior end; **B**, **D**, posterior end. **A**, **B**, *Limifossor talpoideus*, subclass Chaetodermomorpha; **C**, **D**, *Spengelomenia bathybia* of the subclass Neomeniomorpha. **an**, anus; **arp**, antero-ventral radular pocket; **bcm**, buccal commissure; **bl**, bolster; **cbg**, cerebral ganglion; **cte**, ctenidia; **da**, dorsal aorta; **dco**, dorsal caecum; **dgl**, digestive gland; **ft**, foot; **gd**, gonad; **gif**, gill fold; **gmp**, gametopore; **gpd**, gonopericardial duct; **ht**, heart; **int**, intestine; **lgd**, lower gametoduct; **lnc**, lateral nerve cord; **mc**, mantle cavity; **mg**, midgut; **ocv**, oral cavity; **oes**, oesophagus; **osh**, oral shield; **pcd**, pericardium; **pcg**, precerebral ganglion; **peg**, pedal gland; **ph**, pharynx; **ppt**, pedal pit; **rad**, radula; **rs**, radular sac; **sgl**, salivary gland; **spg**, suprarectal ganglion; **sr**, seminal receptacle; **st**, stomach; **ugd**, upper gametoduct; **vnc**, ventral nerve cord; **vrs**, vertical septum; **vs**, ventral septum; **vsb**, vestibule; **vsi**, ventral sinus. (After author's drawings, modified from A, Heath 1911; B, Heath 1912) [K. Hollis]

Body Cavities

Most of the internal space not occupied by muscles and organs is haemocoel, divided by a fine ventral muscular horizontal septum to produce a ventral or pedal sinus (Fig. 2.2A). Transverse septa may be present near the anterior or posterior ends. Coelomic spaces are restricted to the posterior pericardium, which is large relative to the size of the heart (Scheltema 1973, 1988, 1993), and to the reproductive organs – gonads and upper gametoducts.

Feeding and Digestion

Aplacophorans are either carnivores or selective detritivores. Neomenioids feed on Cnidaria and chaetoderms eat small organisms and organic detritus (Salvini-Plawen 1981; Scheltema 1981). Like other molluscs, chaetoderms and most neomenioids have a discrete buccal mass with a radula, radular sac, and paired or fused bolsters with their protractor and retractor muscles (Fig. 2.2A, C). Only prochaetodermatids have jaws (Fig. 2.6C). Radulae vary morphologically and several neomenioids have none. The most generalised radula is distichous, with rows of two opposed, mirror-image, denticulate teeth (Fig. 2.13C) on a unipartite or bipartite radular membrane. A central tooth is lacking, except in prochaetodermatids which have a medial flat plate (Scheltema 1981, 1988). The teeth, produced by odontoblasts at the proximal end of a radular sac, decrease in size from newest to oldest. Denticle number can vary both within and between rows of a single radula (Figs 2.11E, 2.13C). The paired bolsters are often chondroid-like in cell structure (Scheltema 1981; Scheltema *et al.* 1994).

Apparently the radula does not function as a rasping organ except in the Prochaetodermatidae, the only taxon in which distal teeth show wear (Scheltema 1981). Feeding has not been observed in most aplacophorans, and the use of the radula is only inferred from its position in fixed material (for example, Heath 1911) or movements in living specimens (Baba 1940b; Salvini-Plawen 1981). In *Epimenia*, the teeth hook into the soft coral prey, holding the head in place, while the pharynx sucks in the polyps (Scheltema & Jebb 1994).

The foregut consists of a mouth, an oral cavity, a pharynx into which salivary glands open and which contains the radula, and sometimes an oesophagus. The midgut has a simple stomach either united with a digestive gland in neomenioids or separate from a sac-like digestive gland in chaetoderms. The hindgut comprises a long or short intestine that bends ventrally to empty posteriorly through the anus into the mantle cavity.

Circulation

A heart consisting of a ventricle and (usually) paired auricles lies posteriorly within the pericardium (Fig. 2.2B, D). Blood either passes forward from the heart through a dorsal aorta that empties near the cerebral ganglion, or the heart empties directly into the dorsal haemocoel. The remainder of the circulation is open, with blood moved freely through the haemocoel and its sinuses by movements of the body. There are three types of blood cells: erythrocytes, amoebocytes and platelets. The erythrocytes in *Epimenia* are probably haemoglobin carriers (Baba 1940b) and in most living aplacophorans a pink tinge is visible through the body wall (A.H. Scheltema personal observations). The form of the erythrocytes differs in each of five pairs of closely related sister species of Antarctic and Subantarctic Proneomeniidae (Salvini-Plawen 1978b). Phagocytosis by the amoebocytes has been demonstrated only in the Epimeniidae (Baba 1940b). Salvini-Plawen (1968a, 1968b) observed heart rates of 19 to 42 beats per minute.

Excretion

Excretion seems to occur in at least two ways. In epimeniids, phagocytosed material passes directly into the midgut and thence into the mantle cavity (Baba 1940b). Nearly all aplacophorans have epidermal cells or papillae filled with granular material which, histologically, appear to discharge to the outside through the cuticle. If the cuticle is thick, the papillae are stalked (Hoffman 1949). Whether the ctenidia, mantle cavity folds, or the gametoducts function in excretion is not known. Podocytes have been demonstrated in the pericardial coelom of a neomenioid (Reynolds, Morse & Norenburg 1993). Kidneys are lacking.

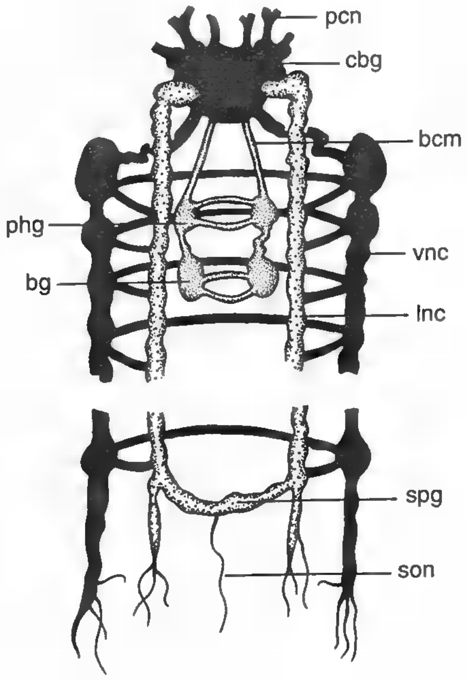

Figure 2.3 The nervous system of *Micromenia fodiens* of the subclass Neomeniomorpha. **bcm**, buccal commissure; **bg**, buccal ganglion; **cbg**, cerebral ganglion; **lnc**, lateral nerve cord; **pcn**, precerebral nerve; **phg**, pharyngeal ganglion; **son**, nerve to dorsal sensory organ; **spg**, suprarectal ganglion; **vnc**, ventral nerve cord. (After Scheltema *et al.* 1994, modified from Schwabl 1955) [K. Hollis]

Respiration

Chaetoderms have paired ctenidia in the mantle cavity (Fig. 2.2B) and neomenioids have simple mantle-wall folds – the gill folds (Fig. 2.2D) – or papillae. Blood cells have been observed to circulate in both (Pruvot 1891; Salvini-Plawen 1968a) and they are assumed to serve in respiration.

Sense Organs and Nervous System

The nervous system is ladder-like (Heath 1904b; Hyman 1967; Salvini-Plawen 1985b). Two pairs of ganglionated nerve cords, a lateral and a ventral, arise separately or from a common root from a large, bilobed antero-dorsal cerebral ganglion and run the length of the body (Figs 2.2, 2.3). The lateral cords unite in a posterior suprarectal commissure, sometimes as a greatly enlarged ganglion in chaetoderms. Several pairs of nerves arise anteriorly from the cerebral ganglion to innervate the mouth and sensory vestibule (neomenioids) or oral shield (chaetoderms). Cross-commissures run between the lateral and ventral cords and link both ventral cords. The cross-commissures are more numerous in the footed neomenioids than in chaetoderms. The lateral cords contribute nerves to the body wall and internal organs. In chaetoderms they descend, run parallel to the ventral cords and fuse with them posteriorly. A pair of buccal connectives link the cerebral ganglion or the common roots of the longitudinal nerve cords to a pair of buccal ganglia connected by one or two commissures in the region of the radula. There may also be pharyngeal ganglia and nerve rings. Posteriorly, a single nerve or a pair of nerves link the suprarectal commissure to a dorsal sensory organ (Salvini-Plawen 1972, 1985b).

The function of sensory organs in the Aplacophora is not known. A protrusible, posterior, dorsal sensory organ is usually present, and may function in reproductive behaviour (Haszprunar 1987). Some neomenioids have additional sensory pits on the body surface. The vestibule of neomenioids, located antero-dorsal to the mouth (Fig. 2.2C), is lavishly provided with papillae and a nerve plexus, and bears large, stiff cilia around a sensory rim (Pruvot 1891; Salvini-Plawen 1968b; Haszprunar 1986). It is held open as the animals creep, and may function in food detection. Water currents were seen to pass in and out of the vestibule of *Epimenia australis* (Scheltema & Jebb 1994). When an individual was presented with a second individual, increased motion ensued. *Epimenia australis* responded to a needle-touch to the stiff frontal cilia by moving the head away from the stimulus (Scheltema & Jebb 1994). A small interstitial *Meiomenia* species uses the stiff frontal cilia to detect obstructions during locomotion (Scheltema personal observations). In *E. australis* and *Meiomenia* species the head moves from side to side during locomotion, presumably testing mechanically as well as by olfaction. The innervated oral shield of chaetoderms may serve in food detection as well as in burrowing. Antero-ventral statocyst-like sacs have been found in gymnomeniid species (Salvini-Plawen 1967, 1988a; Scheltema 1981; Haszprunar 1986) and Pruvotinidae (Scheltema *et al.* 1994).

Reproduction

The Chaetodermomorpha are dioecious, whereas neomenioids are hermaphroditic. The paired gonads, often fused in adult chaetoderms, lie dorsally and run the length of the midgut (neomenioids) or digestive gland (chaetoderms) (Fig. 2.2). The gonads empty directly through (usually) paired gonopericardial ducts into the anterior end of the pericardium. Eggs or sperm are often seen to fill the pericardium in sectioned material. Normally, paired U-shaped gametoducts (also called gonoducts, coelomoducts, pericardioducts plus spawning ducts, or shell glands in the literature) run from the pericardium to the mantle cavity. The upper gametoducts leave from the ventral, posterior end of the pericardium, turn anteriorly and then ventrally to join the lower gametoducts. These extend posteriorly to open through paired gametopores (coelomopores), or, in most neomenioids, through a single gametopore.

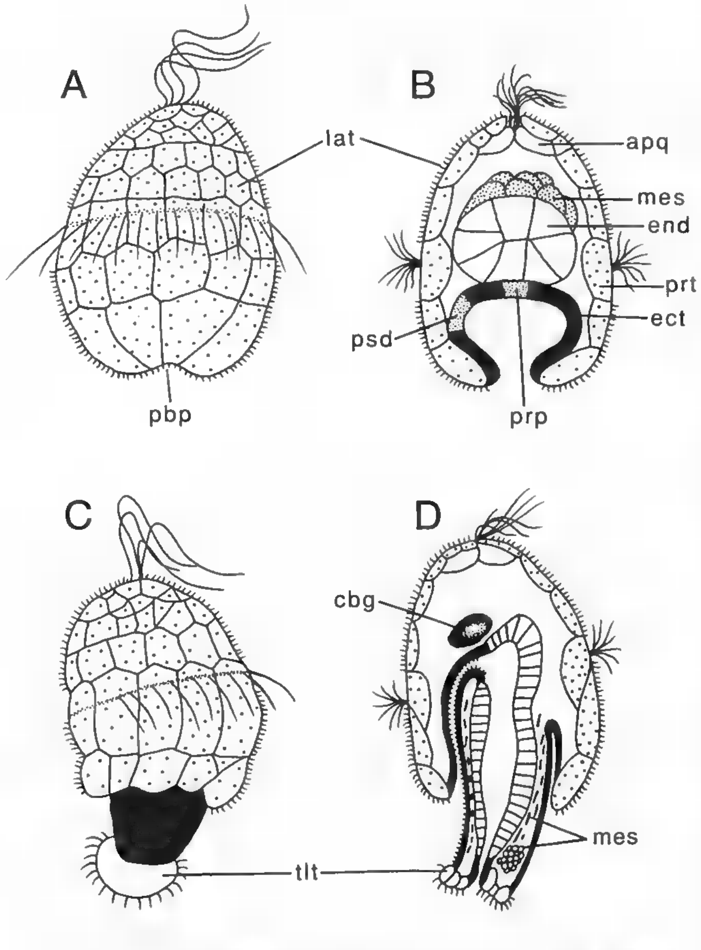

Figure 2.4 Development in *Neomenia*. **A**, **B**, 4- and 3-day larvae, respectively; **C**, **D**, 10-day larvae. **apq**, apical quartet; **cbg**, cerebral ganglion; **ect**, definitive ectoderm; **end**, endoderm; **lat**, larval test; **mes**, mesoderm; **pbp**, pseudoblastopore; **prp**, prospective proctodeum; **prt**, prototroct; **psd**, prospective stomodeum; **tlt**, telotroch. (After Thompson 1960)
[K. Hollis]

The form of chaetoderm sperm suggests that Chaetodermomorpha spawn their gonadal products into the sea (Franzén 1956; Buckland-Nicks & Chia 1989). Neomenioids have internally fertilising sperm (Scheltema *et al.* 1994; Buckland-Nicks & Scheltema 1995), copulatory spicules, and usually seminal receptacles. Copulation probably occurs; pairing has been observed in *Epimenia*. The egg masses of chaetoderms are unknown. Neomenioids spawn fertilised eggs singly or in mucous ribbons, or sometimes brood them (Pruvot 1890; Heath 1918; Baba 1940c; Salvini-Plawen 1978a).

Embryology & Regeneration

Hadfield (1979) and Salvini-Plawen (1985b) have reviewed the published works on reproduction and embryology in the Aplacophora.

Development has been observed in part for a few neomenioid species, but is unknown for any chaetoderm species. Brooding is reported in the neomenioid family Pruvotinidae. Developmental observations on living material are restricted to single species in the genera *Epimenia*, *Nematomenia*, *Rhopalomenia* and *Neomenia* (Pruvot 1890, 1892; Baba 1938, 1940c, 1951; Thompson 1960). Early cleavage is spiral and unequal in *Epimenia* (Baba 1940c). Gastrulation by epiboly (Pruvot 1890), by delamination (Heath 1918), or by invagination (Baba 1940c) has been reported in different species.

Embryogenesis in *Epimenia* species, which sometimes brood larvae for part of their development, differs from that in the other three neomenioids in the formation of a blastopore. Non-brooding species have an abapical pseudoblastopore which is the precursor to the definitive ectoderm, whereas the rest of the outer cell layer of the gastrula forms a ciliated larval test that has an apical tuft and equatorial prototroch (Fig. 2.4). A constant number of cells form the larval test (Thompson 1960). A mass of cells within the test forms the endoderm and mesoderm. The larva, called a pericalymma, swims but does not feed and resembles that found among the protobranch bivalves. Stomodeal and proctodeal invaginations of the definitive ectoderm form the foregut and mantle cavity. The solid endodermal mass differentiates into midgut and intestine; the mesoderm, differentiated from the internal cell mass, gives rise to muscles, and later the heart and pericardium. Only part of the nervous system in adults is derived from the larval test. There is some evidence that the upper gametoduct is coelomic, derived from the pericardium, and the lower gametoduct is ectodermal, derived from the mantle cavity (Baba 1940b; Salvini-Plawen 1972). Metamorphosis occurs gradually in 1–10 days, either by casting off larval structures or by engulfing the larval test with the proliferating ectoderm. At no stage has metamerism been observed.

NATURAL HISTORY

Little is known about the life history or ecology of Aplacophora. Living *Epimenia australis* collected by divers have provided the opportunity to observe habitat, feeding, locomotion, sensory perception, and diurnal activity (Scheltema & Jebb 1994). Individuals of *Prochaetoderma yongei* at depths of 2000 m reach adult size in two months and sexual maturity in a year, based on colonisation of experimental boxes of azoic mud, and on measurements of individuals and eggs from large epibenthic sled samples (Scheltema 1987). Longevity and fecundity are unknown for any species, though length frequency spectra for several species show normal curves, which indicate low recruitment.

Aplacophora are slow-moving creatures, sometimes nearly inert. The Chaetodermomorpha are burrowers. The Neomeniomorpha creep, either on the bottom or on the corals and hydroids upon which they feed. Ciliary action of the non-muscular ridge-like foot moves the animals along a mucous string laid down by glands of the anterior pedal pit and ventral furrow (Salvini-Plawen 1968b). The foot is not protruded during locomotion in *Epimenia australis*; rather, the mucous string acts as a monorail within the ventral groove (Scheltema & Jebb 1994).

Diurnal activity was observed in *Epimenia australis*, which remained quiescent underneath rocks during the day but moved about the aquarium at night (Scheltema & Jebb 1994).

Changes in the distribution of certain species over time reflect alteration in the physical environment of a region. For example, *Chaetoderma argenteum*, common a century ago in Monterey Bay, California, has been replaced by a species of *Falcidens*, probably owing to an increase in temperature, the result of El Niño (Scheltema, Buckland-Nicks & Chia 1991).

Stenotopy is inferred in most Chaetodermatidae. *Chaetoderma nitidulum canadense* from Cape Cod Bay, Massachusetts, is restricted to temperatures of less than 10°C and to sediments with not more than 20% clay (A.H. Scheltema unpublished data).

BIOGEOGRAPHY

The Australian aplacophoran fauna of the continental shelf is the consequence of several influences. Some genera reflect an ancient Tethyan distribution, occurring in the Mediterranean, Atlantic, and south-eastern Australia, but apparently not in the eastern Pacific (Scheltema 1990). Two genera found in Bass Strait, *Nematomenia* and *Neomenia*, occur worldwide, and one tropical Indo-Pacific genus, *Epimenia*, was collected on the shelf off north-western Australia. Antarctic affinities are indicated by the Phyllomeniidae in Bass Strait and the genus *Ocheyoherpia* from Macquarie Island.

Only one genus in each of the families Pruvotinidae, Phyllomeniidae (provisionally), and the unique genus *Notomenia* appear to be Australian endemics. Lack of endemicity at shelf depths may be the result of colonisation from a Tethyan fauna at upper slope depths, where aplacophorans worldwide reach their greatest numbers and diversity (Scheltema 1990). Endemicity at the species level cannot yet be determined because the Pacific aplacophoran fauna is too poorly known. However, the radiation expressed by very closely related species within genera of the Pruvotinidae, Lepidomeniidae and Chaetodermatidae suggests that endemicity may be high in southern Australia.

The aplacophoran shelf fauna of the Bass Strait area of southern Australia is one of the most diverse known, with 32 species in nine or 10 families and 14 to 16 genera. Collections at 32 localities yielded 376 specimens. Though approximately equal in numbers of individuals, the two subclasses are very different in diversity. The Chaetodermomorpha represent two families, three or four genera, and four species, but 98% of specimens collected belonged to a single species *Lepoderma chiastos*. There are 28 species of neomenioids in 12 or 13 genera and seven or eight families. One new pruvotinid, *Eleutheromenia* sp., accounted for 30% of all neomenioids collected. The two genera *Notomenia* and *Ocheyoherpia* are unique, and do not fit into any of the presently recognised families. In this chapter they are treated as *incertae sedis*, and will be described in full elsewhere (Scheltema in preparation). In Bass Strait, some species are not known from depths exceeding 125 m, whereas other species found at 140 m have also been collected from the upper slope. Cleveland and Halifax Bays, North Queensland, comprise the only other shelf area in Australia that has been sampled systematically using fine screens. Only a few specimens of two undescribed species have been collected, one in the Lepidomeniidae and the other in the Pruvotinidae. A species of *Falcidens* has been collected by divers from amongst the rhizomes of sea grass at 3 m depth in water around Rottnest Island, Western Australia (Scheltema 1995).

The neomenioid family Proneomeniidae and the chaetoderm genus *Chaetoderma* (Scheltema 1989; in press), commonly found on continental shelves in other parts of the world, are unknown from the shelf off continental Australia. However, both taxa are found on the slope below 200 m, and a proneomeniid species has been recorded from shelf depths off Macquarie Island (Salvini-Plawen 1978a).

METHODS OF STUDY

Hard parts (spicules and radulae) and external characters such as overall shape, and spicule attitude and arrangement, are useful taxonomically. New species of Neomeniomorpha require histological preparation to determine higher classification. Aplacophorans should be preserved in relatively large volumes of buffered 80% ethanol to preserve spicules. Inadequate preservation can denude specimens of spicules. Permanent slides of holotype spicules should be prepared.

Most aplacophorans have been collected with dredges, box cores, or grabs. The entire contents of such a sample should be sieved through a 0.5 mm screen using a flotation method (Sanders *et al.* 1965), fixed for 24 hours in buffered formalin, and then preserved in 80% buffered alcohol. The addition of rose bengal to a sample before sorting differentiates organisms collected alive from detritus.

Interstitial aplacophorans can be captured alive by collecting coarse sand subject to swift currents or wave action: (1) by dredging with a canvas-lined anchor dredge; (2) by divers using buckets or suction guns; or (3) intertidally with a spade from around boulders where tidal amplitudes are greater than 8 m (Morse & Scheltema 1988). Moist sand is left standing in tubs for up to several days. Surface sand is then subsampled into a small bucket. Sea water is added with vigorous stirring and rapidly decanted through a 42 µm mesh screen. The organisms so retained are washed into a dish for examination under a dissecting microscope.

CLASSIFICATION

Two classifications are currently in use. In one, the two aplacophoran groups Caudofoveata and Solenogastres are placed in separate classes, on grounds that the worm-like form in each evolved independently (Salvini-Plawen 1972, 1985b). However, the worm-like shape of the Aplacophora is here considered to be an autapomorphy, and, as in Table 2.1, the Aplacophora (= Solenogastres) comprises two groups, the subclasses Neomeniomorpha (= Ventroplicida Boettger, 1956; Class Solenogastres Gegenbaur, 1878 (in part), *sensu nomine* Salvini-Plawen, 1967) and Chaetodermomorpha (= Caudofoveata Boettger, 1956) (Scheltema 1978, 1988, 1993).

The division of the Neomeniomorpha into four orders has not been maintained (Salvini-Plawen 1978a; Boss 1982), because as presently constituted the orders are paraphyletic.

Key to the subclasses of Aplacophora

1 (a)	Ventral furrow absent, oral shield present	Chaetodermomorpha
(b)	Ventral furrow present, oral shield absent	Neomeniomorpha

Table 2.1 Classification of the extant Aplacophora.

- **Class APLACOPHORA**
  - Subclass CHAETODERMOMORPHA
    - Family Chaetodermatidae
    - Family Prochaetodermatidae
  - Subclass NEOMENIOMORPHA
    - Family Dondersiidae
    - Family Lepidomeniidae
    - Family Neomeniidae
    - Family Phyllomeniidae
    - Family Pruvotinidae
    - Family Proneomeniidae
    - Family Epimeniidae

Subclass CHAETODERMOMORPHA

The burrowing chaetoderms are recognised by their cuticular oral shield (Figs 2.5B, 2.6B) and lack of a ventral furrow and foot. The three families are characterised by shape, by the way the spicules are born in the cuticle, and by radular morphology. There are 11 genera and 93 known species worldwide.

Although all families and six genera of Chaetodermomorpha are known to occur on the continental slope off south-eastern Australia, only two families with three or four genera are represented in the collections from the shelf, from Bass Strait and off Rottnest Island.

Spicules extend for part or most of their length beyond the cuticle and are held either flat against the body or raised slightly or perpendicularly to the body. Both flat and raised spicules may occur on the same specimen. All spicules, except those held vertically, overlap like shingles. They are orientated parallel to the mid-body axis (Fig. 2.5A, B) or at an angle to the axis (Fig. 2.6A, B). The usual longitudinal orientation of ridges on spicules presumably helps maintain spicule orientation as the animal moves. An exception to lengthwise sculpture is found in the Australian species *Lepoderma chiastos* (Fig. 2.5D).

The placement of four heavy longitudinal muscle bands defines body shape. Measurements of body regions as defined by muscle bands are important taxonomic characters (Scheltema 1976, 1985, 1989). In *Scutopus* species and some Chaetodermatidae, these muscles run the length of the body, and the body is of nearly equal width throughout. In most Chaetodermatidae the longitudinal muscle bands are thickest anteriorly (Fig. 2.5A) or posteriorly, that region then being narrowest (Fig. 2.5E). In the Prochaetodermatidae, the thick muscle bands are posterior and the species are all 'tailed' (Fig. 2.6A). The site of attachment for muscles running anteriorly is marked by a constriction of the body, setting off a 'neck' in the Chaetodermatidae and *Scutopus* species (Fig. 2.5A, E).

Burrowing is slow, and complete burial may take hours (A.H. Scheltema personal observations). It is effected by pushing the anterior end into the sediment hydrostatically, while the ring of usually long, needle-like spicules around the mantle cavity acts as an anchor (Fig. 2.5A, E). Contraction of the heavy longitudinal muscles then brings the rest of the body forward (Wirén 1892a; Salvini-Plawen 1985b). Chaetodermatids can turn the anterior end through nearly 360° around the long axis of the body, and dorsally to ventrally through about 180° (A.H. Scheltema personal observations). The oral shield, with mucous cells opening beside and through it (Scheltema *et al.* 1994), thus becomes an effective shovel.

The radula may be distichous, with two teeth per row on a radular membrane, or specialised. In the Prochaetodermatidae, the radula is a rasping organ with distichous teeth and a central plate reminiscent of that of many gastropods (Scheltema 1981). Examination of fixed specimens indicates that prochaetodermatids ingest large clumps of organic matter, foraminiferans, or other organisms into an expandable pharynx where the food is held between large cuticular jaws and rasped with the teeth (A.H. Scheltema personal observation; manner of feeding stated incorrectly by Scheltema 1981). In Chaetodermatidae, the radula consists of a large cone with two small distal teeth (Fig. 2.5C, G; Scheltema 1972). This apparatus may transport material (Ivanov 1979) or form pincers to grab the organisms

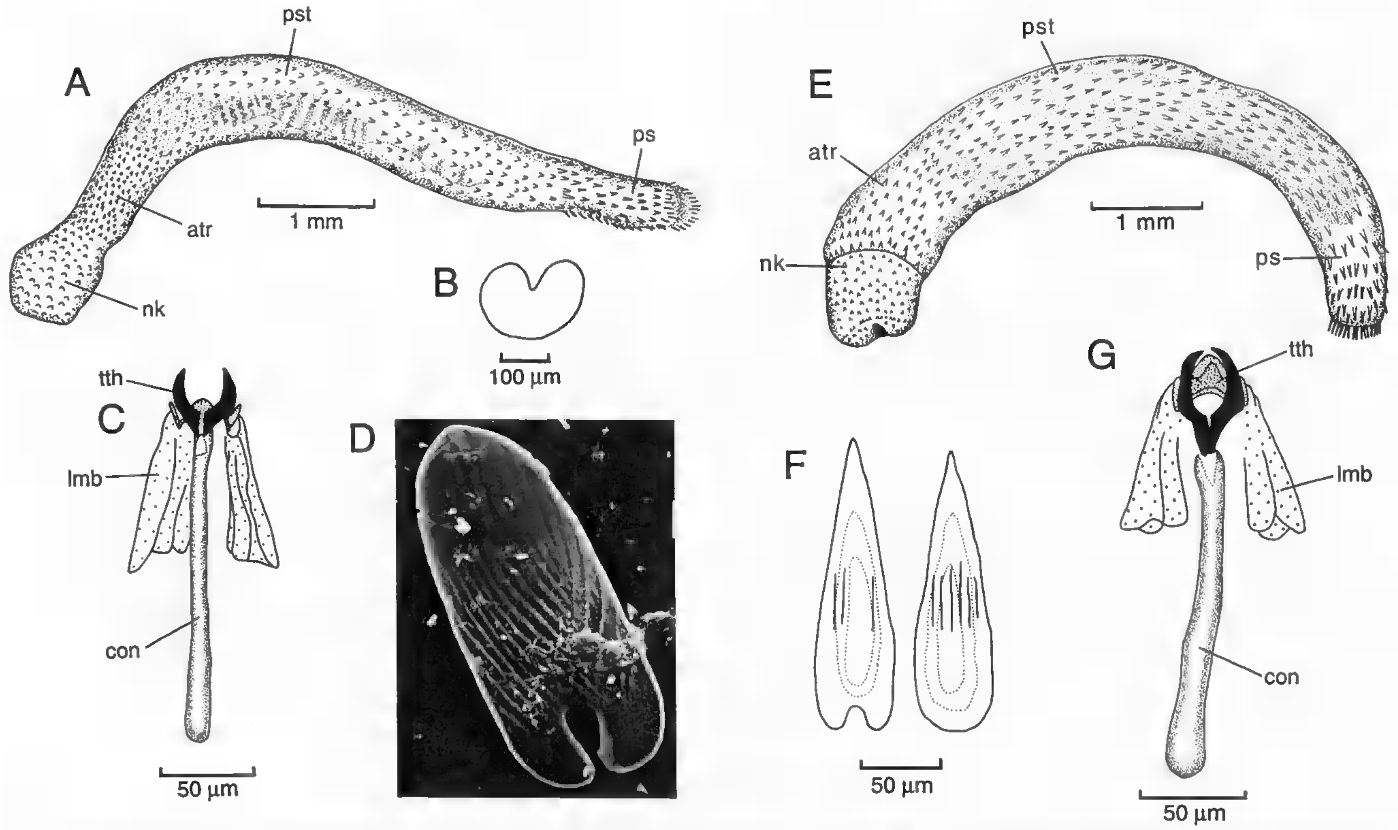

Figure 2.5 Australian Chaetodermatidae from Bass Strait. **A–D**, *Lepoderma chiastos*; **E–G**, *Falcidens lipuros*. **A, E**, external appearance; **B**, oral shield, which is entire; **C, G**, radulae; **D, F**, spicules. **atr**, anterior trunk; **con**, cone-shaped piece; **lmb**, lateral membrane; **nk**, neck; **ps**, posterium; **pst**, posterior trunk; **tth**, tooth. (A–C, E–G, after Scheltema 1989; D, from Scheltema 1989) [A–C, E–G, K. Hollis]

upon which chaetodermatids feed. Muscles of the various radular types among families are homologous (Deimel 1982). The pharynx passes via a tubular oesophagus or directly into the stomach (Fig. 2.2A). The stomach may be short or more than half the body length. Chaetodermatids have a gastric shield at the opening of the digestive gland. At the same level, a mucoid rod projects from a ciliated style-like sac of the intestine where it joins the stomach (Scheltema 1978, 1981). Because the Chaetodermatidae are a more specialised group within the subclass, this gastric shield is considered to be analogous, but not homologous, to the gastric shield in other Mollusca. The digestive gland is a large, blind sac that fills most of the posterior part of the body except the 'tail', if present. Digestion appears to be extracellular (Salvini-Plawen 1988b). The long intestine extends from the stomach dorso-laterally along the digestive gland and gonad. It bends ventrally to open into the mantle cavity between the ctenidia.

Besides probable excretion from integumental papillae, a yellow deposit seen frequently on the outside wall of the mantle cavity suggests there is excretion from the mantle cavity.

The paired ctenidia in the mantle cavity, often very large, are typically molluscan in form but not in orientation, for the efferent membrane is dorsal. In life, the ctenidia extend beyond the opened mantle cavity, and elongate lateral cilia of the ctenidial folds pass water from the dorsal to ventral surfaces between the leaves of the ctenidium (Salvini-Plawen 1985b).

The paired or fused gonads lie posteriorly, but anterior to the 'tail', if this is present. The gonopericardial ducts are short or long, depending on whether there is a 'tail'. The gametoducts are simple and open separately into the mantle cavity. The male gametopore may be on a muscular papilla. The female gametopore opens onto a tract of mucous cells that may secrete a substance to bind emerging eggs into a mass. There are no copulatory spicules. Animals in Scandinavia are reported to be ripe in the autumn and winter (Salvini-Plawen 1985b).

Useful taxonomic characters are: (1) the morphology of the spicules and radula; (2) the absolute and relative measurements of body regions and oral shield; and (3) the arrangement of the spicules along the body and around the mantle cavity (for example, see Salvini-Plawen 1967, 1969; Scheltema 1976, 1985, 1989).

Key to the families of Australian continental shelf Chaetodermomorpha

1 (a) With oral shield entire and four body regions (Fig. 2.5A, B, E) .... Chaetodermatidae

(b) With divided oral shield and tail-like posterium (Fig. 2.6A, B) .... Prochaetodermatidae

Family Chaetodermatidae

The family is distinguished by having four distinct body regions: (1) the anterior neck set off by a usually distinct constriction; (2) the anterior trunk containing the stomach; (3) the posterior trunk with digestive gland and gonad; and (4) the posterium which may be short or tail-like. The oral shield is undivided. The radula is specialised with two small denticles at the end of a large cuticular cone (Fig. 2.5C, G; Salvini-Plawen 1968a; Scheltema 1976, 1989).

The family comprises four genera: *Chaetoderma*, *Falcidens*, *Caudofoveatus* and *Lepoderma*.

Body regions vary in relative length among species, and may bear morphologically similar or dissimilar spicules within a species. Spicules can be rather plain or ornamented with numerous ridges and there is often a medial keel. Bolsters are formed of anastomosed muscle fibres and connective tissue. They lie between the radular cone and cuticular membranes that rest on the outside of the buccal mass. Chaetodermatids selectively eat foraminiferans, small snails, worms, and perhaps crustaceans. The pericardium often has large lateral extensions. In some species there is an aortal bulb and a ventricle which is capable of great expansion (Scheltema 1973). Auricles are generally paired.

Lepoderma chiastos (Fig. 2.5A–D) occurs in Bass Strait at depths of 22–120 m and at densities of up to 180/m^2. *Lepoderma targotegulatus* is a junior synonym. A second species, *Falcidens lipuros*, occurs at depths greater than 100 m in Bass Strait and continues down onto the slope (Fig. 2.5E–G). A closely related species, *F. poias*, has been found at Rottnest Island at 3 m depth. The genus *Chaetoderma* occurs only on the slope at depths greater than 1000 m (Scheltema 1989).

Family Prochaetodermatidae

Prochaetodermatids are less than 6 mm long and are recognised by a divided oral shield, a tail-like posterium, and large, paired pharyngeal cuticular jaws (Fig. 2.6; Scheltema 1985, 1989).

Off Australia, the family is known from two genera, *Prochaetoderma* and *Rhabdoderma*, at slope depths (Scheltema 1989; A.H. Scheltema unpublished data), and one damaged, unidentified specimen from the shelf. These are the first records in the West Pacific for the family, which is now known to be distributed worldwide from the shelf to depths exceeding 7000 m.

Subclass NEOMENIOMORPHA

Neomenioids are recognised by the presence of a narrow foot within a ventral furrow, and by the absence of an oral shield. There are 24 named families with 71 genera and 194 species worldwide.

The 28 neomenioid species known from the Australian continental shelf and Macquarie Island are grouped in 14 or 15 genera. Generic and familial placements of single specimens belonging to two species have not been determined. Two genera are here placed in *incertae sedis* as their familial status is undecided.

The integument and spicules together form a character that links genera or families to one another (Salvini-Plawen 1978a). A thin cuticle usually bears thin, flat spicules as seen in the Dondersiidae or Lepidomeniidae (Figs 2.7, 2.8). The thick cuticle of the Neomeniidae bears short, solid, near-vertical spicules. A number of genera have a thick cuticle with solid or hollow, elongate spicules. These skeletal (tangential) spicules cross over each other at 90°, forming a strong, reticulated network (Figs 2.10, 2.11F). Upright (radial) spicules extend beyond the cuticle, in a variety of shapes, such as paddles, hooks, or scoops. The morphology of upright spicules in conjunction with radula type is used here to define families.

Neomenioid species creep by ciliary action of the foot along a sticky, mucous track produced from the ciliated, eversible pedal pit at the anterior end of the pedal groove (Fig. 2.2C; Pruvot 1891; Salvini-Plawen 1968b; Scheltema & Jebb 1994). Both pedal groove and pedal pit are supplied by many mucous glands. The head end anterior to the pedal pit is held above the substratum and is moved freely. Species of *Neomenia* burrow using the proboscis-like pharynx (Wirén 1892b). *Epimenia australis* can right itself if turned over (Scheltema & Jebb 1994).

Neomeniomorpha feed on cnidarians – stony and soft corals, hydrozoans, zooantharians, or gorgonians. Sometimes prey specificity is evident. The sensory vestibule above the mouth is probably olfactory (Fig. 2.2C; Scheltema & Jebb 1994). Circular muscles surrounding the pharynx, sometimes in series of bands, suggest the function of a buccal pump. The pharynx is sometimes

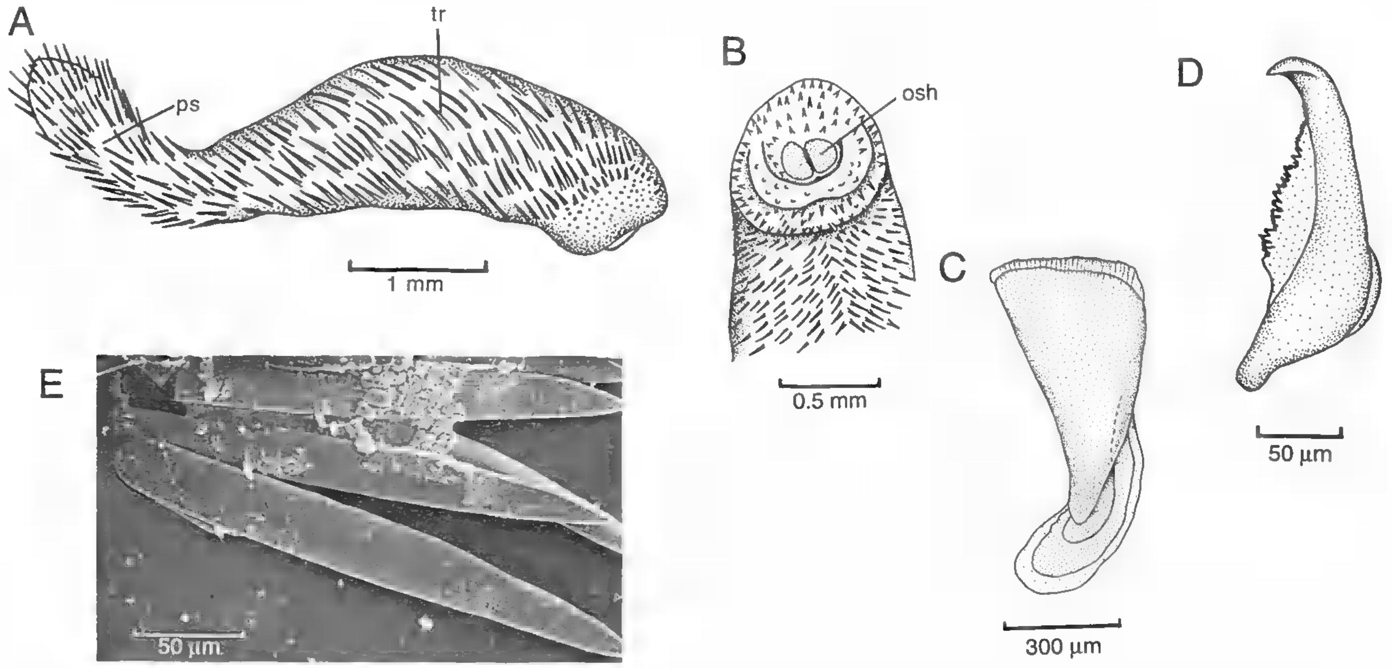

Figure 2.6 Australian Prochaetodermatidae. *Rhabdoderma australe* from a depth of 1200 m off the coast of New South Wales. A, external appearance; **B**, ventral view, showing divided oral shield; C, jaw; **D**, radular tooth; **E**, spicules. **osh**, oral shield; **ps**, posterium; **tr**, trunk. (A–D, after Scheltema 1989; E, from Scheltema 1989) [A–D, K. Hollis]

protrusible and proboscis-like. The radula may be large to very small or even absent. It is situated where the pharynx joins the midgut, unless an oesophagus is present. In some families, the distal rows of teeth bend ventrally into paired or single antero-ventral pockets (Fig. 2.2C). Digestion starts in the pharynx (Baba 1940b), which is well supplied by secretory glands. There is nearly always a pair of discrete ventral salivary glands that open into the pharynx at the level of the radula. In addition there are diffuse, separate gland cells or distinct, paired or single dorsal glands. Different morphological types of ventral salivary glands have been used to classify families (Salvini-Plawen 1978a).

The midgut serves both as stomach and digestive gland. In the Epimeniidae, experimentation has shown that cells lining the cavity are the site for extracellular and intracellular digestion. Often a single or paired anterior extension of the midgut forms a dorsal caecum above the pharynx. The lumen of the midgut in histological preparations is filled with unexploded nematocysts. A dorsal ciliated typhlosole or fold runs the length of the midgut, which passes posteriorly into the ciliated hindgut, or intestine. The latter bends ventrally and opens into the mantle cavity.

All neomenioids are hermaphroditic and have paired gonads. Ova usually are produced on the medial walls and spermatozoa on the lateral walls. The reproductive system is elaborate but follows the general plan of paired U-shaped gametoducts passing from pericardium to the mantle cavity. There are usually one to many seminal receptacles, which sometimes are stalked, where the upper and lower gametoducts join (Fig. 2.2D). There may be seminal vesicles along the upper gametoduct near the pericardium. The large lower gametoducts are lined along their length with secretory cells and form egg casings (Baba 1940b) ('shell gland' of authors). The lower gametoducts may open on paired gametopores, or they may unite terminally or over most of their length to open on a single gametopore which is sometimes a muscular penial sheath. Paired, protrusible copulatory spicules are present in many families (Figs 2.8, 2.9, 2.11, 2.12, 2.15). They range from a pair of single, simple or helical needles to paired groups of two or more, sometimes attaining one-third or more of total body length. Their morphology is sometimes elaborate. There are often specialised spicules on each side of the inner mantle cavity wall which appear to be accessory to the copulatory spicules.

The most important taxonomic features of the Neomeniomorpha, in addition to those used in the Chaetodermomorpha, are morphology of the copulatory spicules if present, height and breadth of the anterior and posterior body, spicule arrangement along the foot groove, shape of integumental papillae, type of ventral salivary glands, and elaborations of the reproductive system (Scheltema & Kuzirian 1991).

Key to the families of Australian continental shelf Neomeniomorpha

1 (a) Spicules birefringent, dissolve in acid 2

(b) Spicules not birefringent, do not dissolve in acid .... *Notomenia*

2 (a) Skeletal (tangential) spicules absent (Fig. 2.7) 3

(b) Skeletal (tangential) spicules present (Fig. 2.10A, 2.10D) 6

3 (a) Spicules solid, extending upright from cuticle 4

(b) Spicules solid, lying flat, scale-like 5

4 (a) Many harpoon-shaped spicules (Fig. 2.9C) .... Neomeniidae

(b) Few fishhook-shaped spicules (Fig. 2.15D) .... *Ocheyoherpia*

5 (a) Spicules of two types; body dorsally carinate (Fig. 2.7) .... Dondersiidae

(b) Spicules of one type; body without dorsal carina, copulatory spicules evident (Fig. 2.8) .... Lepidomeniidae

6 (a)	Upright spicules solid, paddle-shaped (Figs 2.10B, 2.10F, 2.12E)	7
(b)	Upright spicules hollow	8
7 (a)	Radula with 2 teeth per row (distichous)	Phyllomeniidae
(b)	Radula with many teeth per row (polystichous) (Fig. 2.12C)	Proneomeniidae
8 (a)	Upright spicules similar to skeletal spicules; animal > 60 mm in length	Epimeniidae
(b)	Upright spicules fishhook-shaped; animal < 15 mm in length (Fig. 2.11)	Pruvotinidae

Family Dondersiidae

Dondersiids are characterised by a unique, tiny, monostichous (one tooth per row) radula in which the two medial denticles are fused at their tips. The radula is sometimes lacking. Two types of spicules are present, one paddle-shaped, the other somewhat oval, with or without a proximally thickened rim. The posterior end of the body is usually drawn out to a point and covers the mantle cavity opening (Salvini-Plawen 1978a).

The body is slender and may vary from 1 or 2 mm up to 40 mm, even within a genus. A dorsal carina is often present (Fig. 2.7A). Discrete dorsal lobate salivary glands may be absent. The paired ventral salivary glands are often small. Gill folds are often absent. In some genera mantle cavity pockets are present. A dorso-terminal sensory organ may be absent. Seminal vesicles and seminal receptacles are usually present, though copulatory spicules are usually lacking. There is a single gametopore.

The family is widely distributed in the world oceans. Certain species of *Nematomenia* appear to be very widespread. *Nematomenia platypoda* occurs in the Aleutians and in the Gulf of California (A.H. Scheltema unpublished data), and *N. flavens* has been taken from off the Shetlands and in the Mediterranean. A single specimen of a *Nematomenia* species was collected recently in a rock sample from Bass Strait.

Family Lepidomeniidae

Lepidomeniids have overlapping, leaf-like spicules of a uniform shape within a species (Fig. 2.8C). The radula has distichous rows of denticulated, hooked teeth (Fig. 2.8D). The family differs from the very similar Gymnomeniidae Odhner 1921 (= Wireniidae Salvini-Plawen 1978a) in the form of the ventral salivary glands and the lack of statocysts (Salvini-Plawen 1988a).

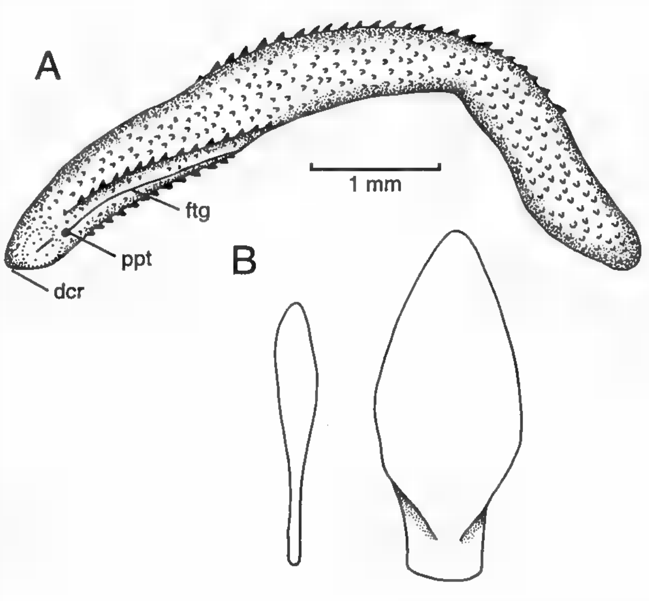

Figure 2.7 Australian Dondersiidae. *Nematomenia* sp. from Bass Strait. A, external appearance; B, spicules. Radula probably lacking. **dcr**, dorsal carina; **ftg**, foot groove; **ppt**, pedal pit. (After author's drawings) [K. Hollis]

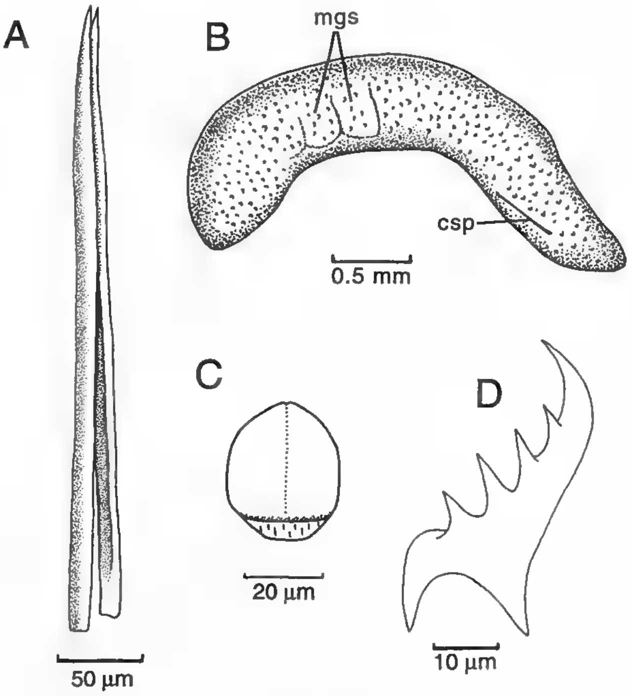

Figure 2.8 Australian Lepidomeniidae. *Tegulaherpia* sp. from Bass Strait. A, distal half of copulatory spicules; B, external appearance; C, spicule, proximal (lower) end thickened; D, single tooth from right side of radula. **csp**, copulatory spicules; **mgs**, midgut sacculations. (After author's drawings) [K. Hollis]

Lepidomeniids are usually less than 3.5 mm in length, translucent, and glistening with a silky sheen. The leaf-like spicules are thin, 4 µm or less in thickness. Most species have paired copulatory spicules with two or more spicules per pair (Fig. 2.8A). Integumental unstalked papillae are present in the thin cuticle. The pedal pit is usually large and protrusible. Paired ventral salivary glands are follicular and have a duct. The dorsal salivary glands are diffuse. Midgut sacculations are usually only weakly formed or are absent. There is a single gametopore, which often opens on a large, muscular, penial papilla.

These meiofaunal forms are found in sands and sandy muds. Five species of the genus *Tegulaherpia* have been collected from Bass Strait in depths of 55–140 m (Fig. 2.8B); one may be *Tegulaherpia tasmanica* (Salvini-Plawen 1988a). Another new species occurs in Cleveland Bay off Townsville, Queensland. The family has previously been reported only from the eastern, western, and southern Atlantic Ocean and the Mediterranean Sea.

Family Neomeniidae

Species of the monogeneric family Neomeniidae may be very large, measuring more than 100 mm in length, with breadth one-third the length. The spicules form a shiny fuzz on the distinctive, plump body which is rounded at both ends (Fig. 2.9A). The cuticle is thick, with large epidermal papillae and a distinctive combination of trowel-shaped, harpoon-like, and solid needle-shaped spicules (Fig. 2.9C–E; Salvini-Plawen 1978a).

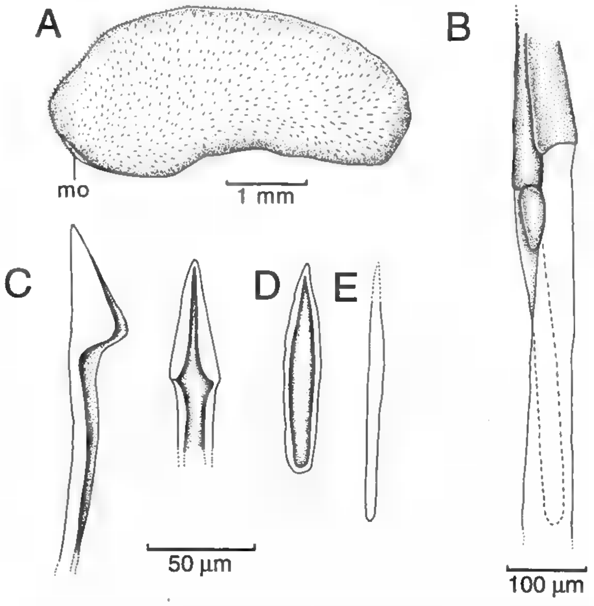

Figure 2.9 Australian Neomeniidae. *Neomenia* sp. from Bass Strait. **A**, external appearance; **B**, distal part of copulatory spicules with thickened ends, distal-most ends missing; **C**, harpoon-like spicule, lateral and posterior views; **D**, trowel-shaped spicule; **E**, needle-shaped spicule. **mo**, mouth. (After author's drawings) [K. Hollis]

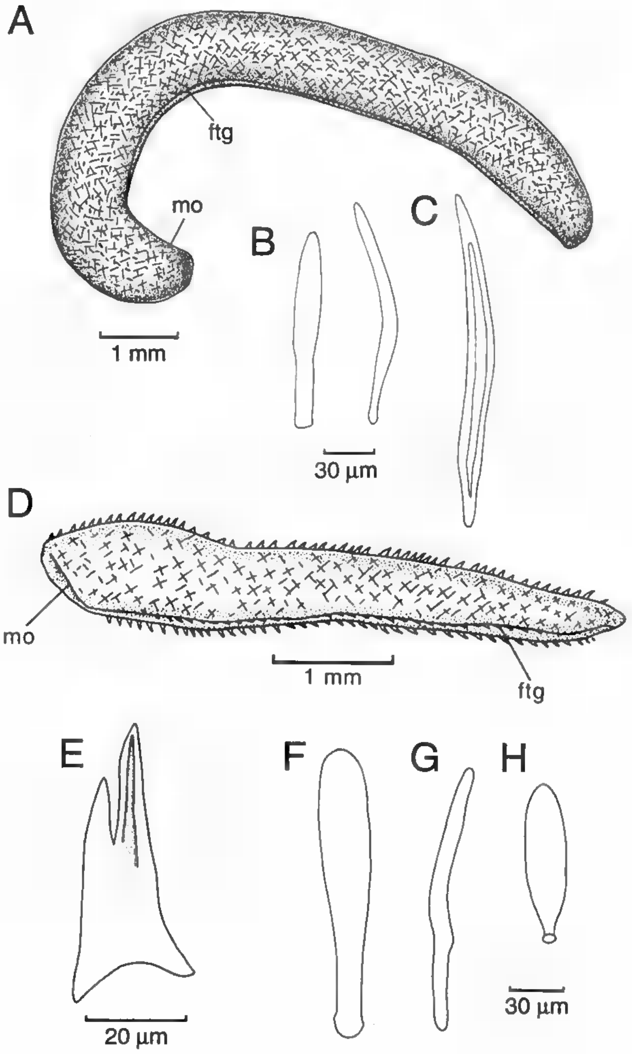

Figure 2.10 Australian Phyllomeniidae. **A–C**, a new species, genus *?Phyllomenia*, from Bass Strait; **D–H**, a new genus and species from Bass Strait. **A, D**, external appearance; **B, F, H**, upright spicules; **C, G**, skeletal spicules; **E**, tooth from left side of radula. **ftg**, foot groove; **mo**, mouth. (After author's drawings) [K. Hollis]

Similar harpoon-like spicules also occur in the Hemimeniidae, which differ from neomeniids by having a thin cuticle, no papillae, and a polystichous radula (many teeth per row) (Thiele 1906).

A dorsal carina is present on the body in several species. A thick, dense dermis lies directly beneath the epidermis. It consists of a homogeneous matrix in which are embedded muscle fibres, nerve fibres, and blood spaces containing blood cells. A radula and salivary glands are lacking. The eversible pharynx is ringed by heavy muscles. The midgut is sacculate. Respiratory folds, vestibular papillae and a dorso-terminal sensory organ are present. Copulatory spicules (Fig. 2.9B) coupled with accessory glands are present and there is a single gametopore.

Five specimens of an undescribed *Neomenia* species, the largest nearly 6 mm long by 2.5 mm in diameter, have been collected in Bass Strait at 140 m (Fig. 2.9A).

Neomeniidae have been collected from the eastern and western north Atlantic, the Mediterranean, the Subarctic and Subantarctic, and from northern Japan. The largest species occur at latitudes higher than 42°.

Family Phyllomeniidae

Members of the Phyllomeniidae have solid skeletal spicules and upright paddle-shaped spicules, a distichous radula with denticulated hook-like teeth, and usually a pointed posterior which covers the mantle cavity (Fig. 2.10). The family definition (Salvini-Plawen 1978a) is expanded here provisionally to include species with hollow skeletal spicules.

Phyllomeniids are slender and 12 mm or less in length. The upright paddle-shaped spicules are conspicuous, sometimes producing a glitter against a smooth background (Fig. 2.10B, C, F–H). The thick cuticle bears plump papillae. Gill folds are lacking. A dorso-terminal sensory organ is usually present. The reproductive system in *Phyllomenia* is unique in having true gonoducts. Gonopericardial ducts are absent in adults and the gonads empty directly into mantle cavity pockets (Salvini-Plawen 1970). Copulatory spicules and usually seminal vesicles and seminal receptacles are present.

Eleven specimens in two genera and three species of Bass Strait neomenioids provisionally are placed in this family. At least one of the genera is new and has a unique radula (Fig. 2.10E).

The Phyllomeniidae have previously been collected only from the Antarctic and Subantarctic south of 52°S. The Bass Strait species thus extend the family's range to north of 40°S.

Family Pruvotinidae

The presence of fishhook-like upright spicules defines the family Pruvotinidae, members of which may be spiny or smooth and range, as adults, from 2–12 mm in length. All genera have skeletal integumental spicules.

Species in the Pruvotinidae are the most numerous and diverse neomenioids in Australia. There is great radiation within some genera, which include morphologically very similar species. There are 12 species in five genera. Of all 172 neomenioids collected in Bass Strait, 110 belong to 11 pruvotinid species. Pruvotinids occur at two-thirds of the aplacophoran localities in Bass Strait and one species of *Eleutheromenia* accounts for nearly one-third of all neomeniomorph specimens in collections (Fig. 2.11).

The Pruvotinidae are morphologically diverse. The fishhook-like spicules may be abundant (Fig. 2.11A) or extremely sparse (Fig. 2.11F). Some species are short and stubby, less than 4.5 mm long, and very spiny or somewhat rough, whereas others may be thin and up to 8 mm, and either spiny or smooth. Integumental papillae may be present and may be club-shaped. The distichous radula has denticulated hook teeth (Fig. 2.11E). Paired dorsal salivary glands that open through a papilla into a dorsal pharyngeal pocket may be present. Copulatory spicules with or

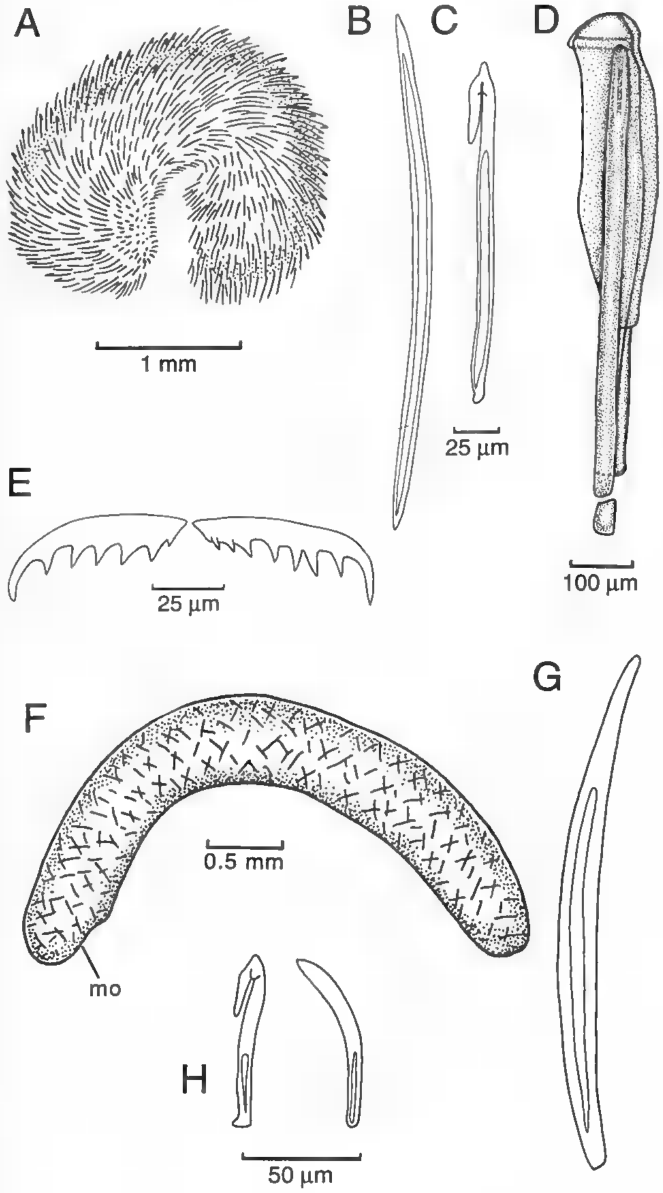

Figure 2.11 Australian Pruvotinidae. A–E, *Eleutheromenia* sp. from Bass Strait; F–H, a new genus and species from Bass Strait. **A**, **F**, external appearances; **B**, **C**, **H**, upright spicules; **D**, copulatory spicules; **G**, hollow skeletal spicule; **E**, single radular row of teeth, denticle number of teeth unequal. **mo**, mouth. (After author's drawings) [A, C. Eadie; B–H, K. Hollis]

without accessory glands may be present, and have taxonomic importance in distinguishing *Eleutheromenia* species. In this genus, there is a large accessory 'ovigerous' gland connected with the pericardium. Gill folds may be present as papillae or as only a few low folds.

The genera *Eleutheromenia* and *Pararrhopalia* were first reported from the Mediterranean (Pruvot 1891). In addition to the numerous new species found in Bass Strait, a new species of *Pararrhopalia* has been collected in Halifax Bay, North Queensland. Two new pruvotinid species from the deepest locality at 140 m in Bass Strait also occur in a sample from the adjacent continental slope at 400 m, where pruvotinids are as numerous and diverse as in the continental shelf stations of Bass Strait (Scheltema 1990). Six new species of an elongate, smooth pruvotinid belong to a new, as yet unnamed genus that so far is known only from Australia (Fig. 2.11F).

Family Proneomeniidae

The family Proneomeniidae is defined by a polystichous radula and an elongate, smooth body with hollow skeletal spicules and small upright paddle-shaped spicules (Fig. 2.12). There are two genera, *Proneomenia* and *Dorymenia*.

The family ranges up to 130 mm in length in the Arctic. The posterior end of *Dorymenia* species is sometimes produced into a finger-like projection (Fig. 2.12A). Species may be tricarinate or quincarinate. The small upright spicules are scarcely evident above the smooth body with many layers of skeletal spicules within a thick cuticle. The numerous epidermal papillae have long, sometimes branched stalks. The long, tubular ventral salivary glands extend posteriorly beneath the midgut. There are deep mantle cavity pockets, numerous accessory copulatory spicules in the mantle cavity wall, and a single gametopore. Up to five dorso-terminal sensory organs have been reported. Only the presence of copulatory spicules distinguishes *Dorymenia* from *Proneomenia* in which they are lacking. However, this character is suspect, as they are resorbed in some *Dorymenia* species (A.H. Scheltema personal observations).

The family is speciose and widespread, found from the Arctic to the Antarctic and in both the eastern and western Atlantic and Pacific Oceans from the shelf to 3000 m. A single specimen of *Dorymenia harpagata*, a small species 20 mm in length, has been reported from Australian waters, from a depth of 100 m off Macquarie Island (Salvini-Plawen 1978a).

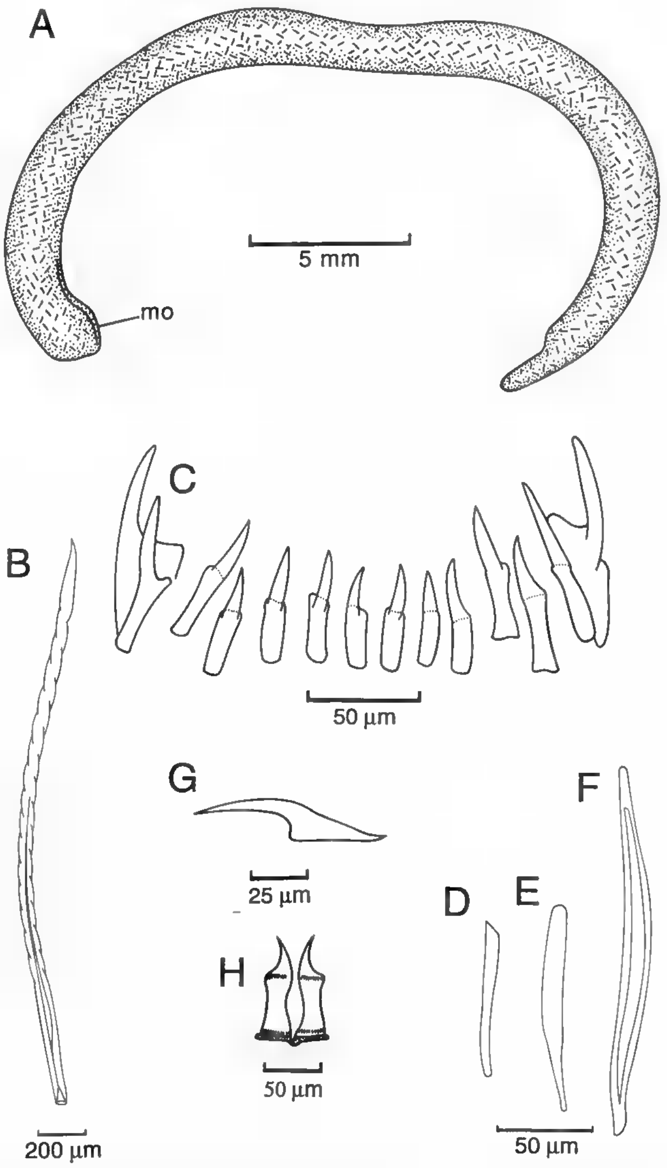

Figure 2.12 Proneomeniidae. The genus *Dorymenia* from the eastern Atlantic and Macquarie Island. A, a new Atlantic species, external appearance; **B**, copulatory spicule of same; **C–F**, *Dorymenia sarsii*, Norway: **C**, one row of radular teeth; **D**, accessory copulatory spicule from mantle cavity wall; **E**, upright, solid paddle-shaped spicule; **F**, hollow skeletal spicule; **G**, **H**, *Dorymenia harpagata*, Macquarie Island: **G**, lateral, and **H**, medial pair of radular teeth. **mo**, mouth. (A–F, after author's drawings; G, H, after Salvini-Plawen 1978a) [C. Eadie]

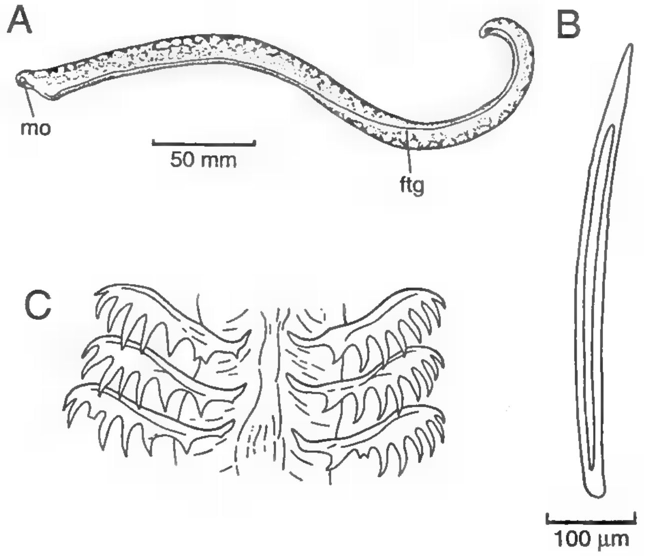

Figure 2.13 Pacific Epimeniidae. *Epimenia* sp. from Amakusa, Japan. **A**, external appearance; **B**, hollow spicule; **C**, portion of distichous radula, showing three pairs (rows) of teeth with unequal denticles. **ftg**, foot groove; **mo**, mouth. (After Baba 1939) [K. Hollis]

Family Epimeniidae

Species in the monogeneric family Epimeniidae are elongate and among the largest Aplacophora, some specimens measuring up to 300 mm in length by 10 mm in diameter (Fig. 2.13; also Fig. 1.3C). In life they are colourful, orange-red to dark brown, with a chrome-yellow dorsal stripe or with bright violet, yellow, green or blue patches (Pl. 7.1; Nierstrasz 1902; Baba 1939, 1940a; Scheltema & Jebb 1994). Skeletal and upright spicules are hollow and needle-shaped (Fig. 2.13B). The anterior end of the body is rounded, the posterior tapered. The radula is distichous with denticulated hook-like teeth (Fig. 2.13C).

The first species of *Epimenia* was described from a single specimen collected at 108 m off north-western Australia, *E. australis* (Thiele 1897). Eleven more specimens taken nearby at depths of 32–112 m by the *Siboga* Expedition were described as *E. verrucosa*, which is synonymous with *E. australis*. It has since been discovered off Madang, Papua New Guinea, at 15–24 m depth in an area of steeply sloping coral rock with swift currents, where a soft-coral species of *Scleronephthya* on which *Epimenia australis* feeds is abundant (Scheltema & Jebb 1994). Animals were found, often in tangled masses, beneath rock slabs and rubble broken from the rock face. *Epimenia oshimai* and *E. arabica* have been described from southern Japan and the Red Sea, respectively (Baba 1940a; Salvini-Plawen & Benayahu 1991).

Its size and the ease with which it is collected off Amakusa, Japan, made an *Epimenia* species, referred to *E. verrucosa*, a unique source for observation and experimentation by Baba (1940b). The body bears two or three types of integumental papillae with small, bulbous ends on long, narrow stalks. The contents of the papillae give the body colour and their exudate can cause a dermatitis (Scheltema & Jebb 1994). The pedal gland excretes mucus exclusively. *Epimenia* species feed on the coenosarc and polyps of nephthyid alcyonarians. The foregut can be everted like a proboscis, bringing the radula to the exterior. The ventral salivary glands are long and tubular, with a glandular section and a long duct. Extracellular digestion starts in the pharynx. In the midgut both extracellular and intracellular digestion take place, the latter preceded by phagocytosis of particles by the club-shaped cells of the villi which line the midgut. At senescence, the villous cells contain vacuoles with uric acid crystals and are released into the lumen of the midgut. Nematocysts are seldom taken up by the villous cells but remain in the lumen. Shed cells and undigested material are passed to the intestine and into the mantle cavity. Erythrocytes (most numerous), amoebocytes, and platelets are distributed in the heart, sinuses, and haemocoel around the digestive tract, and especially in lacunae at the tips of the midgut villi. Amoebocytes phagocytose injected black ink, and discharge the ink particles directly into the midgut lumen between the villous cells, but not into the integumental papillae.

There are no copulatory spicules. The pericardium is large. Seminal vesicles are numerous and stalked. The lower gametoducts unite and empty through a single gametopore. The *Epimenia* species studied in Japan by Baba (1951) matures at 90 mm, and breeds from June to October. In Madang, Papua New Guinea, specimens of *E. australis* were found in reproductive condition in January and February. Baba reported spawn laid as a pair of flat mucous bands each bearing 40 or more uncleaved eggs or developing larvae after a period of brooding. Development from egg to larva, whether spawned or brooded, requires about four days, and the larvae swim for only two days after release before settling and metamorphosis.

Starved individuals of *E. australis* lived in running seawater aquaria for more than one month at Madang. Those supplied with rocks and *Scleronepthya* for food retained healthy-looking tissues and many were found paired, presumably in pseudocopulation. In many individuals, cleaving eggs and embryos present in the mantle cavity were either in several stages of development or developing synchronously.

The Epimeniidae appear to be a widespread family in tropical West Pacific waters at depths of 100 m or less, with recent records from Hong Kong, Papua New Guinea and New Caledonia (Scheltema & Jebb 1994). Although collected only once from the Australian shelf, *Epimenia* can be expected among nepthyid alcyonarians in areas of swift currents.

Incertae sedis

Genus *Notomenia*. The single species in this genus is unique in having non-calcareous spicules. *Notomenia clavigera* was described by Thiele (1897) from a single specimen taken at 37 m in Torres Strait. The unusual occurrence of haemotoxylin-staining spicules (Thiele 1902c) was corroborated by a second specimen

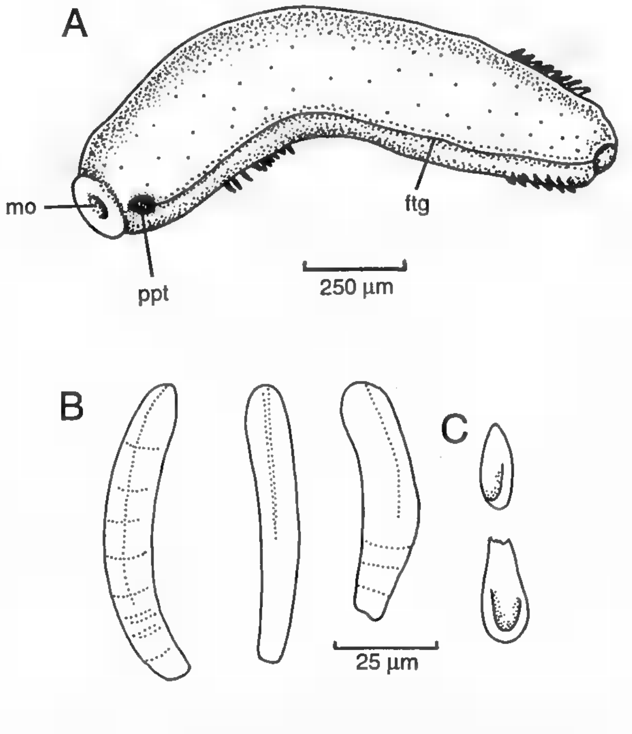

Figure 2.14 Australian Notomeniidae. *Notomenia clavigera* from Bass Strait. **A**, external appearance, most of the spicules lost during collection; **B**, club-shaped and **C**, rimmed non-calcareous spicules. **ftg**, foot groove; **mo**, mouth; **ppt**, pedal pit. (After author's drawings) [K. Hollis]

recently collected in Bass Strait from 40 m (Fig. 2.14). Spicules show no birefringence under cross-polarised light, nor do they dissolve in hydrochloric acid.

Notomenia clavigera is 4 mm or less in length, brown, and bears club-shaped spicules up to 100 µm long and 15 µm wide. The mouth is surrounded by a rim. The mantle cavity is overlain by a knob-like protuberance. Radula, copulatory spicules, gill folds, and dorso-terminal sensory organ are lacking. Unique are: (1) the ring of ganglia surrounding the vestibule; (2) the position of the mantle cavity dorsal to the pericardium, gametoducts, and intestine; (3) the opening of paired gametopores directly to the outside and not into the mantle cavity; (4) the dorsal opening of the intestine into the mantle cavity; and (5) the openings of the pericardium into the upper gametoducts anterior to the bend between upper and lower gametoducts.

The affinities of this unique genus and species are unknown.

Genus *Ocheyoherpia.* This genus, originally placed in the Phyllomeniidae (Salvini-Plawen 1978), is unique in the form of the radula combined with spicule morphology. The two species in the genus are distinguished by thick, solid fishhook-shaped spicules and spines, the lack of skeletal spicules, and a distichous radula in which the denticles arise from a long bar, with the outer two denticles fused in an inverted V-shape (Fig. 2.15C). One of the two known species of *Ocheyoherpia* occurs at Macquarie Island, where several individuals were collected by divers from rocks at depths of 6–14 m (Fig. 2.15B).

The species are small, up to 6.5 mm long. The spicular coat is rough to spiny and a dorsal carina may be present. The anterior midgut caecum is paired. The paired ventral salivary glands are acinar. Two or more paired copulatory spicules are present.

The genus is apparently restricted to the Subantarctic continental shelf (Salvini-Plawen 1978a) and subtidal regions.

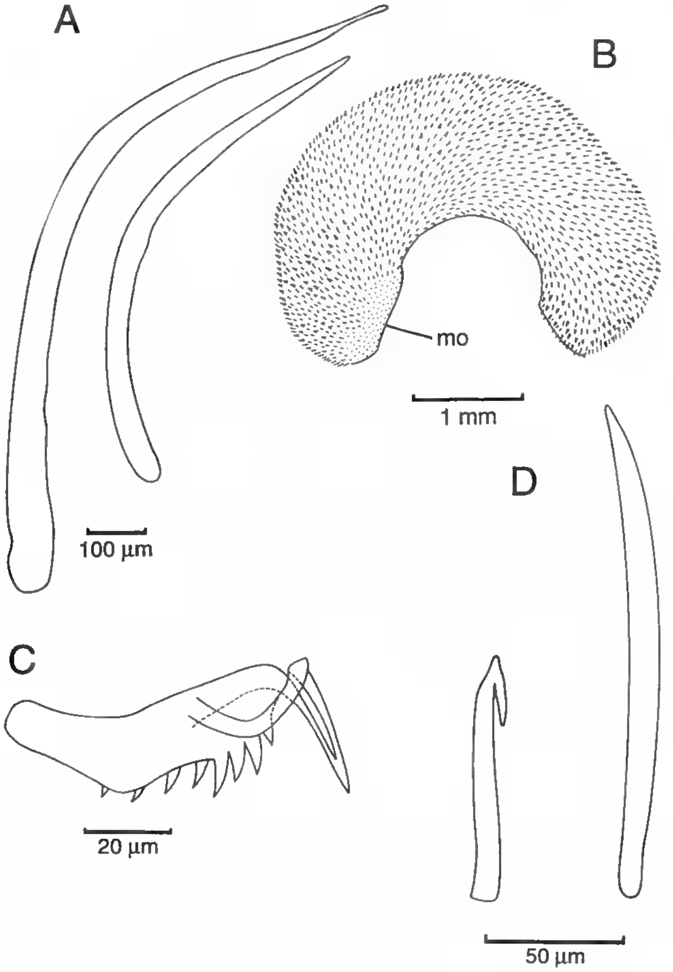

Figure 2.15 Australian *Ocheyoherpia* sp. (family *Incertae sedis*) from Macquarie Island. **A**, copulatory spicules; **B**, external appearance; **C**, single tooth from radula; **D**, spicules. **mo**, mouth. (After author's drawings)
[C. Eadie]

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Contribution No. 7655 of the Woods Hole Oceanographic Institution, Woods Hole MA 02543 USA

CLASS POLYPLACOPHORA

CHAPTER 3

DEFINITION AND GENERAL DESCRIPTION

The Polyplacophora, commonly called chitons, are slow-moving, bilaterally symmetrical, marine molluscs. They are typically grazers living attached to hard substrata in intertidal and shallow coastal waters (Fig. 3.1). However, the Abyssochitonidae, Xylochitonidae, most of the Lepidopleuridae, Hanleyidae and a few species of other groups occur in deeper waters, and the cosmopolitan *Leptochiton alveolus* is found to depths of 5000 m. Chitons occur throughout the world, but are most diverse in Australasia and the tropical Pacific coasts of America. They range in length from a few millimetres to some 100 mm although the west American *Cryptochiton stelleri* reaches 300 mm. Worldwide there are some 10 families and about 750 living species, of which at least 180 species are known from Australian waters.

Chitons are dorso-ventrally flattened, oval to elongate molluscs. They are characterised by eight dorsal, articulating shell plates, termed valves, which are frequently obvious and brightly coloured and/or sculptured (Pls 7–9). They contain unique microscopic structures called aesthetes which appear to have both sensory and secretory functions. The valves are embedded to varying degrees in a fleshy, muscular girdle which may bear calcareous scales or spicules and is sometimes highly coloured or patterned. The valves are very reduced in some members of the Acanthochitoninae where the girdle may grow over most of the valves. The flexible girdle and articulating valves enable many species to curl up when disturbed.

The large foot which dominates the ventral surface is used for creeping over the substratum. The dorso-ventral flattening of the animal has resulted in a remarkable forward extension of the mantle cavity, developing into two narrow pallial grooves extending along the total length of the foot. The pallial groove surrounding the foot contains up to 40 gills (ctenidia) and separates the foot from the ventral surface of the girdle. Anterior to the foot is the simple head, which bears the mouth, but lacks eyes or tentacles, and the anus is located on a papilla posteriorly. There is a large, well-developed radula in which each row contains 17 teeth.

Chitons are dioecious, but lack any form of sexual dimorphism. They usually lay eggs and develop via a short-lived larval stage, but several species are known to brood the eggs in the pallial groove.

HISTORY OF DISCOVERY

Georgius Everhardus Rumphius (1705), an official of the Dutch East Indian Company on Amboina (= Ambon, Indonesia), provided one of the earliest records of chitons when he included *Limax marina* in his book on various natural products. From his description (p. 38) and figure (pl. X no. 4), this is probably *Acanthopleura gemmata*, a widespread Indo-Pacific species and a common inhabitant of tropical northern Australian shores.

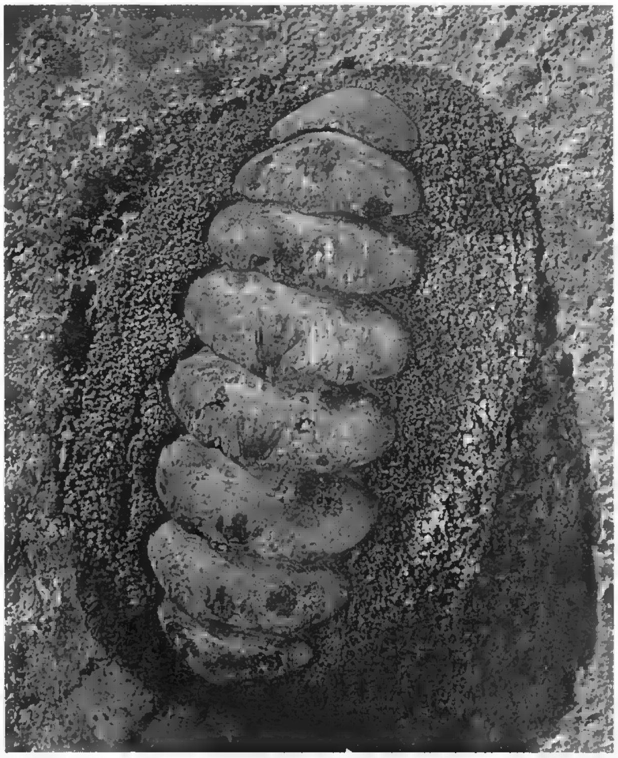


Figure 3.1 *Acanthopleura gemmata* (Chitonidae), showing the characteristic eight shell valves embedded in the girdle. [K. Atkinson]

Linnaeus (1758) described four species of *Chiton* in the 10th edition of *Systema Naturae*, placing the genus within the Vermes Testacea. Nine species were described in the twelfth edition (1767), and the thirteenth edition, compiled by Gmelin (1791), contained 28 species, including (and validating) the 25 species described and depicted by J.H. Chemnitz in vols 8 (1785) and 10 (1788) of Martini's *Neues Systematisches Conchyliencabinet.*

In 1797 the Danish naturalist and antiquarian L. Spengler, a close friend of Chemnitz, wrote the first comprehensive monograph of 'the many-valved genus of conchs that Linnaeus called *Chiton*', in which 27 species are described and some are illustrated. No Australian representatives appeared in Wood's (1815) list of 37 species of chitons, and the first valid species of chitons from the areas of 'New Holland' were reported more than a century after Rumphius.

François Péron and Charles Alexander Lesueur brought home many fine samples of chitons, collected during Baudin's expedition 'aux terres Australes' (1800–1804). The first Australian chitons were described by Lamarck from this material in 1819. He introduced the generic name *Chitonellus* for two species of the aberrant genus presently known as *Cryptoplax.* The bulk of the material collected by Péron and Lesueur, however, was described by another famous French scientist, H.M.D. de Blainville, who in 1825 listed as many as 64 species of 'oscabrions', a vernacular name for chitons; three of the 18 reported from Australia are in error.

Two other famous French naturalists, J.R.C. Quoy and J.P. Gaimard, took part in two voyages visiting Australia, those of the *Uranie* and the *Physicienne*, and of the *l'Astrolabe*. Although some of the collections were examined by de Blainville, Quoy & Gaimard (1835) described and illustrated 22 species from the *l'Astrolabe* material; two of these were from Australia, but both had been described already.

From the beginning of the 19th century, conchology rapidly gained popularity, especially in England, where the establishment of museums of curiosities became a favourite mania. The famous and perhaps the greatest collector of shells in the world, the merchant Hugh Cuming (1791–1865), built a huge collection of shells, mostly gathered personally during his many voyages all around the world, but also by other voyagers, ship's captains and traders. From this extensive source, G.B. Sowerby I and II (1832–1848), L. Reeve (1847–1848), the brothers Henry and Arthur Adams (1854–1866) and others, described many more species from Australia (for example, see Sowerby II 1832–1840; Sowerby Jr 1840; 1841; Reeve 1847–1848; Adams, A. 1854; Adams & Adams 1854–1854).

Meanwhile in 1847, J.E. Gray, then curator of Mollusca at the British Museum (Natural History), wrote an important paper, *On the Genera of the Family Chitonidae*, which he introduced as follows: 'This family now contains so many species, offering such varied modifications of form and structure, that it becomes necessary to separate it into several genera, for the purpose of more accurately determining the species and showing their relations to each other.' Fifteen genera were recognised, based on surficial structure of the girdle, the slitting of the insertion plates, the position of the mucro on the tail valve and other external morphological features. Nine of the ten new genera described are recognised still as valid.

Between the years 1884 and 1875, P.P. Carpenter divided the Polyplacophora into two sections. Species with the end plates similarly articulated were classed as 'regular chitons' (four subsections), and those with an abnormal tail plate or with a sinus behind were termed 'irregular chitons' (five subsections). Unfortunately, Carpenter died before the completion of his two volume monograph on Polyplacophora, which contained all known species and as many newly described ones. His system, however, was published (1879) almost unaltered by the noted American conchologist W.H. Dall. Then the Carpenter manuscripts came into the hands of another American conchologist, Dall's close friend Henry A. Pilsbry, who extensively incorporated Carpenter's work into his monograph of 'Polyplacophora' in Tryon's *Manual of Conchology*, vols 14 and 15 (Tryon 1892–1893). He not only described and illustrated all

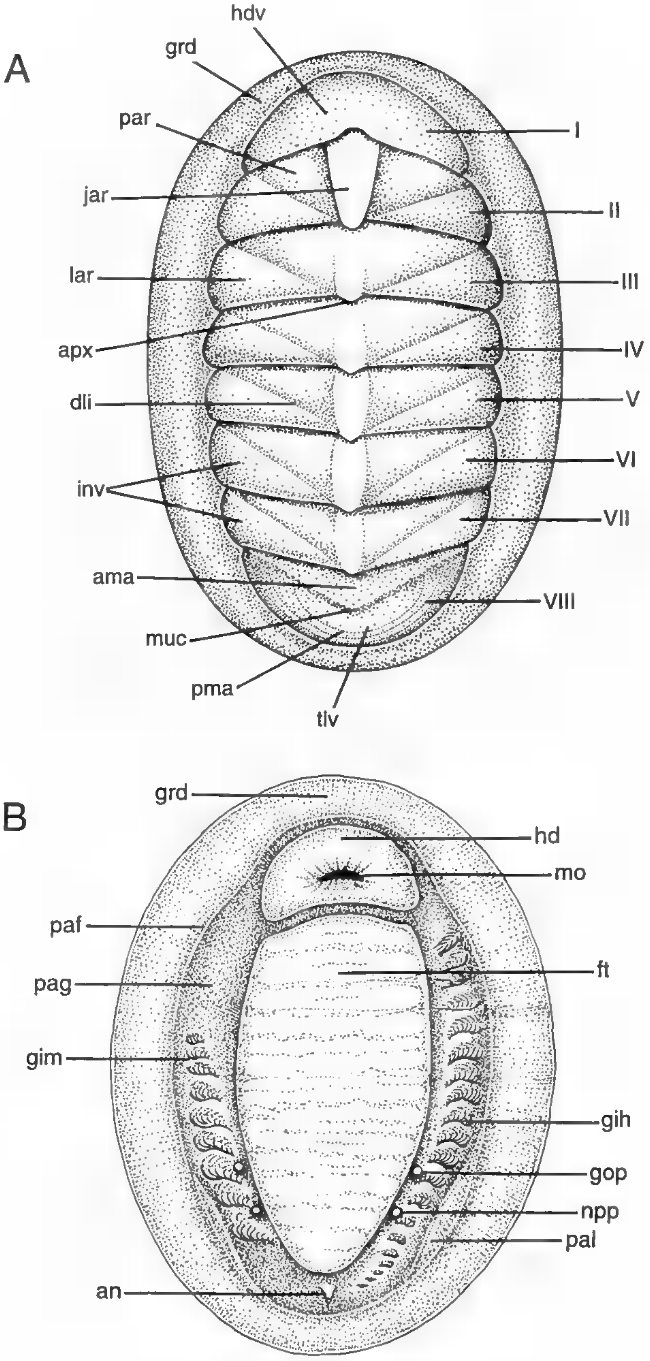


Figure 3.2 External features of the Polyplacophora. **A**, dorsal view. **B**, ventral view showing two gill arrangements. **ama**, antemucronal area; **an**, anus on a papilla; **apx**, apex; **dli**, diagonal line; **ft**, foot; **gih**, gills, holobranchial adanal; **gim**, gills, merobranchial abanal; **gop**, gonopore; **grd**, girdle; **hd**, head; **hdv**, head valve; **I – VIII**, shell valves; **inv**, fifth and sixth intermediate valves; **jar**, jugal area; **lar**, lateral area (lateral triangle); **muc**, mucro; **mo**, mouth; **npp**, nephridiopore; **paf**, pallial fold; **pag**, pallial groove; **pal**, pallial lappet; **par**, pleural area (median triangle); **pma**, postmucronal area; **tlv**, tail valve. [A, D. Wahl; B, P. Kaas]

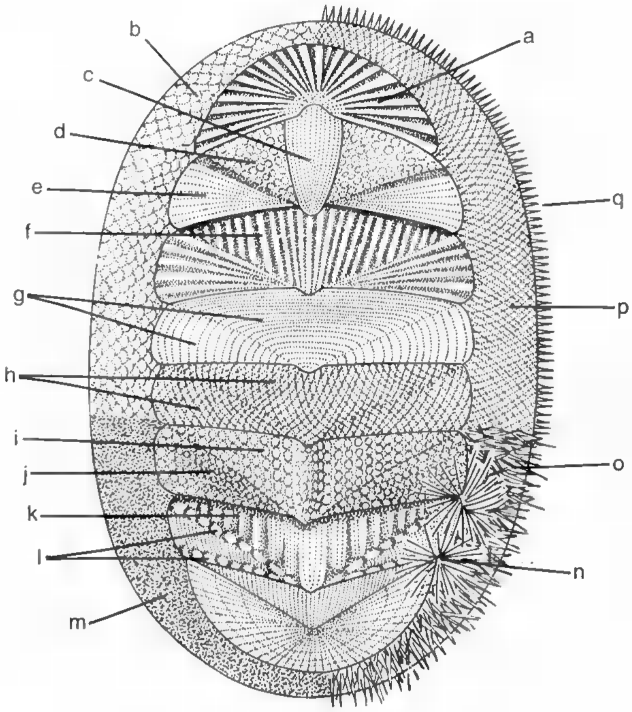


Figure 3.3 Dorsal view of a chiton showing the possible ornamentation and sculpture of the valves and the girdle. **a**, radially sulcate; **b**, imbricating striated scales of girdle; **c**, finely longitudinally striate; **d**, quincuncially pustulose; **e**, radially sulcate; **f**, longitudinally sulcate; **g**, concentrically striate; **h**, quincuncially granulose; **i**, longitudinally pustulose; **j**, radially pustulose; **k**, longitudinally sulcate; **l**, tuberculate radial ribs; **m**, leathery girdle; **n**, spinulose sutural tuft; **o**, spiculose girdle; **p**, granulose girdle; **q**, marginal spiculose girdle-fringe. [D. Wahl]

known living species, including those described in Carpenter's manuscript, but also drew up a new phylogenetic system of classification to replace the purely morphological system of Carpenter and Dall.

Pilsbry's work stimulated the study of chitons enormously, especially in Australia, which is richer in species diversity or abundance than any other continent. Collectors of shells, like J. Bracebridge-Wilson, J.C. Cox, E.H. Matthews, Sir Joseph Verco and many others provided not only Pilsbry, but local workers such as W.T. Bednall, W.G. Torr and Edwin Ashby, all living in South Australia, with a constant stream of specimens. Ashby produced no less than 75 papers on chitons in half a century (1898–1946), a few of them in cooperation with Torr, Cotton or Hull, and described 52 new living and 19 fossil Australian chiton taxa. Major contributions to the knowledge of the group at that time include the works by Pilsbry (1892–1894), Bednall (1897), Bednall & Matthews (1906), Torr (1911, 1912), Thiele (1911), Iredale & May (1916) and Ashby (1918a, 1918b, 1923a).

W.L. May in Tasmania, J.H. Gatliff and C.J. Gabriel in Victoria, and C. Hedley and A.F.B. Hull in New South Wales, also contributed much to the knowledge of the Australian chiton fauna. The most comprehensive work on the Australian Polyplacophora was undoubtedly Iredale and Hull's 'Monograph of the Australian Loricates', which was published in sections between the years 1923–1927, and incorporated into a single monograph on the group in 1927. Interest in the Australian Polyplacophora declined after this period, and the group was largely neglected during the next generation, with the exception of work on the southern Australian chitons by B.C. Cotton and his co-workers (Cotton & Weeding 1939; Cotton & Godfrey 1940; Cotton 1964). Recently, there has been a revival of interest in the Polyplacophora on a worldwide scale (Ferreira 1974, 1978, 1986; Starobogatov & Sirenko 1975; Kaas & Van Belle 1980, 1985a, 1985b, 1987, 1990, 1994; Van Belle 1983; Bullock 1985, 1988a).

MORPHOLOGY AND PHYSIOLOGY

External Features

The external features and associated terminology of chitons are summarised in Figures 3.2–3.4. The gross morphology of generalised chiton valves is illustrated in Figure 3.4 using terminology defined by Boyle (1976). Shell valves are of three distinct types. The head valve is semi-circular and overlaps the first of the six intermediate valves. The posterior tail valve is distinguished by a projection, or mucro, that divides the surface into antemucronal (central) and postmucronal (posterior) areas. Each side of an intermediate valve is often divided into two triangles by a diagonal line, fold or ridge which radiates from the postero-medial apex. These are termed the pleural and lateral areas; they are often separated by a jugal area (Fig. 3.4B). The dorsal surface may exhibit a variety of sculpturing, including granules, pustules, ribs and sulci (Fig. 3.3). Growth lines may be visible at both macro and micro scales (Jones & Gowlett-Holmes 1992). The sculpturing and morphology of the valves are closely related to the abundance and distribution of the aesthete canals that perforate the various lateral and ventral valve surfaces.

The valves are complex structures internally (Haas 1972). They are composed of four main layers differentiated by their organic content and crystalline structures. The inorganic content of the shell comprises 98% calcium carbonate, as aragonite, with small amounts of magnesium carbonate, calcium sulphate, calcium phosphate and oxides of silicon, aluminium and iron (Hyman 1967; Rhoads & Lutz 1980).

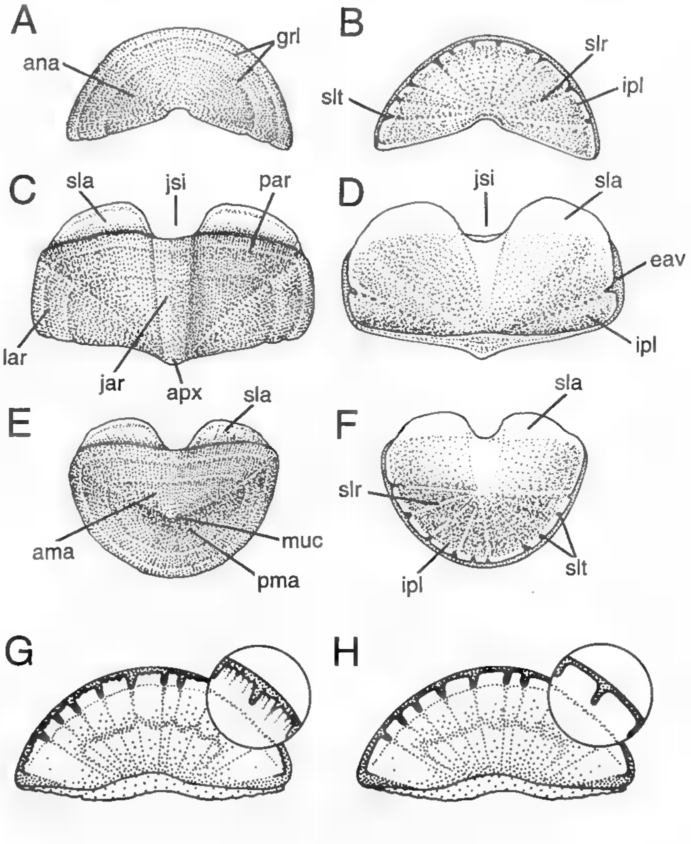


Figure 3.4 Generalised shell valves of a chiton showing the main regions and structures: **A**, **B**, head valve; **C**, **D**, intermediate valve; **E**, **F**, tail valve; **A**, **C**, **E**, dorsal view; **B**, **D**, **F**, ventral view. **G**, head valve with pectinate insertion teeth; **H**, head valve with smooth insertion teeth. **ama**, antemucronal area; **ana**, anterior area; **apx**, apex; **eav**, eave; **grl**, growth lines; **ipl**, insertion plates (teeth); **jar**, jugal area; **jsi**, jugal sinus; **lar**, lateral area (lateral triangle); **muc**, mucro; **par**, pleural area (median triangle); **pma**, postmucronal area; **sla**, sutural lamina; **slr**, slit rays; **slt**, slits. (Modified after original drawings by P. Kaas and A.M. Jones)
[A–F, P. Kaas; G, H, C. Eadie]

The outermost layer is the periostracum, a very thin, proteinaceous film overlying the tegmentum. It may be eroded to expose the underlying tegmentum. The tegmentum consists of an organic matrix of conchiolin impregnated with calcium carbonate. It is usually penetrated by many horizontal and vertical canals containing extensions of the mantle epithelium. These terminate at the valve surface in the unique structures called aesthetes that have been considered sensory and/or secretory in function (Baxter, Jones & Sturrock 1987). The outer edges of the tegmentum which overhang the underlying insertion plates and sutural laminae are called eaves (Fig. 3.4). The eaves maybe solid or porous in different families.

The articulamentum lies beneath the tegmentum, and projects anteriorly and laterally beyond it to form the sutural laminae and insertion plates. This is usually the thickest layer, composed of calcium carbonate crystals in a crossed-lamellar crystal pattern that gives it great strength and solidity. The sutural laminae (= sutural plates or apophyses) are wing-like extensions on the anterior margin of the intermediate and tail valves. They project forwards beneath the posterior margin of the preceding valve, to which they are connected by muscular tissue. Insertion plates occur on the lateral valve margins of all families except the Leptochitonidae. They are usually divided into insertion teeth by slits that are the points of entry for major aesthete canals. However, the insertion plates are penetrated throughout by holes for the entry of smaller aesthete canals (Fig. 3.18B) and are often described as spongy when this is conspicuous. The outer edges of insertion teeth maybe smooth, as found in most families, or pectinate with radiating grooves as in the family Chitonidae.

The thin fourth and innermost layer, the hypostracum, consists of a layer of columnar crystals which lines the ventral surface of the valves.

The valves are embedded in the mantle that forms the tough, flexible girdle running around the margin of the animal. The dorsal side of the girdle may bear various structures including calcareous scales, granules, spicules and spines or chitinous hairs; these are embedded in pockets of the chitin-containing cuticle (Hyman 1967). Ventrally, the girdle is usually clothed with rectangular, flat scales or with dense spicules, and is only rarely naked. The extent to which the girdle covers the valves is variable. As it never grows over the tegmentum, dorsal extension of the girdle results in the simultaneous reduction of this shell layer. Valves are so strongly reduced in the worm-like Cryptoplacidae that the posterior four or five may lose contact with each other. This trend culminates in the condition seen in the New Zealand species *Cryptoconchus porosus* and the huge, northern Pacific *Cryptochiton stelleri*, in which the tegmentum has almost totally disappeared.

The dorsal surface of chitons is generally strongly coloured whereas the ventral surface usually lacks colouration. The colour and pattern of valves and girdle vary with species. Some may be cryptic, such as *Choriplax grayi*, in which the colour of the girdle and tegmentum closely matches that of the host red alga. Valves and girdles of members of the Lepidopleurina and Acanthochitonidae are often rather drab, being grey, brown, tawny or green; deep-water species living in little or no light are usually off-white. However, many littoral and sublittoral species of the Ischnochitonidae and Chitonidae exhibit bright colours and/or elaborate patterns.

The ventral surface (Fig. 3.2B) is dominated by the flat foot and the simple head containing the mouth at the anterior end. The mantle cavity encircling the animal is reduced to shallow pallial grooves between the foot and the girdle, which contain the numerous gills or ctenidia. The anus generally opens on a papilla at the posterior end of the animal.

Muscular System and Locomotion

The musculature of chitons is complicated (Hyman 1967; Wingstrand 1985). Four major groups of muscles (Figs 3.5, 3.6) serve to keep the valves firmly together and closely attached to the body wall as well as providing flexibility. The pair of straight, slender rectus muscles near the median line keep the animal extended. Each pair connects the anterior margin of the jugal sinus region of each valve with the body wall beneath the anterior part of the preceding valve. The paired oblique muscles, also attached to the antero-ventral surface of the jugal sinus of each valve, diverge antero-laterally towards their attachment on the body wall beneath the preceding valve. Both rectus and oblique muscles are absent under the tail valve. The unpaired transverse muscles consist of short dorso-ventral fibres. They connect the dorsal side of the sutural laminae with the underfolded posterior margin of the preceding valve to form a flat, elastic cushion. The lateral longitudinal muscle encircles the animal just beneath the outer margins of the valves. Its ventral fibres are mostly continuous, but the more dorsal ones run from valve to valve. Around the head and tail valves, the fibres of the left and right side meet medially and are intertwined. Contraction of the lateral longitudinal muscle causes the animal to curl up, a means of self-defence when the animal loses contact with the substratum.

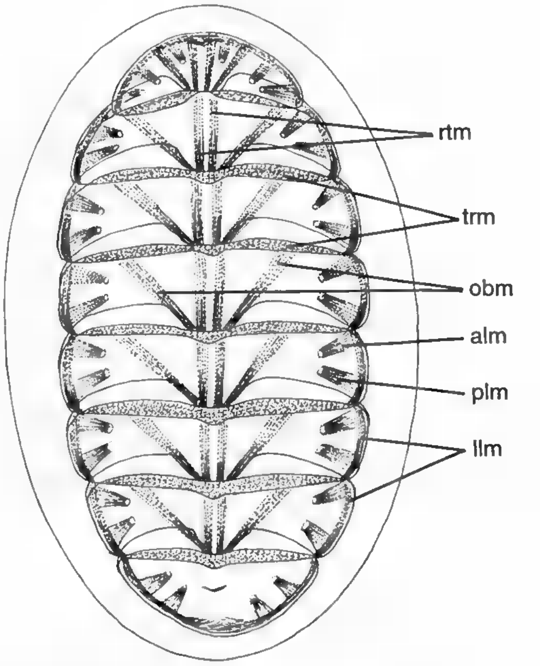


Figure 3.5 Musculature of a chiton, dorsal view. **alm**, anterior latero-pedal muscle; **llm**, lateral longitudinal muscle; **obm**, oblique muscles; **plm**, posterior latero-pedal muscle; **rtm**, rectus muscles; **trm**, transverse muscles. (Modified after Henrici 1912) [P. Kaas]

The valves are strongly connected to the foot by a system of latero-pedal muscles (Figs 3.5, 3.6), comprising an anterior pair and a posterior pair for each valve. Each is divided into three bundles. The inner and outer ones cross in the roof of the pallial groove, are attached to the pleural parts of the articulamentum and radiate into the foot where they intermingle with the diffuse fibres of the foot musculature. The valves are connected to the girdle by the paired inner mantle muscles. These run from the underside of each valve, not far from the outer margin, along the mantle wall bordering the outer side of the pallial groove.

The girdle contains many longitudinal and lateral oblique fibres. These muscles allow it to flex, to clamp down onto the substratum when threatened or to minimise desiccation when exposed to air. Together with the foot muscles, they are responsible for providing a firm attachment to the substratum. They also facilitate ventilation of the gills or gamete release when the girdle is raised.

Chitons are generally slow-moving animals. Although usually slower than gastropods of equivalent size, some members of the Ischnochitonidae are comparatively fast, and disturbed *Ischnochiton maorianus* can normally attain speeds of 100 mm/min (Boyle 1977). Some *Cryptoplax* species also move quite rapidly and can show great flexibility, the body being able to twist easily through 180°. Many chitons can turn over when unattached and upside down, a capability only possible because of the flexibility provided by the articulating valves and associated musculature. They can creep over very rough surfaces and sharp ridges without losing contact with the substratum, again reflecting the flexibility of the body and girdle.

Normally chitons creep forward slowly using antero-posterior (retrograde) contractile waves of the foot musculature. This is accomplished by antagonistic contraction and relaxation of successive longitudinal muscle fibres concentrated in the basal part of the foot. They are also able to move backwards and to rotate, but the direction of the foot wave does not appear to change. Most species are capable of strong adhesion to the substratum by pressing the foot and the girdle against the substratum, and they can be very difficult to remove without damage once clamped to the surface. If a chiton becomes dislodged its normal reaction is to curl up tightly to protect its soft parts.

Body Cavities

A large body cavity (Fig. 3.6), termed the visceral sac, contains the digestive tract and accessory organs. This cavity is not coelomic, however, as neither it, nor the digestive organs is covered with peritoneal tissue. It is a blood sinus and the existence of any true coelom is still a matter of dispute. The visceral sac is divided into a small anterior and a large posterior compartment in most chitons by a nearly vertical, incomplete partition of connective tissue, the diaphragm, at about the level of the transverse groove separating the head from the foot. The radular sheath and the oesophagus pass through this diaphragm and there is a large oval opening in it for the passage of the radular retractor muscles.

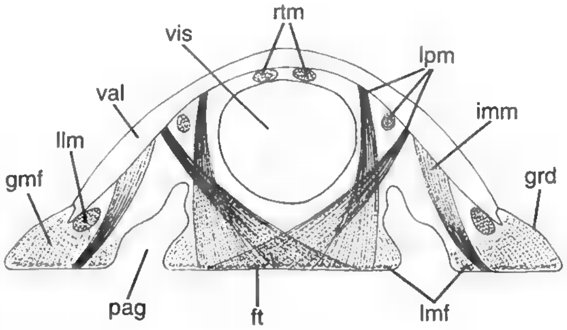


Figure 3.6 Cross-section through the body of a chiton, showing musculature. **ft**, foot; **gmf**, girdle muscle fibres; **grd**, girdle; **imm**, inner mantle muscle; **llm**, lateral longitudinal muscle; **lmf**, longitudinal muscle fibres in foot and girdle wall; **lpm**, latero-pedal muscles; **pag**, pallial groove; **rtm**, rectus muscles; **val**, shell valve; **vis**, visceral sinus. [P. Kaas]

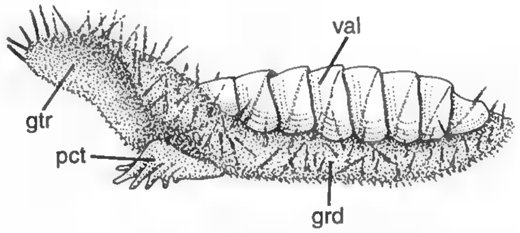


Figure 3.7 *Placiphorella velata* (Mopaliidae) in offensive attitude with raised girdle. **grd**, girdle; **gtr**, girdle trap; **pct**, precephalic tentacles; **val**, shell valve. (After McLean 1962) [P. Kaas]

Feeding and Digestion

Most chitons are generalist grazers (herbivores and omnivores) of hard substrata, feeding mainly on the microflora, algae and small encrusting animals scraped from the substratum using the well-developed radula. The substrata grazed comprise mainly the surface of rocks, empty shells or stems (stipes of algae) and leaves (fronds of algae) of marine plants. Mineral material, constituting as much as 40% of the gut contents, is often ingested together with the various digestible organic materials. Although chitons generally avoid crawling on sand and mud surfaces, some, such as *Pseudotonicia cuneata* and *Bassethullia* species, have been found free-living in sand with undefined feeding substrata. *Callochiton crocinus* is a specialist algal grazer (Kangas & Shepherd 1984), whereas *Ischnochiton torri*, *Stenochiton longicymba* and *Stenochiton cymodocealis* are specialist seagrass feeders. Deep-water chitons, found to depths of 8000 m and mainly members of the suborder Lepidopleurina, appear to feed on detritus or on sunken wood; skeletons of diatoms, foraminiferans, radiolarians, larvae of crustaceans, molluscs and polychaetes frequently are found in their intestines. The stomach of *Leptochiton vitjazi* from the Bougainville trough in the Solomon Sea contained skeletons of diatoms, foraminiferans, radiolarians and the spicules of calcareous sponges (Sirenko 1977). The gut of *Xylochiton xylophagus* from off New Zealand (Jones & Gowlett-Holmes 1992) contained only wood fragments, raising the possibility that this species feeds on bacteria.

Most carnivorous chitons feed on sedentary animals, including sponges, bryozoans and coelenterates; some larger forms, such as the Californian *Mopalia hindsii*, also feed on young barnacles. *Notoplax speciosa*, like some species of the Northern Hemisphere genus *Hanleya*, appears to be a specialist sponge feeder and is usually found in cavities embedded within the host sponge. An active, carnivorous habit was found by Ludbrook & Gowlett-Holmes (1989) in *Loricella angasi*, resembling that described for *Placiphorella velata* (McLean 1962) and two species of *Craspedochiton* (Saito & Okutani 1992). *Placiphorella velata* and *L. angasi* catch small crustaceans using a much enlarged anterior girdle; they have also a mantle fold bearing sensory precephalic tentacles anterior to the head (Fig. 3.7). The girdle is raised anteriorly while at the same time the precephalic tentacles are pressed onto the substratum. If stimulated by passing prey, the girdle is lowered in less than one second, trapping the prey. The precephalic tentacles hold the prey and direct it to the mouth in a process taking about an hour. The more varied diet of *Craspedochiton* species includes annelids, brittlestars and crustaceans.

Studies of the structure of the alimentary system of chitons (Figs 3.8, 3.9) were reviewed by Hyman (1967); no Australian examples are available. The digestive tract of *Acanthopleura echinata* from the Pacific coast of South America was treated thoroughly by Plate (1897–1901) and Fretter (1937) described the anatomy and histology of the gut of the European species *Lepidochitona cinerea* in detail. Several regions can be distinguished: the mouth and buccal tube, the buccal cavity, the pharynx, the oesophagus, the stomach and digestive gland, the intestine, and the rectum and anus.

The rounded or oval mouth is situated in the centre of the ventral surface of the head. It expands considerably when the radula and/or the subradular organs are protruded while feeding. The wall of the short buccal tube (Fig. 3.9) leading from the mouth is strongly folded longitudinally. Via a sphincter, this tube leads to the wide and complex buccal cavity, which is strengthened ventrally by a thick cuticle. The roof of the anterior part of the buccal cavity bears a pair of small, oval, more or less arborescent, buccal glands which secrete mucus, but which are not homologous with the salivary glands of other molluscs. A blind sac, the subradular pouch, extends backwards from the posterior wall of the buccal cavity and contains two small cushions of tall, ciliated epithelial cells, the subradular organs, among which sensory cells occur. The latter may be protruded through the buccal tube and are presumed to be chemosensory and used for testing the substratum for food.

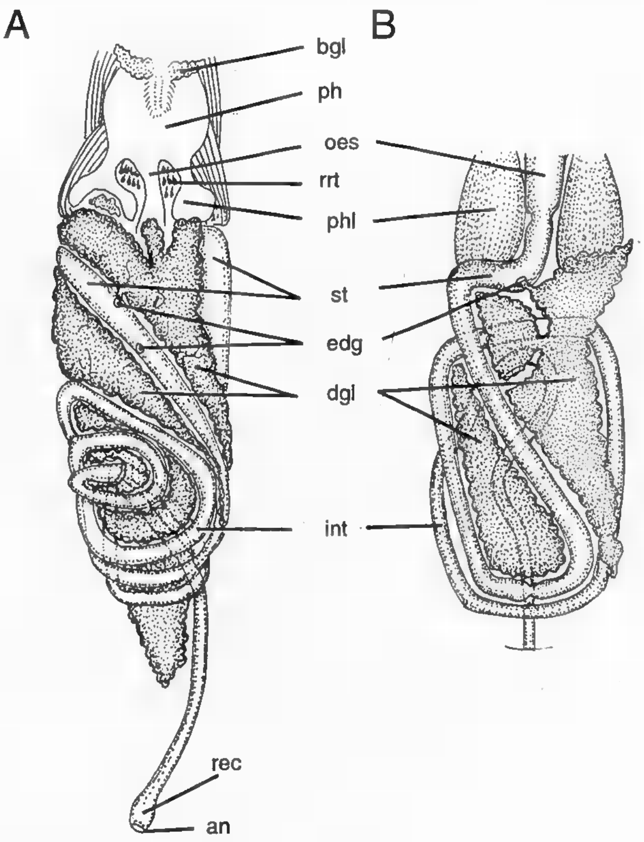


Figure 3.8 Digestive tracts of chitons, dorsal view. A, *Chiton cumingsii* (Chitonidae). B, *Hanleya hanleyi* (Hanleyidae). **an**, anus; **bgl**, buccal gland; **dgl**, digestive gland; **edg**, entrance of digestive gland into stomach; **int**, intestine; **oes**, oesophagus; **ph**, pharynx; **phl**, pharyngeal gland; **rec**, rectum; **rrt**, radula retractors; **st**, stomach. (After Plate 1899) [P. Kaas]

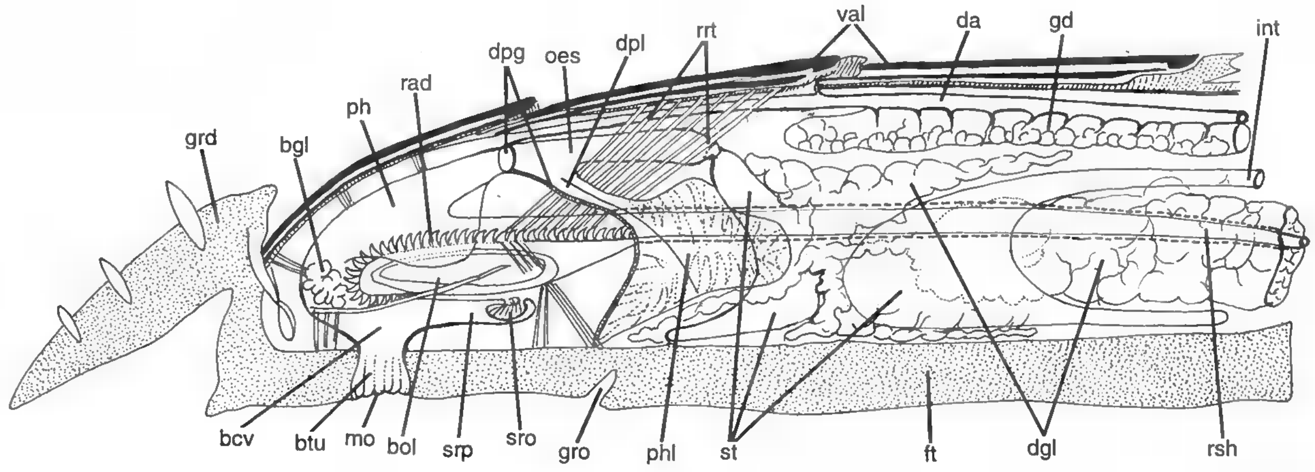


Figure 3.9 A lateral view of the anterior body of *Acanthopleura echinata* (Chitonidae) in sagittal section. **bcv**, buccal cavity; **bgl**, buccal gland; **bol**, bolster; **btu**, buccal tube; **da**, dorsal aorta; **dgl**, digestive glands; **dpg**, diaphragm; **dpl**, duct of pharyngeal gland; **ft**, foot; **gd**, gonad; **grd**, girdle; **gro**, groove between head and foot; **int**, intestine; **mo**, mouth; **oes**, oesophagus; **ph**, pharynx; **phl**, pharyngeal gland; **rad**, radula; **rrt**, radula retractors; **rsh**, radula sheath; **sro**, subradular organ; **srp**, subradular pouch; **st**, stomach; **val**, shell valves. (After Plate 1897) [P. Kaas]

The radula (Fig. 3.10) projects into the posterior wall of the buccal cavity at the entrance to the pharynx, and is used for rasping food materials. This very long, horny, toothed structure is enclosed in an elongate sheath which extends backwards beneath the digestive tract to about the level of the posterior margin of the third valve. The radula is formed as a long, narrow ribbon at the distal end of the radular sheath where special cells secrete a basal membrane of proteins and chitin. The teeth, many of which are simply flat plates, are formed by odontoblasts arranged in groups at the posterior end of the radular sheath; the surface shape of the odontoblasts determines the form of the teeth. The radula lengthens anteriorly through continuous growth, and the teeth develop gradually as they move forward where they replace the anterior working teeth as they are worn away.

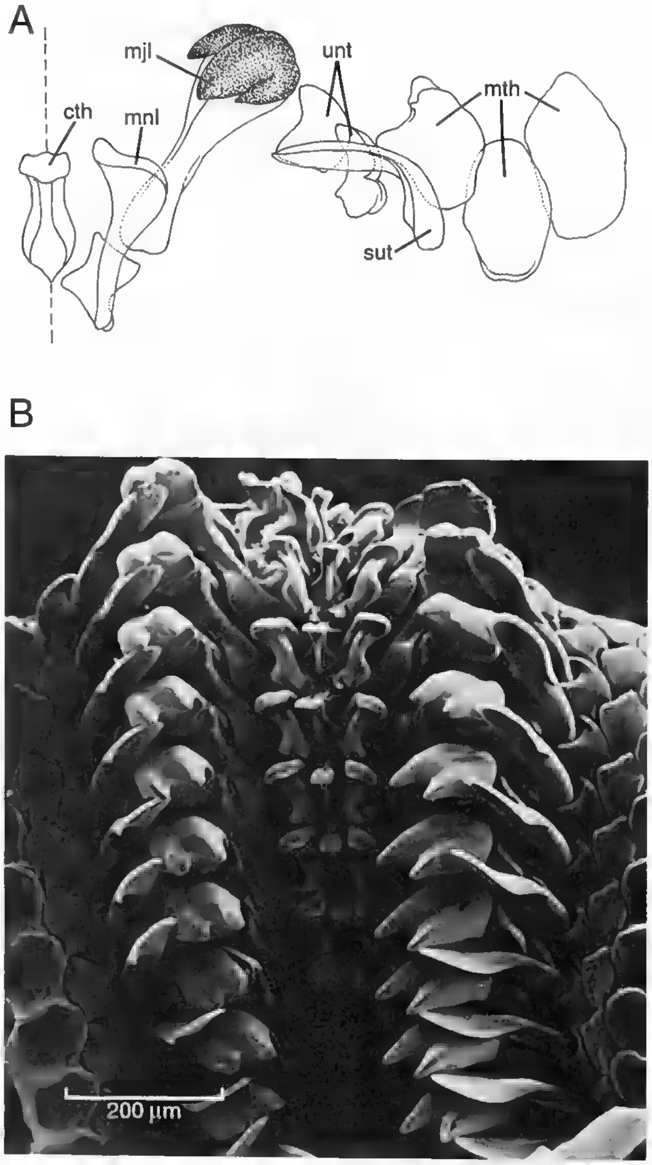


Figure 3.10 Radulae of members of the Ischnochitonidae. **A**, half a radular row of *Lepidochitona cinerea*. **B**, rows of radular teeth of *Ischnochiton elongatus*. **cth**, central tooth; **mth**, marginal teeth; **mjl**, major lateral tooth; **mnl**, minor lateral tooth; **sut**, spatulate uncinal tooth; **unt**, simple uncinal teeth. (A, After Kaas & Van Belle 1985a) [A, P. Kaas; B, A.M. Jones]

The radula has a remarkably uniform construction, consisting of numerous transverse rows of 17 teeth each; only in the genus *Juvenichiton* are 13 to 15 teeth found. The number of transverse rows varies considerably, from about 30 to more than 80, but is fairly constant within a species, although more rows are present in older animals than in young ones. Chiton radulae comprise several distinct components (Fig. 3.10). The central tooth is usually small and elongate with a narrow cutting edge, and arises medially from a basal plate. On each side of it is a larger, variously shaped first, or minor, lateral tooth, which often bears a basal laterally directed wing, and may have a narrow blade distally. The major lateral tooth is by far the largest and most conspicuous. Its long shaft is crowned by a large, black, recurved, cutting edge that may bear up to four more or less sharply pointed cusps. Studies of these strong and effective scraping structures in *Acanthopleura hirtosa* (Evans, Macey & Webb 1990, 1991) show that they have a complex internal structure. The black colouration is the result of impregnation with various iron biominerals, such as magnetite, which harden the edge.

Three uncinal teeth flank the major lateral tooth. The first and second of these are simple polygonal plates without cutting edges whereas the third or spatulate uncinal tooth is long and inwardly curved, usually with a cutting edge. The outer margin is lined by a further three flat, polygonal marginal plates. Although the radula has a remarkably uniform construction in being composed of 17 teeth per row, the individual shape and characteristics of the teeth are variable, and are taxonomically useful, especially when combined with other taxonomic characters. The radula is supported anteriorly by a pair of gas-filled bolsters which also serve as an attachment point for the very complicated muscular system used to move the radula, bolsters and the adjacent buccal area (Wingstrand 1985). Plate (1897, 1899, 1901) distinguished

38 paired and six unpaired muscles in *Acanthopleura echinata* which are used to protrude and retract the radula and bolsters or move them up and down while scraping food from the substratum.

Posterior to the radula, each side of the pharynx is usually expanded laterally into a diverticulum lined with glandular tissue of unknown function. The ducts from the large, paired pharyngeal (salivary or sugar) glands enter the pharynx posterior to the diverticula and at the point where it narrows into the oesophagus. The secretion of these glands includes alkaline phosphatase and a powerful diastase which breaks down a range of carbohydrates; however, the sites of enzyme synthesis are still unknown (Boyle 1977).

The pharynx becomes constricted before passing into the narrow, short oesophagus, which has a strong sphincter at the point of entry to the stomach. The stomach is tube-shaped in the Lepidopleurina, hardly wider than the oesophagus, but in the Chitonina and Acanthochitonina it is a wide sac lying between the brownish lobes of the digestive gland (= midgut gland or 'liver'). This voluminous, bilobed gland occupies the space around the stomach and between the coils of the intestine: the left lobe is usually much larger in mature animals. Both lobes open to the stomach through separate or fused ducts just anterior to the sphincter which separates the stomach from the anterior intestine. It is presumed that soluble products from digestion are squeezed into these ducts. The precise roles of the digestive gland in chitons are unclear, but it secretes a strong protease and is considered to store lipid as well as aid in digestion. The size of the digestive gland is correlated with both season and gonadal development (Giese 1969). Digestion in chitons appears to be entirely extracellular (Boyle 1977).

The pattern of coiling of the intestine appears to differ among taxa (for example, Fretter 1937; Saito & Okutani 1992), being coiled back and forth to varying extents in different chiton species and may reach a length of up to four times the length of the animal. It is divided into a short anterior intestine that closely resembles the stomach, and a longer posterior intestine. The two sections usually differ in colouration, and are separated by a muscular valve, unique to the Polyplacophora, which controls the passage of food material into the posterior intestine. The posterior intestine functions mainly to form the faecal pellets using mucus from the abundant mucous glands in this region. The short hindgut or rectum, which is enlarged in some species, opens at the anal sphincter, usually borne on a papilla in the median line of the pallial groove.

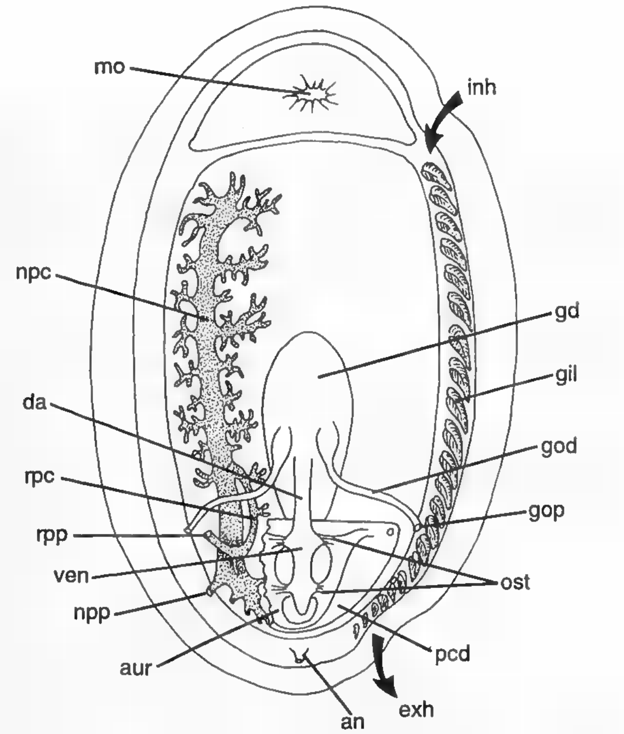


Figure 3.11 Arrangement of the heart, and reproductive and excretory systems of a chiton. The right side of the pericardium has been removed to show the posterior section of the nephridial canal. **an**, anus; **aur**, auricle; **da**, dorsal aorta; **exh**, exhalant current; **gd**, gonad; **gil**, gills; **god**, gonoduct; **gop**, gonopore; **inh**, inhalant current; **mo**, mouth; **npc**, nephridial canal; **npp**, nephridiopore; **ost**, auriculo-ventricular ostia; **pcd**, pericardium; **rpc**, renopericardial canal; **rpp**, renopericardial pore; **ven**, ventricle. (Modified after Götting 1974) [P. Kaas]

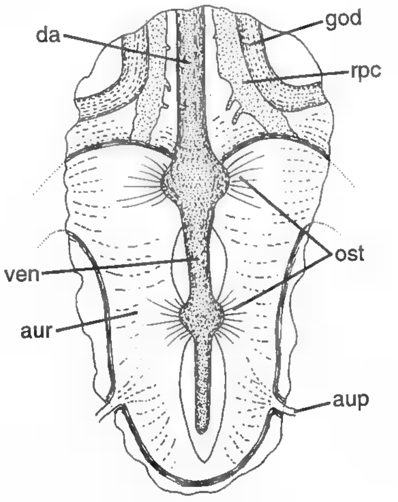


Figure 3.12 Heart of a chiton with two pairs of ostia. **aup**, auricular pore; **aur**, auricle; **da**, dorsal aorta; **god**, gonoduct; **ost**, auriculo-ventricular ostia; **rpc**, renopericardial canal; **ven**, ventricle. (After Haller 1894) [P. Kaas]

During feeding, the sphincter of the buccal tube relaxes and the subradular organs are protruded through the expanded mouth to test the substratum. If the latter is suitable, the subradular organs are withdrawn and the radula is protruded, flattening out as it does so. Since the teeth point backwards, the radula scrapes the surface as it is retracted. Food particles thus removed are then drawn into the buccal cavity where they are bound into a mucous string for passage through the anterior gut.

Circulation

The circulatory system has been well described by Hyman (1967) and Boyle (1977) has discussed the physiology of the body fluids, based mainly on a few, very large species. The amount of haemolymph in chitons is relatively large, and comprises about 44% of the soft-tissue wet weight in the large Californian *Cryptochiton stelleri* (Martin, Harrison, Huston & Stewart 1958). It is a slightly alkaline fluid, isosmotic with seawater. Although colourless, the haemolymph may appear faintly green, orange or brown because of numerous coloured granulae related to the colour of the animal; these are either suspended freely or enclosed in the cytoplasm of amoebocytes. Arvy & Gabe (1949) recognised two kinds of amoebocytes, those with a large nucleus and little cytoplasm and others with a smaller nucleus and much cytoplasm. Both types may contain coloured granulae which resemble mitochondria and occur close to the nucleus. The respiratory pigment of the haemolymph is the copper-based haemocyanin as found in other molluscs. Haemocyanin has a very low affinity for oxygen, but is sufficient to meet the needs of an animal with a sluggish metabolism and a rather large, easily ventilated, branchial surface. Haemoglobin has also been identified from chiton tissues and the deep red pigment found in radular muscles of *C. stelleri* has been identified as a myoglobin.

The description of the circulatory system relies almost entirely on the anatomical studies of Plate (1897–1901). Blood vessels with definite walls are lacking, and the open and diffuse system is based upon a complex system of interior sinuses and tissue interstices filled with haemolymph. The heart is situated dorsally beneath valves VII and VIII within a dorso-ventrally flattened

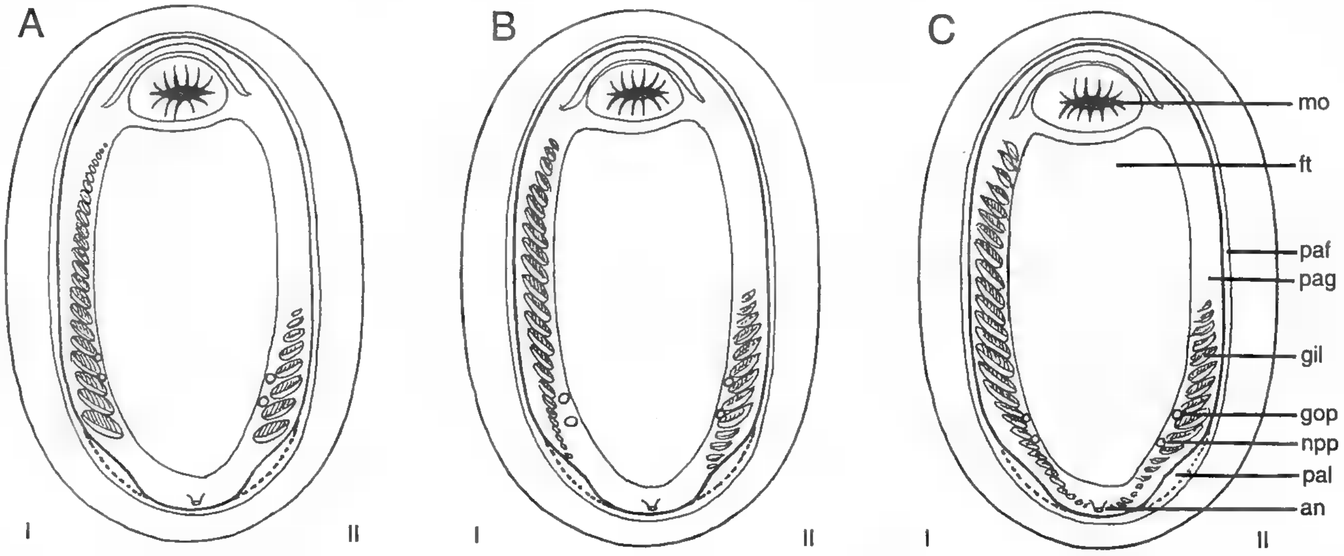


Figure 3.13 Arrangement of the gills in chitons. **A**, abanal. **B**, adanal with interspace. **C**, adanal without interspace. **I**, holobranchial; **II**, merobranchial. **an**, anus; **ft**, foot; **gil**, gill; **gop**, gonopore; **mo**, mouth; **npp**, nephridiopore; **paf**, pallial fold; **pag**, pallial groove; **pal**, pallial lappet. (After Kaas & Van Belle 1985a) [P. Kaas]

pericardium which is filled with a proteinaceous fluid (Fig. 3.11). The heart consists of a tubular median ventricle which ends blindly posteriorly, but opens anteriorly into the dorsal aorta (Fig. 3.12). The ventricle is accompanied laterally by a left and a right auricle (atrium), which connect posterior to the blind end of the ventricle. The auricles communicate with the ventricle via two pairs of auriculo-ventricular ostia; in Lepidopleuridae there is only one pair, whereas in a few other groups there may rarely be three or four pairs. These small, oval openings in the muscular ventricle wall are spanned by a stiff membrane perforated by a narrow slit which can open to let arterial blood pass from the auricle into the ventricle. Despite the presence of a contractile heart, circulation is brought about at least in part by body movements and by contraction of general musculature.

The dorsal aorta, a rather flat channel with a wall of connective tissue, extends forwards between the gonad and the dorsal body wall to which it is attached near the anterior margins of the valves. Intersegmental blood channels branching off the aorta at this point supply the valve muscles, and, ventrally, many channels branch from the aorta into the gonad. The aorta terminates at the level of the diaphragm where it opens into the wide head sinus, a space around the buccal cavity. The haemolymph, still arterial in nature, is collected into the wide visceral artery which accompanies the radular sheath posteriorly. At the end of the radular sheath, this artery, lined with connective tissue, continues and branches out to the viscera. The venous blood from the viscera gathers in the visceral sinus and passes into the foot sinuses.

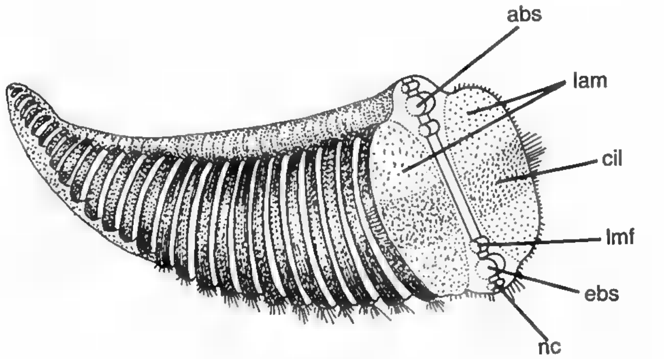


Figure 3.14 Side view of a gill, showing the arrangement of gill lamellae. **abs**, afferent branchial sinus; **cil**, strongly ciliated area; **ebs**, efferent branchial sinus; **lam**, pair of lamellae; **lmf**, longitudinal muscle fibres; **nc**, nerve cord. (Modified after Hescheler 1900) [P. Kaas]

Three other pairs of sinuses diverge from the head sinus. Two of these, the neuro-lateral sinus and the pedal sinus, unite before penetrating the diaphragm to form the important median sinus. The pedal sinus surrounds the pedal nerve cords and the neuro-lateral sinus accompanies the lateral nerve cords to the roof of the pallial groove. The afferent and efferent branchial sinuses are involved directly in the exchange of gases in the gills. Most of the venous haemolymph from the foot sinuses is delivered to the median longitudinal sinus. Near its end, this longitudinal sinus sends transverse branches to the afferent branchial sinuses which in turn branch to each gill. After oxygenation, the blood is collected in the efferent branchial sinus, from whence most of it is transported to the heart, enters the auricles by way of a number of pores, and then continues through the ostia into the ventricle.

Respiration

The gills are cone-shaped organs which hang in a row from the roof of each of the pallial grooves. Considered by Yonge (1939) to be individually homologous with the paired ctenidia of gastropods, each gill consists of a double row of roughly oval lamellae attached to each other medially and to an axis above and below. Gills decrease in size quite rapidly from the base towards the free end. Their number varies widely between taxa and Russell-Hunter (1988) has reviewed the taxonomic significance of gill arrangements. In the Lepidopleurina, there are usually between five and sixteen, confined to the posterior part of the pallial groove, an arrangement termed merobranchial (Fig. 3.13). Most Ischnochitonina, however, have numerous gills, varying from about 40 to 80 per side, arranged in the pallial grooves along the whole foot (holobranchial; Fig. 3.13).

Although their arrangement is specific, the number of gills is not constant for any species and increases with growth. When gills are added only to the anterior end of the gill rows, such that the most posterior gill is the largest, and the rows end before the level of the anus, the arrangement is called abanal (Fig. 3.13A). When gills are added both posteriorly and anteriorly during growth and development, the arrangement is termed adanal; as a consequence, gill size decreases both anteriorly and posteriorly. When the gills are not continuous around the anus, the gap is termed an interspace. Gill rows may be either adanal with interspace (both rows may terminate anterior to the level of the anus: Fig. 3.13B) or adanal without interspace (continuous around the anus; Fig. 3.13C). The number of gills is not even equal on both sides of an individual and there is no certainty that larger individuals of a certain species have more gills than smaller ones (Cochran 1993; A. Jones personal observations).

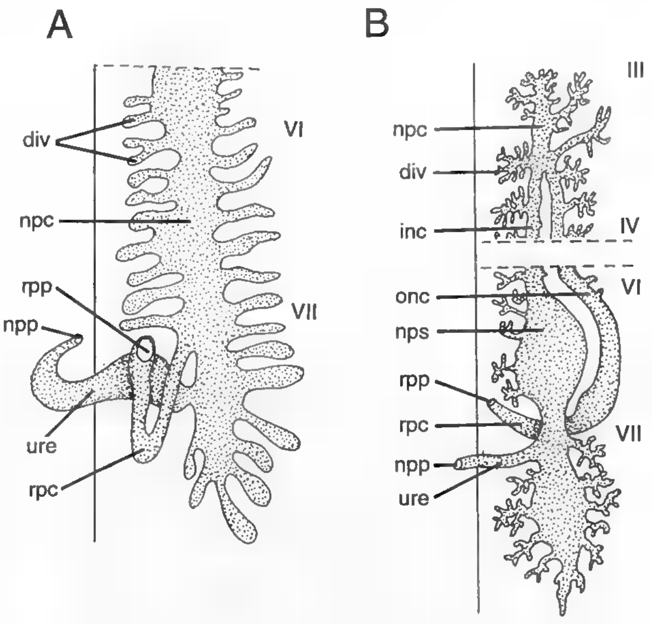


Figure 3.15 Sections of chiton metanephridia. **A**, *Calloplax vivipara* (Ischnochitonidae). **B**, *Chiton (Amaurochiton) magnificus* (Chitonidae). **div**, diverticula; **inc**, inner nephridial canal; **npc**, nephridial canal; **npp**, nephridiopore; **nps**, nephridial sac; **onc**, outer nephridial canal; **rpc**, renopericardial canal; **rpp**, renopericardial pore opening into pericardium; **ure**, ureter. Roman symbols indicate the situation of the anterior margins of the valves. (After Plate 1897–1901) [P. Kaas]

The gill lamellae (Fig. 3.14) are covered by a thin ciliated epithelium on both sides; the cilia are particularly dense in a transverse central area. The epithelium rests on a thin layer of connective tissue which also forms supporting cross bars in the otherwise hollow interior. The lamellae are alternately attached to the axes which contain a nerve cord, longitudinal muscle fibres and two blood sinuses, a branch of the afferent branchial sinus on the upper side and a branch of the efferent branchial sinus on the underside.

The gills effectively form a longitudinal curtain hanging from the roof of the pallial groove, dividing the groove into an outer inhalant chamber and an inner exhalant one (Boyle 1977). Ventilation takes place by lifting the anterior girdle and allowing ciliary currents to draw water into and along the inhalant chamber. The water is drawn over the lamellae by tracts of beating gill cilia, allowing gas exchange to take place. It then passes into the exhalant chamber before being expelled through the uplifted girdle in the anal region. Although water movement is usually the result of ciliary action, in some members of the Schizochitonidae very distinct muscular movements of the posteriorly divided girdle are apparently associated with ventilation. The numerous sensory strips on the gills and in the pallial grooves are presumed to have a role in the regulation of respiratory currents also.

Excretion

The excretory system of chitons (Figs 3.11, 3.15; Hyman 1967; Martin 1983) consists of a pair of large ventral metanephridia each located lateral to the visceral cavity. The complexity of these organs varies from group to group although each begins with a short renopericardial canal; this arises from a renopericardial pore in the antero-lateral corner of the pericardium and leads to the nephridial canal. The renopericardial canal is characterised by an epithelium bearing extremely long cilia. The nephridial canal is a rather wide tube with numerous lateral diverticula and extends from the level of the last valve forwards to the level of the diaphragm. In *Leptochiton* and *Calloplax* (Fig. 3.15A), the renopericardial canal is short and opens directly into the nephridial canal with many simple, digitate diverticula. More often, the renopericardial canal extends anteriorly parallel to the nephridial canal for some distance before opening into it. In the most extreme case, that of *Chiton (Amaurochiton) magnificus* (Fig. 3.15B) it continues forward almost to the anterior end to form a hairpin-shaped tube; it is clearly separable into an inner and an outer nephridial canal, each of which is strongly diverticulate with arborescent appendices. In *Acanthopleura echinata*, diverticula from the outer canal extend anteriorly and posteriorly into the foot where they are associated with the transverse and medial pedal blood sinuses (Hyman 1967). The whole nephridial canal is lined with ciliated epithelium, the cuboidal cells of which are filled with yellow granulae which colour the organs. A pair of short ureters branch from each main nephridial canal at the level of the posterior gills; they carry the excretory products to the nephridiopore, which lies on a papilla in each pallial groove shortly behind the gonopore.

The excretory products, probably the result of ultrafiltration of the haemolymph, are collected in the pericardial cavity. The ultrafiltration of the haemolymph is thought to be associated with the podocytes present in the auricular wall of the heart. Podocytes, which have numerous branched processes known as pedicels, have become closely associated with filtration membranes suggesting that filtration is the initial process of urine formation in chitons (Økland 1980; Wilbur 1983). Movement of the ultrafiltrate from the pericardial cavity to the nephridial canal via the renopericardial ducts is thought to involve the contractile pericardium (Økland 1981). By further excretory and resorption processes during the passage through the nephridial canal, these products are converted or modified before being expelled from the body via the urethra and nephridiopore. Chitons are ammonotelic or ureotelic animals, as is generally true of molluscs.

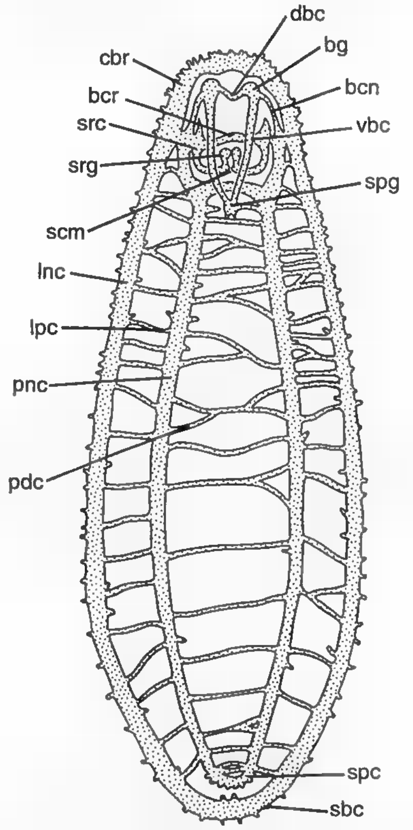


Figure 3.16 Nervous system of *Lepidochitona monterosatoi* (Lepidopleuridae). **bcn**, buccal connective; **bcr**, buccal part of cerebrobuccal ring; **bg**, buccal ganglion; **cbr**, cerebrobuccal ring; **dbc**, dorsal buccal commissure; **lnc**, lateral nerve cord; **lpc**, latero-pedal commissure; **pdc**, pedal commissure; **pnc**, pedal nerve cord; **sbc**, subrectal commissure; **scm**, subradular commissure; **spc**, suprarectal commissure; **spg**, supraradular ganglion; **src**, subradular connective; **srg**, subradular ganglion; **vbc**, ventral buccal commissure. (After Eernisse & Reynolds 1994, modified from Gantner 1987) [C. Eadie]

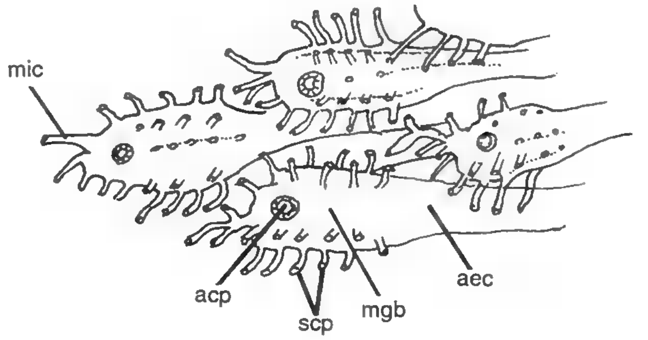


Figure 3.17 Aesthetes of the central area of a decalcified valve of *Callochiton septemvalvis* (Ischnochitonidae). **acp**, apical cap of megalaesthetes; **aec**, aesthete canal; **mgb**, megalaesthete body; **mic**, micraesthete; **scp**, subsidiary cap of micraesthetes. (After Plate 1899)
[P. Kaas]

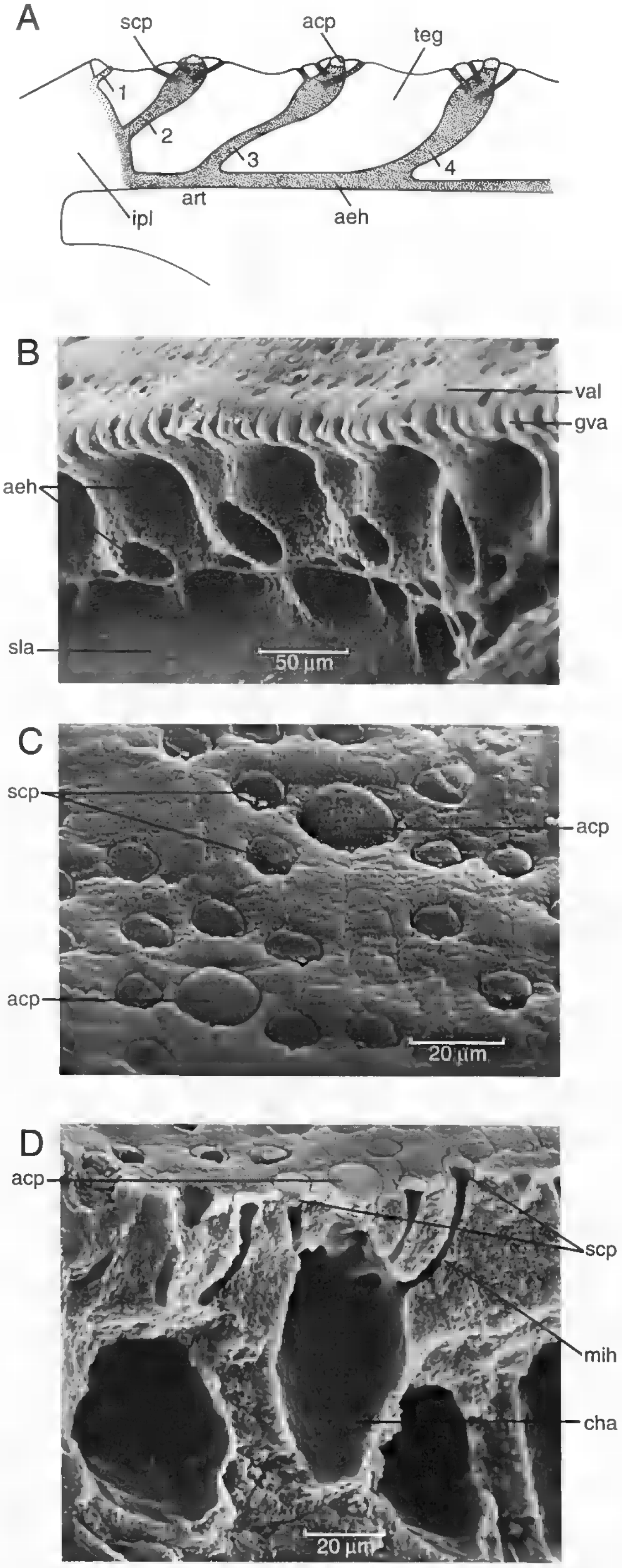


Figure 3.18 Structure of aesthetes in valves. **A**, a vertical section through the lateral edge of a valve showing the arrangement of the aesthete canal system; aesthete canals 1–4 are of increasing age. **B–D**, shell valve structures in *Rhyssoplax calliozona* (Chitonidae): **B**, eave of valve (anterior edge) showing multiple entrance points for the aesthete canals; **C**, dorsal surface of an untreated valve to show groups of aesthete caps; **D**, structure of aesthete chamber revealed in a shell fracture. **acp**, apical cap of megalaesthete; **aeh**, aesthete canal; **art**, articulamentum; **cha**, chamber normally containing aesthete body; **gva**, growing edge of valve; **ipl**, insertion plate; **mih**, micraesthete channel; **scp**, subsidiary cap of micraesthete; **sla**, sutural lamina; **teg**, tegmentum; **val**, dorsal surface of shell valve with aesthete caps.
[A, C. Eadie; B–D, A.M. Jones]

Nervous System and Sense Organs

The basic plan of the nervous system of chitons is simple and very similar to that of aplacophorans except for its lack of cerebral ganglia (Hyman 1967; Boyle 1977; Wingstrand 1985). Although a cerebrobuccal (circum-enteric) ring encircling the buccal tube is present (Fig. 3.16), cerebral ganglia are absent and the ring gives off a pair of longitudinal lateral nerve cords and a pair of pedal nerve cords. These four main nerves are simple in structure, the nerve cells being scattered along the string and not concentrated in ganglia. Chitons are unusual in this respect, as equivalent structures among other classes of molluscs are found only in some primitive gastropods and in *Nautilus* species. A number of ganglia are present, however, such as the buccal ganglion and the subradular ganglion but they are not associated with the nerve cords.

Numerous cerebral nerves branch off anteriorly from the cerebrobuccal ring to the organs in this part of the head (Fig. 3.16). After the separation of the two pairs of nerve cords, the buccal part of the ring narrows considerably and gives rise to subradular connectives to the two subradular ganglia and to buccal connectives to the two buccal ganglia The subradular connectives lead to the subradular ganglia on the roof of the subradular sac, just above the subradular organ. The buccal connectives lead antero-dorsally over the roof of the buccal cavity to the buccal ganglia located near the buccal glands. The ganglia are connected by a dorsal buccal commissure, from which a pair of nerves branch to innervate the buccal cavity and the mouth. The radula sheath and the muscles of the radular apparatus are innervated by a pair of nerves arising from the ventral buccal commissure, which forms a ring around the oesophagus. The buccal ganglia also send well-developed nerves posteriorly to the stomach; these give off branches to the buccal glands, the pharyngeal glands and the oesophagus.

The longitudinal lateral nerve cords proceed posteriorly to the end of the animal where they are united. They pass immediately above the pallial groove, giving rise to numerous branches into the mantle and a pair into each gill, one accompanying the afferent and one the efferent branchial sinuses. The pedal nerve cords are located in the tissue of the dorsal part of the foot on each side of the median axis and give off numerous branches to the foot musculature. They do not meet at the end of the foot, but are linked to each other by many connecting pedal commissures and in some taxa, as in *Acanthopleura* species, to the lateral cord via latero-pedal commissures.

Complex sense organs do not occur in chitons, with the exception of the aesthetes in the tegmentum of the valves and a possible statocyst described for *Cryptoplax mystica* (Currie 1992b). Sensory structures such as elongate neurosensory cells with a terminal bristle are found in small groups or narrow strips in various parts of the body, including the ventral epidermis of the head near the mouth, the epithelium of the subradular organ, the floor of the buccal cavity, and the pallial groove in particular. In many chitons, a pair of sensory strips, presumed to be chemosensory, occur in the roof of the pallial groove near the anus. These have been considered homologous with the chemosensory osphradia of other molluscs (Haszprunar 1987) but their precise function remains undetermined. Other strips of these neurosensory cells are found in the posterior part of the pallial groove and are termed glandular tracts. They occur from the anus to the hindmost gills, and in the anterior part of the groove, where they extend from the first gills to the sides of the head. All these organs in the pallial groove are innervated by branches of the longitudinal lateral nerve cords (for details see Eernise & Reynolds 1994).

The subradular organs, located on the bottom of the subradular pouch a little before its blind end, also contain neurosensory cells, mostly in groups of three. These organs can be protruded through the mouth in order to test the substratum for food and are presumed to act as taste organs.

The extensive shell organs are unique to chitons and form three distinct categories (Boyle 1977): the aesthete (Blumrich 1891), the intrapigmentary ocellus (Nowikoff 1909) and the extrapigmentary ocellus (Nowikoff 1907). All chitons studied have the aesthete type of organ; ocelli occur only in certain genera in the suborder Ischnochitonina. Ocelli have long been considered to be primitive photosensitive organs, but their function is still far from clear and alternative functions have been proposed for the aesthetes. A secretory role was proposed by Baxter *et al.* (1987, 1990), and a mechanoreceptor function has been suggested for the aesthetes of *Mopalia lignosa* by Omelich (1967). Fischer (1988) noted similarities between the cells of aesthetes and the chemoreceptors of insects. The photoreceptive function of the ocellus is well described, for example, in *Onithochiton neglectus* (Boyle 1969), and is not in dispute. However, as the nervous system is largely decentralised, it is probable that diffuse parts of the system respond to stimuli and that the visual perceptivity of chitons, even when equipped with numerous ocelli, must be very limited and restricted to vague perceptions of light and dark such as occur when a shadow passes over the animal.

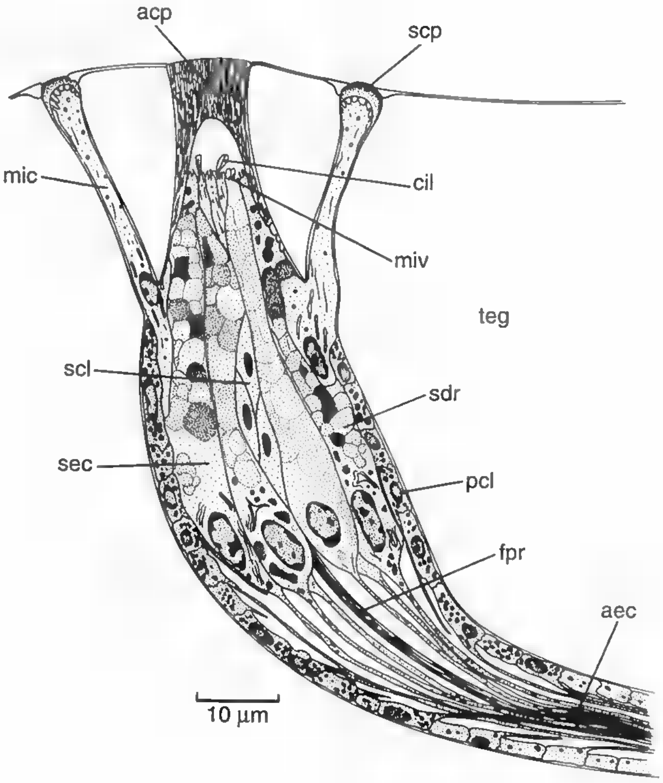


Figure 3.19 Aesthete fine structure in *Lepidochitona cinerea* (Lepidopleuridae) based on light and electron microscopy. **acp**, apical cap of megalaesthete; **aec**, aesthete canal; **cil**, cilium; **fpr**, fine processes of central sensory cells; **mic**, micraesthete; **miv**, microvilli; **pcl**, peripheral cell; **scl**, central sensory cell; **scp**, subsidiary cap of micraesthete; **sdr**, secretion droplet; **sec**, secretory cell; **teg**, tegmentum. (After Boyle 1974) [D. Wahl]

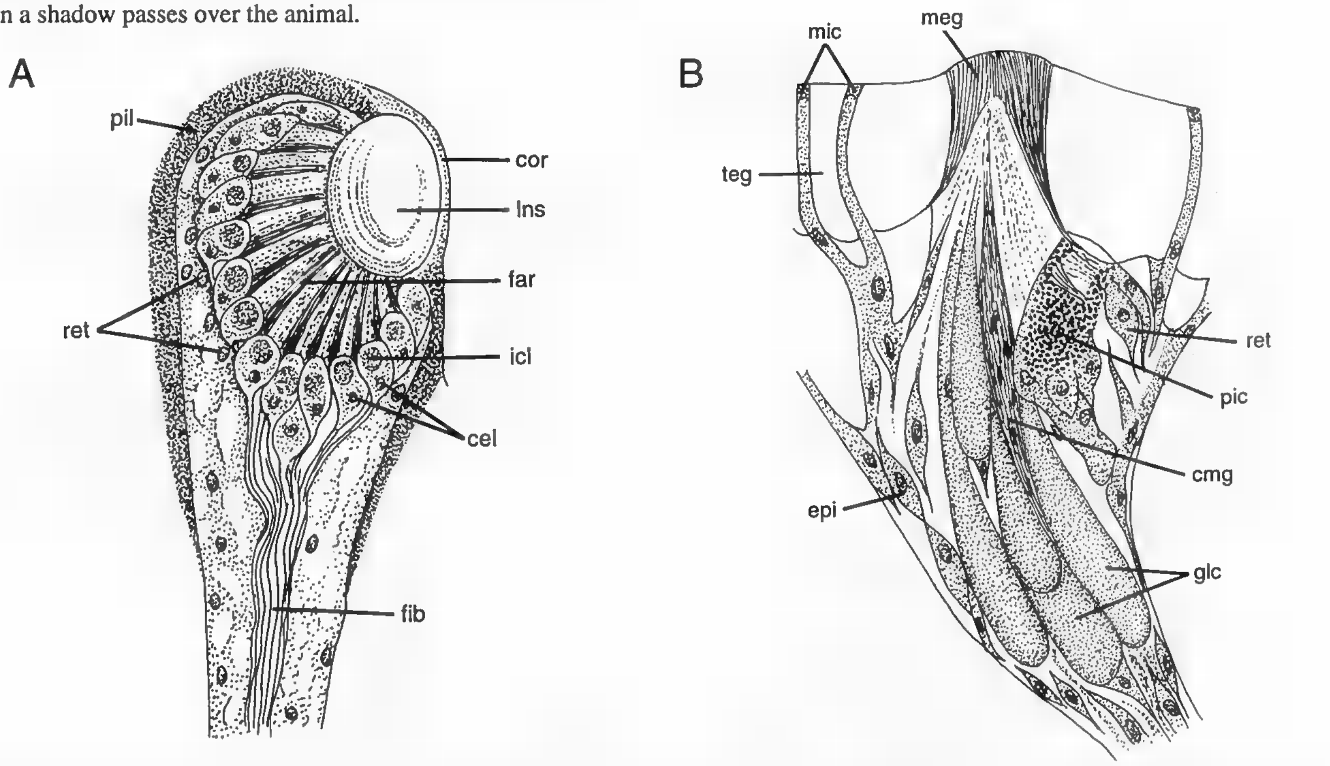


Figure 3.20 Chiton ocelli, in longitudinal section. A, extrapigmentary ocellus of *Acanthopleura* sp. (Chitonidae). B, intrapigmentary ocellus of *Callochiton* sp. (Ischnochitonidae). **cel**, cells of cup; **cmg**, central core of megalaesthete; **cor**, cornea; **epi**, epidermis of fibre cord; **far**, fibrillar area; **fib**, fibre cord; **glc**, glandular cells; **icl**, inclusion; **lns**, lens; **meg**, megalaesthete; **mic**, micraesthetes; **pic**, pigment cup; **pil**, pigment layer; **ret**, supposed retina cell; **teg**, outer layer of tegmentum. (A, after Nowikoff 1907; B, after Nowikoff 1909) [P. Kaas]

The aesthetes (Figs 3.17, 3.18A) are located in canal branches more or less perpendicular to the valve surface. The majority connect proximally to canals running parallel to the surface within the tegmentum and are linked to the mantle epithelium at the anterior and lateral margins of the valve (Fig. 3.18). Alternatively, in specific regions such as the jugal area, they may turn ventrally and pass through the articulamentum to connect with the underlying mantle epithelium (for example, Currie 1992a). The main body of the aesthete contains a variety of structures and cell types (Fig. 3.19) and is termed the megalaesthete. Each central sensory cell bears numerous microvilli and a single cilium. Arising from it are a variable number of finer, unicellular branches called micraesthetes (Figs 3.17–3.20). Megalaesthetes and micraesthetes terminate at the surface in distinct apical or subsidiary caps, respectively (Fig. 3.18C). The caps are usually almost flat and level with the valve surface, although unique, erect subsidiary caps have been described for some deep-water species (Gowlett-Holmes & Jones 1992; Sirenko 1992). These caps occur in a variety of densities and in megalaesthete to micraesthete ratios of up to 1:20 or more. The numbers of these structures may be very high, with over 200 apical caps/mm^2 and 2500 subsidiary caps/mm^2 in *Rhyssoplax calliozona* (Jones unpublished data). The distribution and density of these structures may sometimes be related to the nature of valve sculpturing (for example, Currie 1989). Thus in species with a pustulose tegmentum, such as most acanthochitonids, the megalaesthetes are usually located in the centre of each pustule with the micraesthetes distributed around the outer edge or in the spaces between pustules.

The megalaesthete body (Fig. 3.19) contains several cell types, but mainly comprises large, secretory cells. The direction of the secretory activity, either inwards via the canals or outwards through the porous apical cap, remains uncertain, and there is some evidence for either possibility (Boyle 1974; Baxter *et al.* 1987; Fischer 1988). The cells in the aesthete body maintain a connection with the mantle tissue and the lateral nerve cords also send out branches through the pores in the slit-rays of the articulamentum of the valves; these branches penetrate the tegmentum and 'innervate' the associated aesthetes.

In *Schizochiton* species, the Toniciinae and Acanthopleurinae, some of the megalaesthetes are transformed into extrapigmentary ocelli (Fig. 3.20), so-called because of the pigment layer covering the outer end of the megalaesthete. In these structures, the outer layer of the tegmentum is thin and transparent, forming a cornea covering a convex lens. Behind the lens, epithelial cells containing large globules of secretion form a fibrillar cup. At their base, small wedge-shaped cells, probably retinal cells, are present. From these cells, fine fibrils extend distally to the lens; proximally fibrils join with those of the cup cells to form a strand leading to the interior.

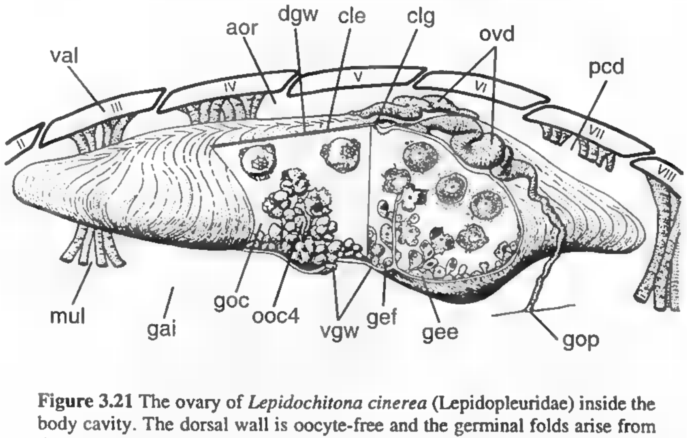


Figure 3.21 The ovary of *Lepidochitona cinerea* (Lepidopleuridae) inside the body cavity. The dorsal wall is oocyte-free and the germinal folds arise from the ventral wall. On the left, oocytes are drawn three dimensionally, and on the right, as they are represented on thin sections. Oocyte stages not in correct scale. **aor**, location of the dorsal aorta; **cle**, ciliated epithelium; **clg**, ciliated groove; **dgw**, dorsal gonadal wall; **gai**, gastrointestinal region; **gee**, germinal epithelium; **gef**, germinal folds of the nutritive tissue; **goc**, gonocoel; **gop**, gonopore; **mul**, dorso-ventral muscle; **ooc4**, oocyte of stage IV; **ovd**, oviduct; **pcd**, location of the pericardium; **val**, shell valve; **vgw**, ventral gonadal wall. (After Richter 1986) [I. Hallam]

A second type of ocellus, the intrapigmentary ocellus, is found in the genus *Callochiton* (Fig. 3.20B). Each is formed of a small pigment cup at the side of some megalaesthetes, well under the tegmental surface and with an opening covered by a small lens. A few cells, which may be regarded as retina cells, give off fine fibrils into the pigment cup. Fibrils from both retina cells and pigment cells form a strand leading inward. Baxter *et al.* (1990) have described the structure of the intrapigmentay ocellus of *Callochiton achatinus.*

Ocelli usually occur in radiating rows in the head and tail valves and the lateral areas of intermediate valves. They may form a single row accompanying the diagonal ridges (as in *Schizochiton* species), a double row, or cover the whole lateral area. Their distribution is closely associated with the slit rays and their related channels.

Reproduction

Polyplacophorans are usually dioecious animals in which sexual dimorphism is rare (Pearse 1979). In *Cryptoconchus porosus* from New Zealand, the olive-green girdle is mottled with orange in males, but dark brown in females (Brewin 1942). As the gonads often differ in colour and this colouration may show through the foot in ripe animals, sex may be determined in some mature animals. Hermaphroditism has been reported for two species of chitons from California, *Lepidochitona caverna* and *L. fernaldi* (Eernisse 1988); in young animals, the gonad is female, but tiny clusters of sperm develop along the walls of the gonad between the oocytes in older animals (Heath 1907). The details of the reproductive process in these two species remain unclear, but based on evidence from animals isolated for up to nine months in the laboratory, they are apparently fully capable of self-fertilisation and the production multiple broods (Eernisse 1988).

Sex ratios in chiton populations vary considerably and generalisation is of little value. In some species, however, smaller size groups tend to be dominated by females whereas larger ones are male dominated, for example, in *Sypharochiton pellisserpentis* (Johns 1960).

The paired gonads are fused in most chitons to form a single mid-dorsal ovary or testis located between the gut and the dorsal body wall (Fig. 3.11); only in the genus *Nuttallochiton* do the components of this reproductive structure remain separated. It extends forward from the level of the sixth to the third valve and is attached to the dorsal wall by strands and membranes of connective tissue; most of it lies free in the spacious visceral sinus. Gametes are released via paired gonoducts, oviducts in females and sperm ducts in males, which arise at the postero-dorsal end of the gonad and lead to the gonopores. The latter open into the pallial groove at the level of the junction of valves VI and VII, between one to nine gills anterior to the nephridiopores.

The organisation of the gonads and details of oogenesis and spermatogenesis are well covered in Pearse (1979). Selwood (1968) made a detailed study of oogenesis in *Sypharochiton* and Sakker (1984) has described both spermatogenesis and sperm morphology in *S. pellisserpentis*, *Onithochiton quercinus* and *Plaxiphora (P.) albida.* A broader review of spermatology is given by Hodgson, Baxter, Sturrock & Bernard (1988). Ovaries contain oocytes at all states of development (Fig. 3.21), the largest and most mature on the inside of the ovarian folds. There is usually a sac-shaped evagination of variable size at the beginning of the glandular part of the oviducts which is itself lined with glandular epithelium; this has been termed a slime sac on the assumption that it secretes the slimy mass in which the eggs may be laid. The sperm ducts usually widen considerably before reaching the gonopore and some investigators consider that this may be a seminal vesicle; however, the storage of sperm has never been demonstrated. Copulatory organs are absent in all chitons and mating behaviour has never been observed.

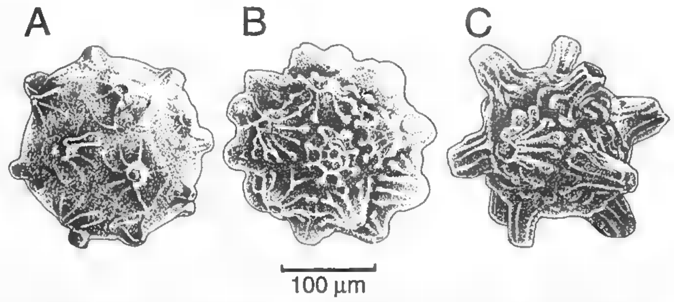


Figure 3.22 Three variations on the same theme: egg hulls of Californian species of *Lepidochitona*. **A**, *Lepidochitona caverna*; **B**, *Lepidochitona dentiens*; **C**, *Lepidochitona berryana*. (After Eernisse 1988) [P. Kaas]

The gametes are usually shed into the pallial groove and are carried out with the exhalant current, aided by movements of the animal. Their precise fate for the first few days is unclear; they may become temporarily planktonic allowing dispersal of the species or they may remain benthic. The eggs may be held together in gelatinous strings or masses (Brewin 1942) or may accumulate in a loose pile behind the female (Thorpe 1962) except in females of species that brood their young. Brooders retain fertilised eggs in the pallial grooves until a relatively advanced stage of development. Brooding was first observed by Kowalewsky (1883) in the Mediterranean species now known as *Lepidochitona corrugata*, but it has since been reported in a variety of chitons including *Callochiton crocinus*, *Eudoxochiton inornatus* and *Callistochiton mawlei* (Turner 1978). All known Australian brooders belong to the Ischnochitonidae. Only one observation of ovoviviparity in chitons has been recorded. Plate (1897–1901) described a female *Calloplax vivipara*, from Chile, which had some 15 embryos in the ovary; how fertilisation of the eggs takes place is unknown.

Most chitons are sexually mature after one or two years. Spawning is performed by lifting up the girdle postero-medially to form a spout but there is no evidence of sexual pairing during spawning. There are conflicting reports with regard to the sequence of gamete release and the stimuli for spawning (see Pearse 1979 for a review). Males are often first to spawn, emitting a double stream of sperm into the water. Soon after, females start spawning, apparently stimulated by the presence of sperm. Experiments have shown that females may be stimulated at a distance of up to 7–8 m from the spawning male. The eggs are usually released individually and are often held together loosely in a mass or string by gelatinous material, probably from the slime sacs of the oviducts. The number of eggs and the mode of their deposition vary with species (Hyman 1967; Pearse 1979), but there are no observations for Australian chitons.

Chitons exhibit marked periodicities in their gonad development and spawning seasons (Pearse 1979). No consistent pattern has emerged, although water temperature changes, photoperiod, and changes in phytoplankton abundance are considered to be the principal environmental factors controlling these processes. Studies of Australian species (Sakker 1986; Wells & Sellers 1987; Currie 1990) illustrate this. *Acanthopleura gaimardi* spawns annually during autumn, *Onithochiton quercinus* and *Sypharochiton pellisserpentis* show a bimodal spawning pattern with unequal spawnings in spring and autumn, and *Cryptoplax mystica*, *Ischnochiton australis* and *Plaxiphora (P.) albida* have extended spawning periods over several months. In *A. gaimardi*, gametogenesis takes place in spring and early summer, but proceeds at a constant rate throughout the year in *C. mystica* and *I. australis*. Chiton species that brood do not exhibit the well-defined seasonal periods of reproduction found in most spawning species, but reproduce throughout most of the year (Creese 1986, 1992; Eernisse 1988; Cochran 1993). The proportion of reproductively mature adults in the population at any given time is usually small; less the 15% in the New Zealand species *Onithochiton neglectus* and up to 17.5% in the southern Australian species *Ischnochiton mayi* (Creese 1986; Cochran 1993), although Eernisse (1984, 1988) found up to 30–80% of three species of *Lepidochitona* (*L. thomasi*, *L. caverna* and *L. fernaldi*) brooding throughout the year in California.

The time of day at which spawning occurs also varies widely with species and habitat, with evidence for correlations with solar, lunar and/or tidal cycles (Boyle 1977). Spawning commonly occurs at night or early in the morning, at low tide, in calm water and at the new or full moon.

Chiton eggs are rich in yolk, spherical and about 200–220 µm in diameter. Their colour varies from species to species; for example, they are light green, pink and off-white in *Rhyssoplax tricostalis*, *R. exoptanda* and *R. calliozona*, respectively. The most common colours are light green, yellow or orange, but colour does vary with the degree of maturity of the eggs. The eggs are always provided with two membranes: an inner one around the egg and an outer, thick hull or chorion, which is frequently ornamented with diverse projections, such as cup-shaped papillae, cones, lobes, flaps or spines (Fig. 3.22; Eernisse 1984, 1986, 1988). In those members of the Lepidopleurina studied to date the egg hulls appear to be smooth. Each species within a genus displays its own specific egg hull pattern, potentially providing an important taxonomic character.

Embryology

Embryological development of the few chitons studied is remarkably similar morphologically, although developmental rates appear to vary considerably, even within the same species, in accordance with environmental conditions such as temperature (Pearse 1979). The development process has been studied extensively (see Heath 1899; Hyman 1967; Pearse 1979). Cleavage is holoblastic, nearly equal, spiral and determinate. The first cleavage of eggs in *Leptochiton asellus* takes place about two hours after fertilisation (Christiansen 1954); the second cleavage, like the first, is total, equal and occurs one hour later. The third, unequal cleavage takes a further hour and results in an eight cell stage with an animal pole of small cells and a vegetative pole of larger cells, making the spiral cleavage distinct. Cleavage then becomes more rapid. At the 64 cell stage the molluscan cross is clearly perceptible (Fig. 3.23). Gastrulation and formation of the blastopore are succeeded by the development of a double cilia zone, the prototroch, and the movements of the cilia are clear within the egg hull. Little more than 20 hours after spawning, the trochophore larva (Fig. 3.24) hatches as an oval body that rotates rapidly round its vertical axis while, at the anterior pole, an apical tuft of only two cilia is formed. These cilia grow into flagella later, the number also increasing to three or four. Gradually, the larva becomes increasingly elongate oval in shape, the cilia of the prototroch grow longer and fine cilia appear on the cephalic part. After four days, the whole body, with the exception of a dorsal area behind the prototroch, is covered with short cilia. By this stage the blastopore has been displaced anteriorly behind the prototroch on the ventral side (Fig. 3.24B).

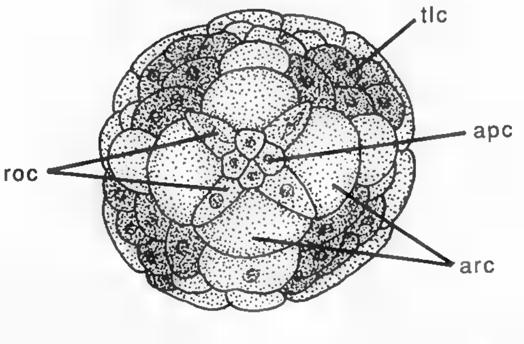


Figure 3.23 Late cleavage stage of the embryo of *Stenoplax heathiana* (Ischnochitonidae), showing the typical molluscan cross. **apc**, apical cells; **arc**, arms of the cross; **roc**, rosette cells; **tlc**, teloblast cells (darkly stippled). (After Heath 1899) [P. Kaas]

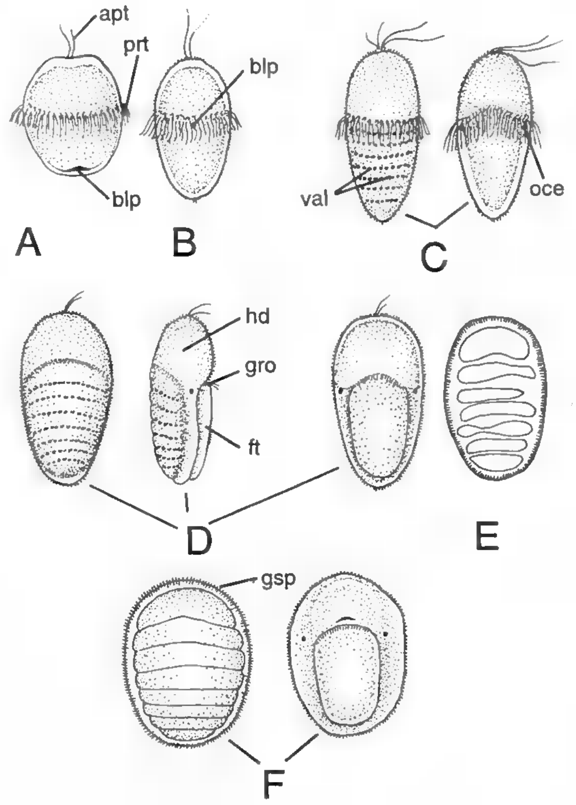


Figure 3.24 Larval development of *Leptochiton asellus* (Lepidopleuridae). **A**, newly hatched trochophore, ventral view. **B**, four day old larva, ventral view. **C**, four and three-quarter day old larva: left dorsal, right ventral view. **D**, newly settled larva: left dorsal view, middle side view, right ventral view. **E**, larva with seven developing valves. **F**, larva nearly two months old: left dorsal view, the eight valves completely covering the back, right ventral view. **apt**, apical tuft; **blp**, blastopore; **ft**, foot; **gro**, groove between head and foot; **gsp**, girdle spicules forming a marginal fringe; **hd**, head; **oce**, ocellus; **prt**, prototroch; **val**, divisions of future valves. (After Christiansen 1954) [P. Kaas]

Metamorphosis starts with a dorso-ventral flattening of the body on about the fifth day. Simultaneously, the first signs of segmentation appear on the dorsal side behind the prototroch in the form of transverse rows of elevated, clear, epidermal cells which secrete the cuticle (Figs 3.24C, 3.25). The epidermis forms transverse grooves between these rows and in these the valves are secreted. On the ventral side, just behind the prototroch, two red ocelli appear; each consists of a single pigment cell embedded in the epidermis beneath the lateral nerve cords (Kowalewsky 1883). The first seven valves form almost simultaneously in most species as irregularly shaped, calcareous deposits, and, according to Heath (1899) and Okuda (1947), the tegmentum forms before the articulamentum. The terminal valve is always the last to appear. By this stage the larva has settled on the bottom and changed from its pelagic mode of life to the more sedentary adult mode. The apical tuft, prototroch and ocelli disappear, the mouth becomes visible and the valves, surrounded by a narrow girdle, occupy the whole dorsum of the young chiton (Fig. 3.24F). Gill formation, however, occurs at a far more advanced stage.

The digestive tract, formed by the endoderm, occupies most of the interior of the trochophore and initially consists of the stomodeum and the midgut. After the closing of the blastopore, the stomodeum breaks through to form the mouth. Ventrally, the stomodeum forms the small, sac-shaped, subradular pouch and, subsequently, a much larger invagination, the radular sac, in which the first radular teeth soon appear (Fig. 3.25). The midgut ends blindly. At a later stage, the proctodeum, a terminal invagination of the ectoderm, gives rise to the anus.

In the adult chiton, the stomodeum forms the mouth and the buccal cavity, and the midgut gives rise to the pharynx, oesophagus, stomach, intestine as well as the buccal, pharyngeal and digestive glands. Just ventral to the mouth, an ectodermal invagination forms a sac-shaped gland called a foot gland (Kowalewsky 1883). Heath (1899) and Hammarsten & Runnström (1924), working with different species, found a transverse row of such foot glands at the anterior end of the future foot.

The duration of the free-swimming stage varies with species but is usually 0.5–4 days (Pearse 1979). The development described above for *Leptochiton asellus* was reported with an unusually long pelagic stage of 10–20 days. Juveniles of several brooding species hatch at a relatively late trochophore stage (Creese 1986; Eernisse 1988; Cochran 1993) and in at least one species, *Ischnochiton subviridis*, are retained within the pallial groove until they metamorphose (Cochran 1993). A limited period of up to two days between hatching and settlement occurs in other species, during which limited movement is possible (Creese 1986; Eernisse 1988). In *Ischnochiton mayi*, the trochophore larvae lack an apical tuft and prototrochal cilia, and metamorphosis occurs within the egg hull; hatching occurs 12–14 days after fertilisation in this species (Cochran 1993).

NATURAL HISTORY

Life History

Most aspects of the life cycle and development of chitons are described in the sections on Reproduction and Embryology. Once metamorphosis is completed, the animal settles on a suitable substratum, which may involve some degree of habitat selection.

Differences in growth rates and longevity vary according to the maximum sizes attained by different species, ecological niches and prevailing environmental conditions. Both growth and age are very difficult to determine in chitons. Arey & Crozier (1919) counted growth marks on the valves of *Chiton tuberculatus* which were considered to represent annual growth marks. On this basis, the oldest animals were some 12 years old, the normal life span is 8 years and sexual maturity occurs in the third year of life. Other workers have questioned the validity of using growth lines and, on the basis of population size-class frequency data, have suggested that growth is faster than reported by Arey & Crozier. Glynn (1970) considered the mean life span of *C. tuberculatus* to be about two years. Estimates of longevity for a number of chitons varied from 2–4 years for *Katharina tunicata* and *Chaetopleura apiculata* to more than 20 years for *Cryptochiton stelleri* (Comfort 1957). Detailed studies of *Lepidochitona cinerea* in Scotland (Baxter & Jones 1978) revealed a growth rate which declined with age, and a longevity of 4–6 years. No information is yet available for Australian species.

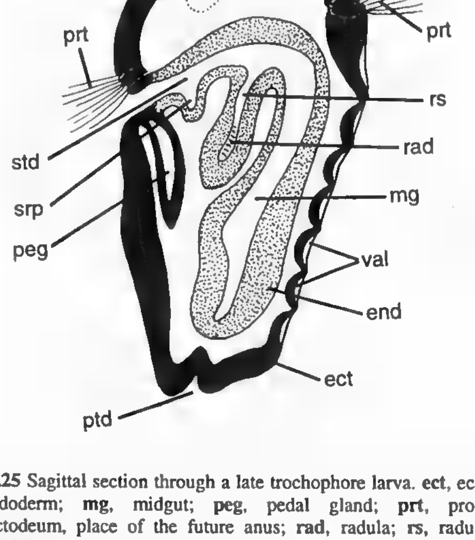


Figure 3.25 Sagittal section through a late trochophore larva. **ect**, ectoderm; **end**, endoderm; **mg**, midgut; **peg**, pedal gland; **prt**, prototroch; **ptd**, proctodeum, place of the future anus; **rad**, radula; **rs**, radular sac; **srp**, subradular pouch; **std**, stomodeum; **val**, shell valves. (Modified after Kowalewsky 1883) [P. Kaas]

Very significant seasonal and annual changes occur in the soft body components of chitons, which must be considered in any studies of growth; these are well reviewed by Giese (1969) and Boyle (1977). Allometric growth of body components has been described for a number of species (for example, Sakae 1968; Baxter & Jones 1986), and changes in morphology during growth have been demonstrated by O'Neill (1984a) for *Onithochiton neglectus*. There is no published information on Australian species.

Ecology and Behaviour

The general ecology of chitons is closely related to their behavioural and physiological adaptations to the environmental conditions of each habitat or microhabitat, including the occurrence of suitable substrata (Boyle 1977; Murdoch & Shumway 1980; Horn 1986; McMahon, Burggren, Pinder & Wheatly 1991). Some species are entirely dependent on the occurrence of their particular food organisms. Thus the South Australian *Stenochiton cymodocealis* lives only where the sea-grass genus *Amphibolis antarctica* can be found. Note that the presence of suitable food species does not mean that chitons will always be present, their distribution and abundance being patchy for as yet unknown reasons. Patchy local distribution is common to many species of chiton, but problems with its interpretation are especially true for Australian species where the basic ecology remains little studied.

Most Polyplacophora live on the shore or in shallow coastal waters, and prefer habitats with plenty of oxygen, light and algal growth. Most require hard substrata, such as bedrock, stones, or dead bivalve shells. Some species, such as *Rhyssoplax exoptanda* (Pl. 8.2) and *R. calliozona* (Pl. 8.4), prefer bedrock covered with a layer of sand, whereas many other species live beneath stones loosely embedded in sand; such species usually emerge from the sand at night when feeding.

Hardy species such as *Sypharochiton pellisserpentis* inhabit bedrock on high-energy rocky coastlines, often living in crevices and beneath overhangs, whereas *Plaxiphora albida* and *Onithochiton quercinus* live in shallow depressions or amongst *Pyura* communities. A few chitons are found in notably different habitats: *Stenochiton* species live on seagrasses, *Pseudotonicia cuneata* is free-living in sand, and *Notoplax* species often are found embedded within crypts in sponges.

Members of the Lepidopleurina have been found living at depths down to 8000 m (Sirenko 1977; Gowlett-Holmes & Jones 1992) and are found on various substrata. The relatively deep-water species of *Hanleya* are found sometimes on sponges. Very deep-water species, like most species of the genera *Leptochiton* (down to 8000 m) and *Stenosemus* (100–2580 m), feed on detritus. Many are found on pieces of decaying, waterlogged wood, the only habitat from which *Xylochiton xylophagus* and most *Ferreiraella* species have been recorded.

Deep-water chitons are usually a drab white or grey colour, sometimes with brownish or blackish patches as a result of metallic deposition on the valves, particularly by manganese. Littoral and sublittoral species, on the other hand, often show bright colours and elaborate patterning. Rock-dwellers exposed to surf, like *Onithochiton quercinus* and *Plaxiphora albida*, are normally strongly eroded and overgrown with algae, serpulids, bryozoans and barnacles: only in very young, small animals are the normal valve and girdle features easily seen.

Chitons are relatively inactive animals, a feature typical of many grazing animals. Some species remain in one area for long periods, exposed-shore animals often having a homescar (home) to which they return regularly when conditions are unsuitable for feeding. Species living under stones or in more sheltered conditions may range more widely. Young individuals of a species are generally more active, although they seldom leave the limited area where they feed. Most chitons are nocturnal in habit, hiding during the day in crevices, under rocks, loose stones or dead shells, or beneath a layer of sediment and emerging at night to feed. With the onset of daylight or adverse conditions, they return to suitable shelter or to a semi-permanent 'home'. Chelazzi, Focardi, Deneubourg & Innocenti (1983) demonstrated this homing behaviour for species such as *Acanthopleura gemmata* and also reported aggressive behaviour in the defence of the homescar area. Homing is likely to be found in many open-coast species, such as *Plaxiphora albida* and *Onithochiton quercinus*; their 'homes' being important in helping to resist the adverse physical conditions during the tidal emersion periods characteristic of these exposed habitats. Whether defensive behaviour occurs remains to be determined. The distance covered on these grazing excursions does not exceed 400 mm (Glynn 1970).

Temperature and desiccation pose the greatest environmental problems for shore species. The few studies of the ecological physiology and behaviour of chitons have been well reviewed by Boyle (1977). Chitons on the shore are usually found in rather moist, cool habitats but some are very resistant to the desiccating effects of wind and sun. Individuals of *Sypharochiton pellisserpentis* can sustain a loss of about 75% of the body water before a mortality of 50% occurs. The effects of drying are more severe on small animals and this is reflected in size distributions of shore species, in which only the larger animals are found in exposed locations. Species normally living beneath stones and subtidally are very susceptible to desiccation. A similar relationship exists for temperature tolerance (Kenny 1958). The clamping behaviour shown by *S. pellisserpentis* restricts osmotic problems resulting from inundation by rain water (Boyle 1969) but again, most species normally living in protected environments have little resistance to salinity change. Practically all chitons appear to be stenohaline; the European *Lepidochitona cinerea*, however, is known to be euryhaline and penetrates into the Baltic Sea to the Isle of Bornholm, tolerating a salinity of 15%.

Many chitons shelter symbionts in the pallial groove. These include sphaeromid isopods (*Eusphaeroma crenulatum*) among the gills of *Chiton tuberculatus* (Arey & Crozier 1919), mites (*Halixodes chitonis*) and protozoans (*Urciolaria korschelti*) (Pelseneer 1899). Ricketts & Calvin (1939) found the pea crab, *Opisthomus transversus*, and the polychaete, *Acholoe vittata*, in the pallial groove of the large *Cryptochiton stelleri*.

Some parasites of chitons are known. The sporozoan *Minchinia chitonis* has dramatic effects on growth of the European *Lepidochitona cinerea* (Baxter & Jones 1978) and *Chitonicium simplex* was reported in the tissues of the Chilean *Ischnochiton inca* (*fide* Plate 1897–1901). The parasitic copepod *Ischnochitonika lasalliana* has been reported by Franz & Bullock (1990) in tropical western Atlantic chitons. Of the ectoparasites, borers such as the bivalved *Lithophaga* species, are known to damage the valves of *Chiton tuberculatus*, *C. stokesii* (Bullock & Boss 1971) and *Acanthochitona hirundiniformis* (*fide* Watters 1981).

The predators of chitons are principally crabs, fishes and birds.

Economic Significance

There are several records of chitons having been eaten by humans. Coastal Aborigines in western Kimberley, Western Australia, are known to have eaten *Acanthopleura spinosa* (Pl. 8.1; O'Connor 1990), and shell heaps on the Lesser Antilles consist predominantly of valves of *Chiton* and *Acanthopleura* species eaten by the original inhabitants of these islands. Arey & Crozier (1919) reported that Bermudans made a soup out of chitons. Native Alaskans were observed to eat *Katharina tunicata* and Indians of Puget Sound ate the foot and eggs of *Cryptochiton stelleri*. Ricketts & Calvin (1939) attempted to eat a thin, tough steak cut from the foot of a *Cryptochiton*, but desisted as it 'radiated such a penetrating fishy odour that it was discarded before it reached the frying pan'. Chitons are clearly of negligible economic significance, although there is much to be learned of their significance for the intertidal community.

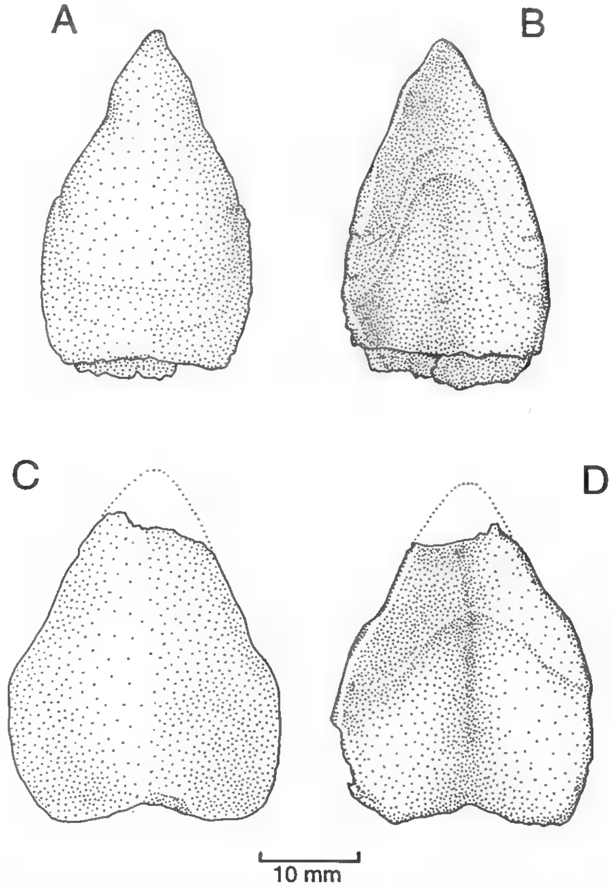


Figure 3.26 Intermediate valves of *Chelodes calceoloides* (Mattheviidae), the first fossil chiton named from Australia. **A**, **C**, dorsal view; **B**, **D**, ventral view. [I. Grant]

Biogeography

Chitons are known from all the world's seas and are found on all Australian coasts, the Subantarctic islands and Antarctica. Australia, with over one-quarter of the world's species, has the highest diversity of any single region. Over 90% of chiton species found in Australia are endemic. The extinct order Phosphatoloricata, containing the family Cobcrephoridae, is known only from Australia (Fig. 3.27).

Several fossil and extant taxa in the order Neoloricata are endemic to Australia: one extinct family, Protochitonidae (Fig. 3.28) and one extant family, Choriplacidae; the extinct genera *Permochiton* and *Pseudoischnochiton* (Lepidopleuridae) and *Oochiton* (family Schizochitonidae and genera, *Mucrosquama* and *Delicatoplax* (Chitonidae), one extinct genus, *Afossochiton* and one extant genus, *Bassethullia* (Acanthochitonidae); three extant genera, *Particulzona*, *Stenochiton*, and *Subterenochiton* (Ischnochitonidae).

Over 85% of species of chitons in Australia are known from the southern and eastern coasts. There is a great paucity of records from the northern and north-western coasts. This probably reflects a lack of specialised collecting in tropical areas rather than a genuine lack of species, as often chiton species have been recorded from adjacent waters, and increased collecting in recent years in northern Western Australia, in particular, has added many new records.

FOSSIL RECORD

The Polyplacophora has been represented continuously in the fossil record since the late Cambrian (Fig. 3.30). Fossil chitons are recorded from the Ordovician, Permian, Miocene and Pliocene in Australia (Runnegar, Pojeta, Taylor & Collins 1979; Van Belle 1981; Smith & Hoare 1987).

The oldest Australian species, *Chelodes whitehousei* is known from the early Ordovician (lower Tremadocian) deposits of the Ninmoroo Formation, Mount Datson, Queensland and is believed to have been a grazer on intertidal and shallow subtidal algal stromatolite domes (Runnegar *et al.* 1979). Another congener, *C. calceoloides* (Fig. 3.26) from the upper Silurian deposits at

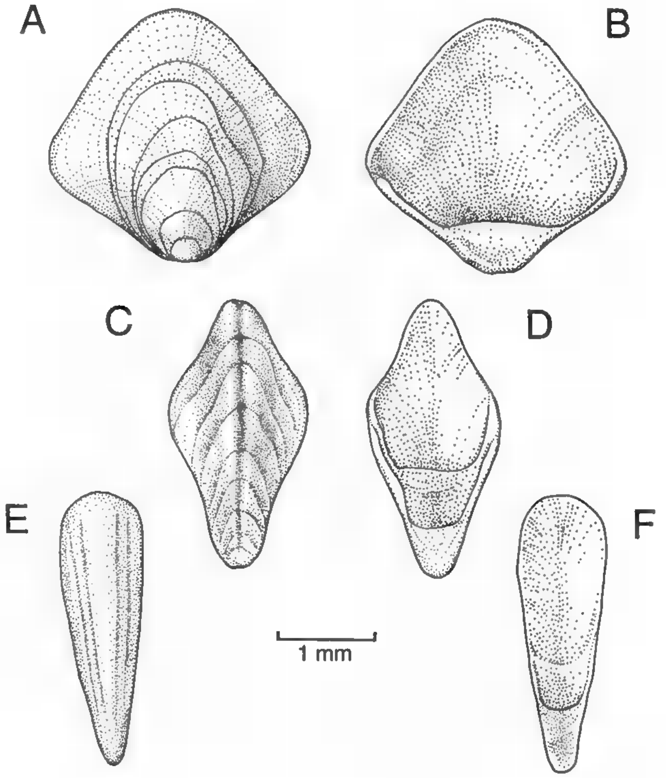


Figure 3.27 Valves of *Cobcrephora silurica*, one of the two fossil species in the Australian endemic family Cobcrephoridae. **A**, **B**, head valve; **C**, **D**, intermediate valve; **E**, **F**, tail valve. **A**, **C**, **E**, dorsal view; **B**, **D**, **F**, ventral view. [I. Grant]

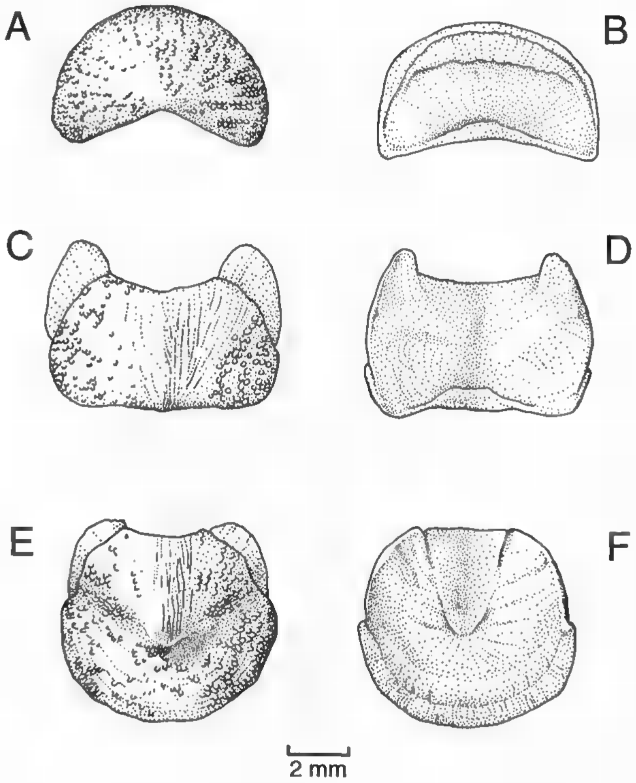


Figure 3.28 Valves of *Protochiton granulosus* (Protochitonidae), known only from the Miocene deposits of Victoria. **A**, **B**, head valve; **C**, **D**, intermediate valve; **E**, **F**, tail valve. **A**, **C**, **E**, dorsal view of valves; **B**, **D**, **F**, ventral view. [I. Grant]

Yass, New South Wales, was the first fossil chiton named from Australia (Etheridge 1897). These species are in the family Mattheviidae (= Chelodidae) and are the only known Australian representatives of the extinct order Paleoloricata.

The extinct order Phosphatoloricata is known only from Australia. This order is unique among the Polyplacophora in that the valves were apparently made of calcium phosphate, and were probably apatitic. The single family in this order, Cobcrephoridae, contains the single genus *Cobcrephora*, which contains the two species *C. silurica* (Fig. 3.27) and *C. corrugata*, from the late Ordovician (Caradocian) and Silurian (Llandoverian, Wenlockian and Ludlovian) deposits near Orange, New South Wales. These species are believed to have lived in an intertidal to shallow-water, high energy environment (Bischoff 1981).

In the order Neoloricata, a single species is recorded from the Permian of New South Wales (Iredale & Hull 1926b, 1927) and a large number of species have been named from the Neogene of south-eastern Australia. Major references for the Neogene chitons of south-eastern Australia are Ashby & Torr (1901), Ashby (1925, 1929), Iredale & Hull (1926b, 1927) and Ashby & Cotton (1939). For an up-to-date placement of most of the Neogene chitons of south-eastern Australia see Gowlett-Holmes & McHenry (1988b). Fossil records for the extant families are dealt with in detail under those families.

The monotypic Protochitonidae are an extinct family in the suborder Lepidopleurina of the Neoloricata known only from the Miocene of Victoria (Fig. 3.28). Intermediate valves of *Protochiton* were recorded by Ashby & Torr (1901) from the Miocene deposits at Mornington, Victoria (Eocene of Ashby & Torr 1901 and Van Belle 1981) under the genus *Acanthochites (Notoplax)*. Chapman (1907) referred a tail valve of *Protochiton* from the Miocene deposits at Balcombe Bay, Victoria to the genus *Ischnochiton (Ischnoplax)*. Head valves of the same species were recorded from the Miocene deposits at Balcombe Bay, Grices Creek and at Muddy Creek, Victoria by Ashby (1925).

The monotypic genus *Lavenachiton* Cotton & Godfrey, 1940 is regarded by Van Belle (1981, 1983) as *incertae sedis*. This genus is based on a single incomplete intermediate valve (Fig. 3.29) recorded from the Miocene deposits at Clifton Bank, Muddy Creek, Victoria, by Ashby & Cotton (1939) who referred it to the genus *Ischnochiton (Radsiella)*.

Most of the fossil chitons recorded from the Neogene of south-eastern Australia are based on few specimens, the majority of which are in very poor condition and incomplete. The exact affinities of many of these are uncertain because of their poor condition and the erosion of diagnostic characters. The majority of these species are in urgent need of revision, but this must await the collection of more and better quality material.

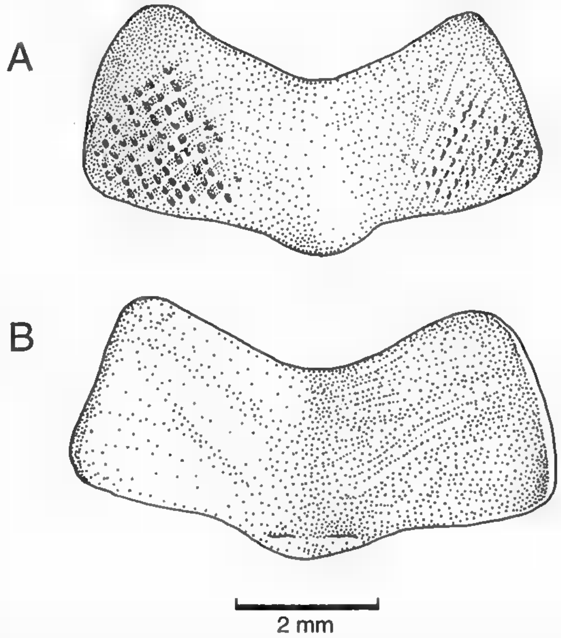


Figure 3.29 Intermediate valve of *Lavenachiton cliftonensis* (family *Incertae sedis*) (holotype). **A**, ventral view; **B**, dorsal view. [I. Grant]

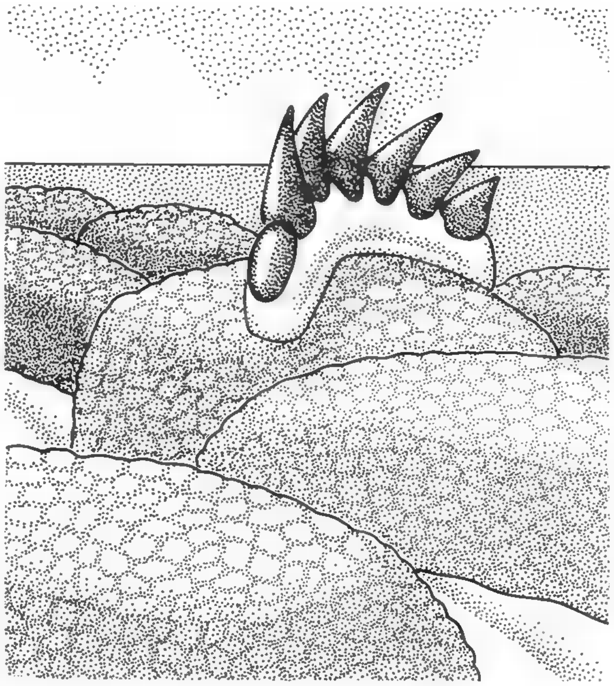


Figure 3.30 Artist's impression of the North American *Matthevia variabilis* grazing Late Cambrian intertidal stromatolites. (After Runnegar *et al.* 1979) [C. Eadie]

CLASSIFICATION

The Polyplacophora has been divided into two orders by Bergenhayn (1955). For the most primitive extinct species the order Paleoloricata was erected, characterised by the absence of an articulamentum on the valves, so that insertion plates and sutural laminae are wanting. Members of this order are known from the Lower Ordovician to the Upper Cretaceous. There is one suborder, Chelodina.

The order Neoloricata was created to accommodate all chitons equipped with an articulamentum forming at least sutural laminae on the valves II–VIII. As outlined in Table 3.1, the order contains four suborders. Two of the 11 families are not known from the Australian region, but have been found in neighbouring waters.

Table 3.1 The classification of the extant Polyplacophora. Families marked with an asterisk are not known from the Australian region.

Class **POLYPLACOPHORA**
Order NEOLORICATA
  Suborder LEPIDOPLEURINA
    Family Lepidopleuridae
    Family Hanleyidae
    Family Xylochitonidae*
    Family Abyssochitonidae*
  Suborder CHORIPLACINA
    Family Choriplacidae
  Suborder ISCHNOCHITONINA
    Family Ischnochitonidae
    Family Schizochitonidae
    Family Mopaliidae
    Family Chitonidae
  Suborder ACANTHOCHITONINA
    Family Acanthochitonidae
    Family Cryptoplacidae

Key to the suborders of the order Neoloricata

1(a)	Valves without or with unslitted insertion plates	2
(b)	At least one of the valves with a slitted insertion plate	3
2(a)	Valves with well-developed tegmentum, without or with unslitted insertion plates	Lepidopleurina
(b)	Valves with reduced tegmentum and large, unslitted insertion plates	Choriplacina
3(a)	Tegmentum always present, valve I with six or more slits in insertion plate	Ischnochitonina
(b)	Tegmentum absent, or number of slits in valve I at most five	Acanthochitonina

Suborder LEPIDOPLEURINA

In this suborder, the valves lack insertion plates, or have unslitted insertion plates on one, several or all valves. The tegmentum is pustulose, colourless or plainly coloured, and the girdle has imbricating striated scales or is pustulose. The gills are merobranchial, and either adanal or abanal. Members are bottom dwellers; most live in deep water, where they feed on decaying wood and detritus. The group is found in all oceans to depths of 8000 m.

The Lepidopleurina includes four extant families. The Lepidopleuridae (= Leptochitonidae) have almost 100 extant species worldwide and the Hanleyidae have no more than four known extant species. Recently, two new families have been assigned to the suborder: the Xylochitonidae which has one species, *Xylochiton xylophagus*, from the deep waters of New Zealand (Gowlett-Holmes & Jones 1992) and the Abyssochitonidae which has six species in the genus *Ferreiraella* found at abyssal depths in most seas (Sirenko 1988; Dell'Angelo & Palazzi 1989).

Key to the families of the suborder Lepidopleurina

1(a)	Girdle with calcareous armament on underside	2
(b)	Girdle without calcareous armament on underside	3
2(a)	Insertion plates absent	Lepidopleuridae
(b)	Insertion plates present, at least on head valve	Hanleyidae
3(a)	Insertion plates absent	Abyssochitonidae
(b)	Head valve, at least, with insertion plate	Xylochitonidae

Family Lepidopleuridae

The members of this family are small to large, oval to elongate chitons, reaching over 50 mm in length (Fig. 3.31; Pl. 9.4). The tegmentum of the valves is generally not coloured and is covered with granulose sculpture. All known Australian representatives are well documented by Kaas & Van Belle (1985a). The family is divided into the subfamilies Helminthochitoninae, a group of small to large fossil chitons, and the Lepidopleurinae, a group of small to medium-sized chitons up to 30 mm long which includes all known extant species. Lepidopleurinae comprise the four genera, *Hanleyella*, *Lepidopleurus*, *Oldroydia* and *Leptochiton*, the latter with three subgenera, *Leptochiton sensu stricto*, *Parachiton* and *Pilsbryella*.

The family is characterised by valves which lack insertion plates and the sutural laminae are small and widely separated (Fig. 3.31C–H). The girdle is clothed with variously shaped scales, spines and spicules (Fig. 3.31B). Gills are merobranchial, adanal or abanal, usually few in number. Most species are less than 15 mm in length.

Most deep-water *Leptochiton* species feed on small organisms such as diatoms, radiolarians, foraminiferans, crustacean and polychaete larvae, and bottom detritus (Kaas & Van Belle 1985a). In the northern European species, *Leptochiton asellus*, both eggs and sperm are shed directly into the water at night. Development includes an extended free-swimming larval stage before metamorphosis and settlement (Christiansen 1954).

In *Leptochiton asellus*, individuals become reproductively mature at about 6 mm in length, at an age of one or two years. Spawning takes place in the northern autumn, from late September to early November, with greatest intensity in October. Christiansen (1954) observed that in culture males always spawn first. About 100 to 500 eggs are shed singly and held together in a slimy mass. The eggs hatch 20–21 hours after spawning, with an extended free-swimming larval stage of 6–10 days before metamorphosis and settlement. The life span is unknown for any species, but it is at least several years (Christiansen 1954). These chitons are found from intertidal to abyssal depths. Intertidal species are usually found under rocks in pools. Deeper water species are found under rocks, on rock under a layer of loose sand, or on cobbles, pebbles and shells in sands and muds. Abyssal forms are usually dredged up on pebbles, or on rock or carbonate fragments.

All known Australian representatives are in two *Leptochiton* subgenera, *L. (Leptochiton)* and *L. (Parachiton)*, and the fauna includes the deep water-abyssal cosmopolitan species *L. (L.) alveolus*. With the exception of the latter and *L. (L.) norfolcensis* from Norfolk Island, Lord Howe Island and the Kermadec Group, Australian representatives are restricted to mainland waters. Several tropical species (for example, *L. (L.) liratellus*, *L. (P.) litoreus* and *L. (P.) capricornicus* are known from restricted localities and few specimens, and may need to be reassessed when larger samples are available. *Leptochiton* species are known from all Australian waters; *L. (L.) liratus* (Pl. 9.4) and *L. (L.) matthewsianus* are the most common species on temperate Australian coasts. *Leptochiton (L.) fairchildi* is recorded from Macquarie Island, and *L. (L.) kerguelensis* is known from the Subantarctic islands and Antarctic waters under Australian jurisdiction. Records from northern Australian coasts are very sparse, and our northern fauna may prove to be much more extensive following additional collecting. The family is not known from Christmas Island.

The fossil subfamily Helminthochitoninae is recorded from the lower Ordovician to lower Jurassic of Europe and North America and the Permian and Miocene of Australia (Van Belle 1981, 1983). The only representative of the genus *Permochiton* was recorded from the Permian deposits at Bundanoon, New South

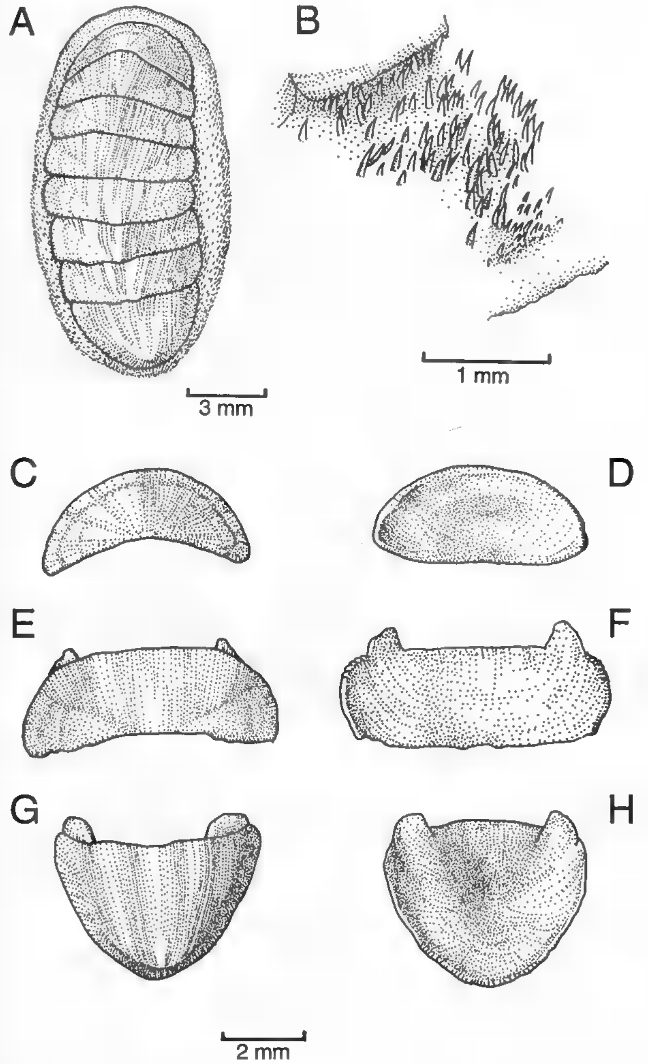


Figure 3.31 Family Lepidopleuridae. *Leptochiton (Parachiton) puppis*, external appearance and valves. **A**, whole animal, dorsal view; **B**, detail of dorsal surface of girdle; **C**, **D**, head valve; **E**, **F**, intermediate valve; **G**, **H**, tail valve. **C**, **E**, **G**, dorsal view of valves; **D**, **F**, **H**, ventral view of valves. [I. Grant]

Wales by Iredale & Hull (1926b, 1927). The genus *Pseudoischnochiton* was placed in this subfamily tentatively by Van Belle (1981, 1983); its only representative was recorded from the Miocene deposits at Table Cape, Tasmania, by Ashby (1930).

Fossil representatives of the subfamily Leptochitoninae are recorded from the Eocene to Miocene of Europe, the Pliocene of North America and the Miocene and Pliocene of Australia and New Zealand (Van Belle 1981, 1983). Head, intermediate and tail valves of several species of *Leptochiton* were recorded by Ashby (1925) and Ashby & Cotton (1939) from the Miocene and Pliocene deposits at Muddy Creek, Victoria.

Family Hanleyidae

Members of this family are small to large, oval to elongate chitons, up to 60 mm in length (Fig. 3.32). The girdle is spiculose. In the two genera comprising the family, the sculpture of the tegmentum of the valves is almost smooth (*Hemiarthrum*) or granulose (*Hanleya*). The most recent revision of the family is that of Kaas & Van Belle (1985a). Only the genus *Hemiarthrum* occurs in Australian waters.

In *Hanleya*, sutural laminae are well developed, and the unslit insertion plates are well developed on the head valve, but more or less absent on the remaining valves. In *Hemiarthrum*, the insertion plates are well developed on the head and tail valves, and absent on the intermediate valves. The girdle is spiculose with longer spines, forming sutural tufts in *Hemiarthrum* (Fig. 3.32A, B). Gills are merobranchial, adanal (*Hanleya*) or abanal (*Hemiarthrum*). Members of the genus *Hanleya* have been recorded feeding on sponges (Kaas & Van Belle 1985a), and *Hanleya nagelfar* has been found embedded in sponges on which they feed (Warén & Klitgaard 1991) in a similar manner to *Notoplax* species (Acanthochitonidae). On Macquarie Island, *Hemiarthrum setulosum* feeds on green algal film, diatoms and encrusting coralline algae, showing a marked preference for the latter (Simpson 1976). The radula of this species bears a row of broad, thin, blade-like central teeth, and major lateral teeth with tridentate cusps, of which the central denticle is the largest. This species broods its young to an advanced stage in the pallial groove (Simpson 1976, 1977).

The reproductive cycle of *H. setulosum* on Macquarie Island is annual (Simpson 1977). Spawning occurs in males from December to March, with peaks in December and February. Females retain the eggs in the ovary until February, eggs appearing in the pallial groove in March, where they are retained while they develop into juvenile chitons before release in June and July. Fertilisation occurs just before or during the transfer of the eggs. Life span and the age of reproductive maturity are unknown.

Members of this family are found from the intertidal to abyssal depths, although members of the genus *Hanleya* are rarely found in shallow water. On Macquarie Island, *Hemiarthrum setulosum* is commonly found in the intertidal zone on encrusting coralline

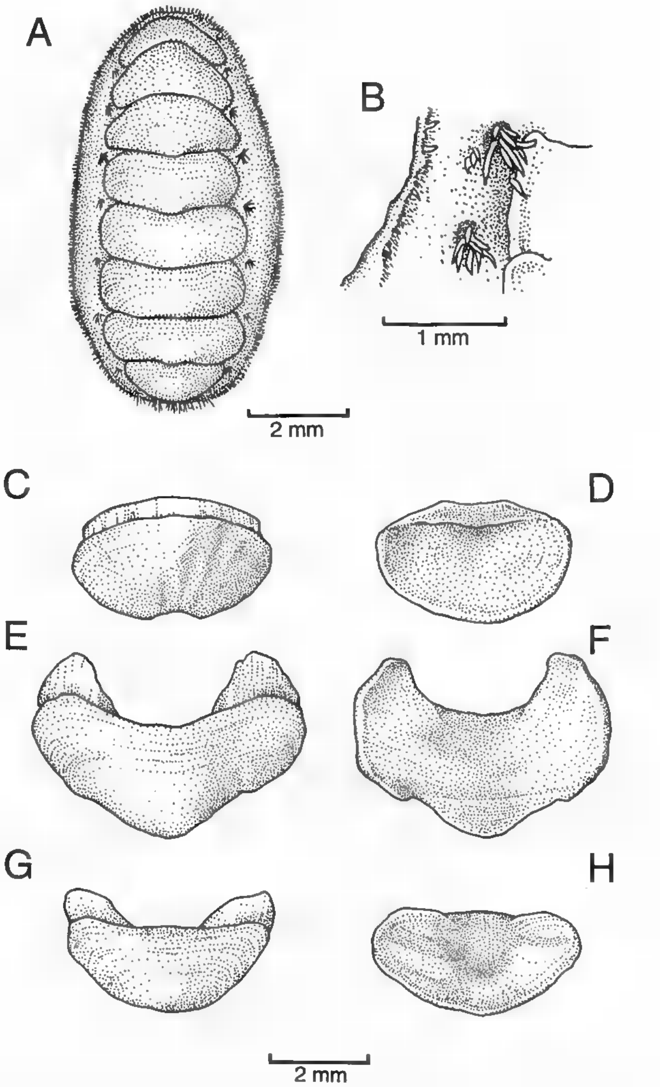


Figure 3.32 Family Hanleyidae. *Hemiarthrum setulosum*, external appearance and valves. **A**, whole animal, dorsal view; **B**, detail of dorsal surface of girdle; **C**, **D**, head valve; **E**, **F**, intermediate valve; **G**, **H**, tail valve. **C**, **E**, **G**, dorsal view of valves; **D**, **F**, **H**, ventral view of valves. [I. Grant]

algae among the holdfasts of the kelp *Durvillea antarctica* and moves little within this habitat (Simpson 1976); this species is also recorded to a depth of 380 m (Kaas & Van Belle 1985a).

The genus *Hanleya* is Holarctic, from deep water Arctic to Northern Hemisphere tropical latitudes in distribution, with several species. The single species of *Hemiarthrum* has a circumpolar Antarctic distribution between the latitudes 45°S and 70°S. It is found on the Subantarctic islands and off the coast of Antarctica under Australia's jurisdiction, but not on the Australian coast, on Norfolk, Lord Howe or Christmas Islands.

Fossil species of *Hanleya* are recorded from the Oligocene and Miocene of Europe. No fossils of *Hemiarthrum* species have been recorded (Van Belle 1981, 1983).

Suborder CHORIPLACINA

The members of this small suborder are small to large chitons with large unslit insertion plates in all valves, a much reduced tegmentum and holobranchial gills. The suborder was reviewed most recently by Gowlett-Holmes (1987). It contains only two monogeneric families, the extant monotypic Choriplacidae from southern Australia and the fossil Glyptochitonidae from the Carboniferous of Europe.

Family Choriplacidae

The sole member of this family, *Choriplax grayi*, is a medium-sized, elongate oval chiton up to 30 mm long (Fig. 3.33). The valves have a much reduced tegmentum, and the girdle is fleshy and microscopically spiculose (Gowlett-Holmes 1987).

In *Choriplax grayi*, the tegmentum of the valves is discrete, very small and bears granulose sculpture. The sutural laminae and unslit insertion plates are large and well developed. The girdle is large and fleshy in life, completely covering the valves with a transparent layer over the tegmentum, drying to a thin horny covering. The gills are holobranchial and abanal. The radula has small central teeth with asymmetrical cusps, and the major lateral teeth have wide tridentate cusps of sharp denticles of equal length. Nothing is known of the internal anatomy, feeding and reproduction of this species. The tegmentum is produced at an early stage of growth in this species and then does not increase in size. The articulamentum grows normally so that the tegmentum in an adult shell is proportionately much smaller than in a juvenile and is more centred on the valves. *Choriplax grayi* lives on the prostrate red alga *Sonderopelta coriacea* in shallow water to 20 m depth. In life, the colour of the girdle and tegmentum matches that of the host plant. The family is endemic to southern Australia being recorded from Port Jackson, New South Wales, to Perth, Western Australia, and south-eastern Tasmania. Very few specimens of *Choriplax grayi* have been collected. This family has no fossil record.

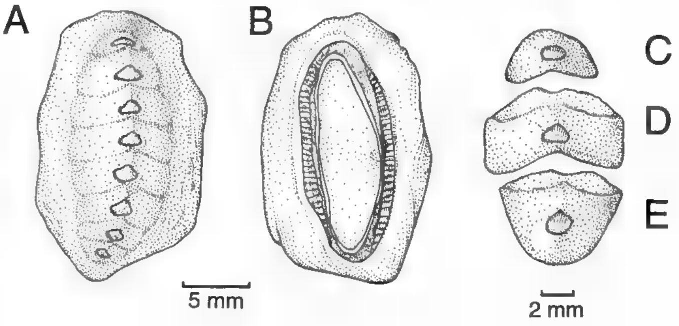


Figure 3.33 Family Choriplacidae. *Choriplax grayi*, external appearance and valves. **A**, whole animal, dorsal view; **B**, ventral view showing holobranchial gills (the head is not visible in this preserved specimen). **C–E**, dorsal view of valves: **C**, head valve; **D**, intermediate valve; **E**, tail valve. [I. Grant]

Suborder ISCHNOCHITONINA

The members of this suborder are characterised by the presence of insertion plates on all valves, and of a tegmentum. The insertion plate of at least the anterior valve is multislitted. The suborder comprises the four families, Ischnochitonidae, Mopaliidae, Schizochitonidae and Chitonidae.

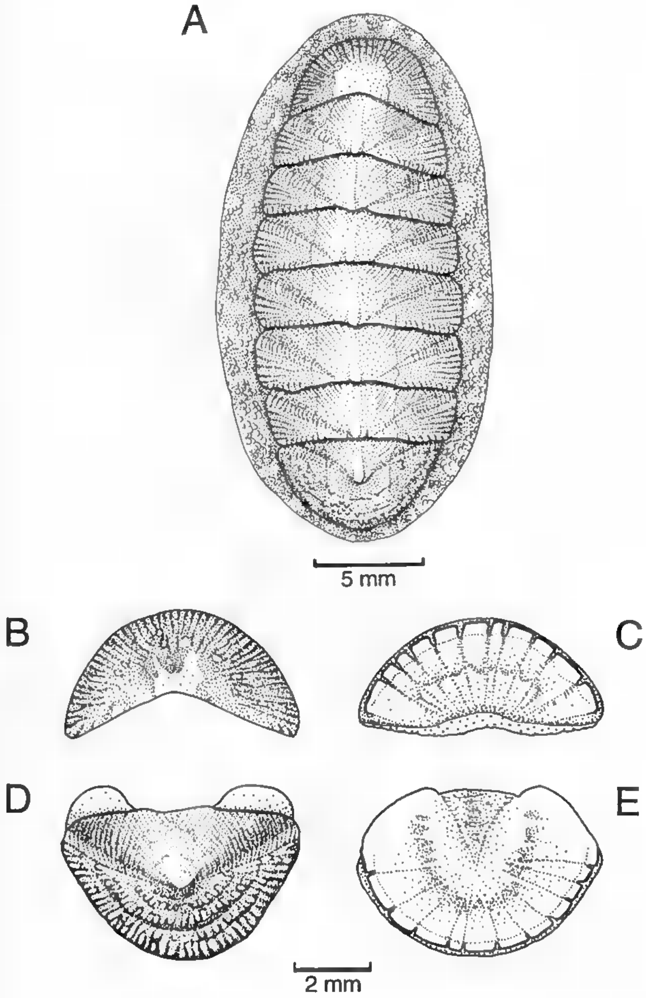
Key to the families of the of the suborder Ischnochitonina

1(a)	Insertion plates not pectinate	2
(b)	Insertion plates pectinate	Chitonidae
2(a)	Tail valve (valve VIII) with a terminal sinus	3
(b)	Tail valve without terminal sinus	Ischnochitonidae
3(a)	Tegmentum without extrapigmentary ocelli	Mopaliidae
(b)	Tegmentum with extrapigmentary ocelli	Schizochitonidae

Family Ischnochitonidae

Members of this large and diverse family (Fig. 3.34; Pls 7.2–7.5) range from ovate to elongate in shape. The valves may be convex to carinate dorsally with a low to moderately high elevation. Though the body length may reach 120 mm, most species are 10–40 mm long. The sculpture of the tegmentum is variable, and the girdle is variously ornamented with spicules, calcareous scales or chitinous processes of different kinds (Van Belle 1983). The head and tail valves are multifissured, and the intermediate valves contain one to many slits. The number of insertion teeth is variable, and some intraspecific variability occurs. No single character distinguishes this family from other taxa; the only characteristics which are shared by all members of the family are the presence of slits in the insertion plates, a multifissured tail valve, and the absence of pectinations in the insertion teeth.

The family Ischnochitonidae was erected by Dall (1889) from the subdivision Ischnoidea which was created by Carpenter (in Dall 1879). Several families have been proposed to accommodate the large number of morphologically diverse species that are now considered to belong to the family Ischnochitonidae (Thiele 1909–1910; Bergenhayn 1955; Smith 1960; Starobogatov & Sirenko 1975). In a series of papers Iredale & Hull (1923, 1924a, 1924b, 1925a, 1925b, 1926a, 1926b, 1926c, 1927a, 1927b; often quoted as Iredale & Hull 1923–1927) recognised three families, the Ischnochitonidae, Lepidochitonidae and the Callistochitonidae, all of which are now included in the Ischnochitonidae as subfamilies. Six subfamilies and 27 genera are currently recognised within the family (Van Belle 1983; Kaas & Van Belle 1985a, 1985b, 1987, 1990, 1994), which has a worldwide distribution. The majority of species occur along the Australian coastline and the west coast of North America. The most recent revisions of Australian species are those by Kaas & Van Belle (1985b, 1987, 1990, 1994) and



Cochran (1993). The Australian representatives of this group belong to ten of the 27 currently recognised genera, and are distributed within all of the subfamilies except Schizoplacinae.

The subfamilial classification of the Ischnochitonidae is based largely on characteristics of the articulamentum, the tegmentum and the morphology of the girdle (Fig. 3.34F–K). So far internal anatomical features have not been studied sufficiently with respect to polyplacophoran systematics to incorporate these structures in diagnoses at the higher levels of classification. The subfamilies are distinguished as follows:

Schizoplacinae (Fig. 3.34F). The intermediate valves are separated into two lateral halves which are united by a ligament. The tegmental sculpture is finely granulose, and the eaves (overhanging edges of the tegmentum) are spongy. The insertion teeth of the articulamentum are obtuse, with a single insertion slit on each side of the intermediate valves, and the girdle is covered with minute, distally-blunt spicules and elongate bristles. This subfamily is represented by a single species, *Schizoplax brandtii*, found in the northern Pacific, and does not occur in Australia.

Callochitoninae (Fig. 3.34G). The sculpture of the tegmentum is finely granulose, and the pleural areas are sometimes deeply grooved or pitted. Ocelli (shell-eyes) may be conspicuous on valves and the eaves are spongy. The insertion teeth are obtuse, and tend to be propped on the outside of the valves. The insertion plates of intermediate valves have one to four slits, with sutural laminae connected or continuous across a narrow jugal sinus. The girdle is spiculose, sometimes with isolated or grouped longer spicules, or with chitinous processes. Two genera, *Callochiton* and *Eudoxochiton*, containing six species (*C. mayi*, *C. elongatus*, *C. klemi*, *C. rufus*, *C. crocinus* and *E. inornatus*; Pl. 7.3) occur around mainland Australia. Five of these six species are endemic and *Callochiton crocinus* also occurs in New Zealand. *Callochiton gaussi* occurs in Australian Antarctic waters. An additional species of uncertain systematic position, *Quaestiplax wilsoni*, which may belong to this subfamily, is endemic to Lord Howe Island.

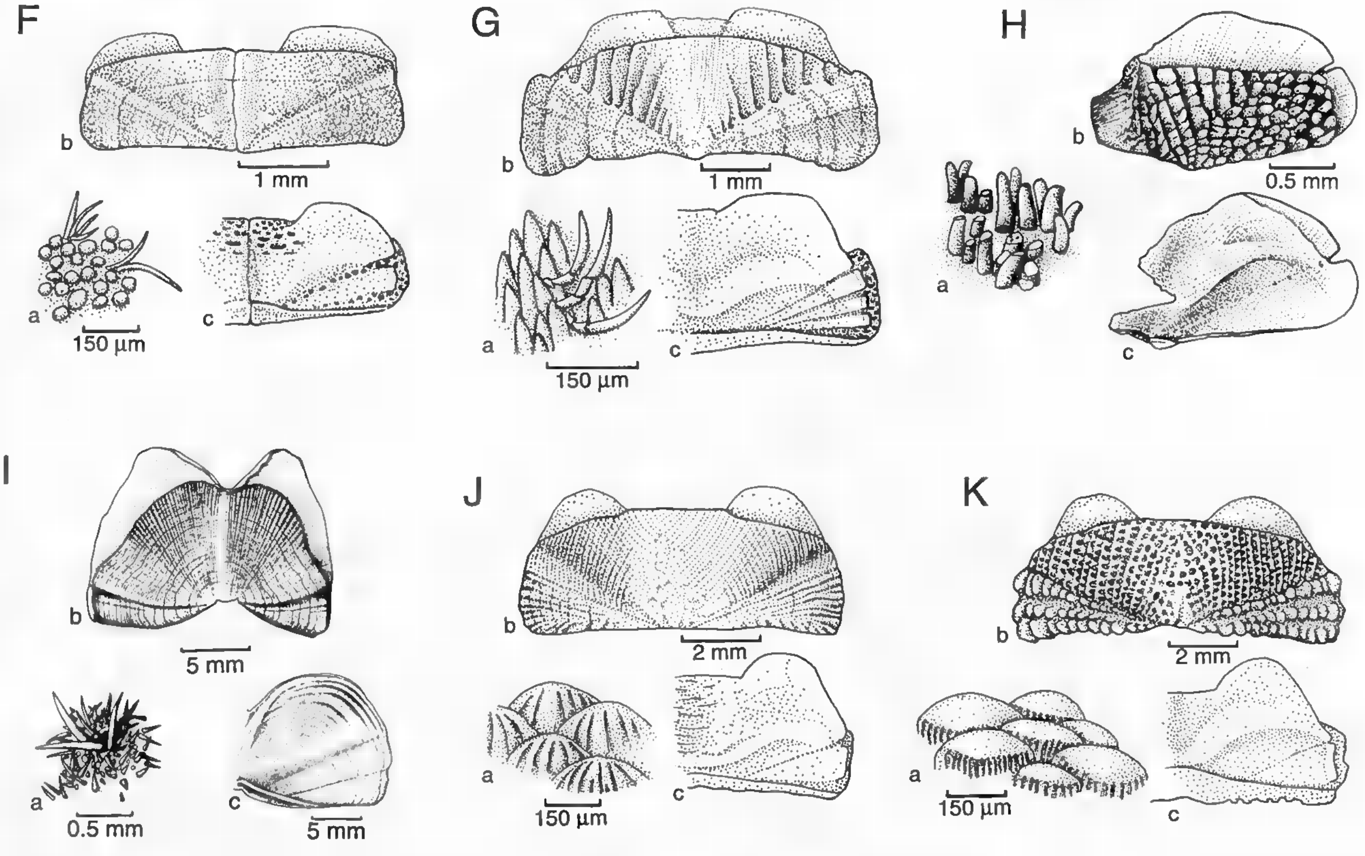


Figure 3.34 Family Ischnochitonidae. **A–E**, *Ischnochiton elongatus*, one of the most common and widespread chitons, external appearance and valves: **A**, whole animal, dorsal view; **B**, **C**, head valve; **D**, **E**, tail valve; **B**, **D**, dorsal view; **C**, **E**, ventral view. **F–K**, morphological features of the six subfamilies: **F**, Schizoplacinae (*Schizochiton brandtii*); **G**, Callochitoninae (*Callochiton mayi*); **H**, Lepidochitoninae (*Particulazona milnei*), showing half the intermediate valve, dorsal view; **I**, Chaetopleurinae (*Nuttallochiton mirandus*); **J**, Ischnochitoninae (*Ischnochiton elongatus*); **K**, Callistoplacinae (*Callistochiton antiquus*). **a**, girdle; **b**, intermediate valve in dorsal view; **c**, right half of intermediate valve in ventral view. [A–G, J, K, T. Cochran; H, I, J. Thurmer]

Lepidochitoninae (Fig. 3.34H). The sculpture of the tegmentum is almost smooth to finely granulose, and the eaves are generally porous. The insertion teeth are obtuse, sometimes rugose, and insertion plates of intermediate valves have one or more slits. The girdle is naked or covered with non-imbricating, calcareous corpuscles, with or without chitinous processes. Most members of the subfamily Lepidochitoninae are found in the northern Atlantic and Pacific Oceans, and along the coast of South Africa. This subfamily is represented in Australia by the endemic genera *Subterenochiton* and *Particulazona*. *Subterenochiton* contains two species, *S. gabrieli* and *S. bednalli* (Kaas & Van Belle 1985b), whereas *Particulazona* is represented by a single species *P. milnei*, which is known only from Darwin, Northern Territory (Kaas 1993).

Chaetopleurinae (Fig. 3.34I). The tegmental sculpture is radially or randomly arranged with beaded, longitudinal riblets on the pleural areas, and the eaves are solid. The insertion teeth are sometimes rugose with a single insertion slit on each side of the intermediate valves, and the sutural laminae are wide, almost connecting across the jugal sinus. The girdle is leathery and covered with spicules. This subfamily is represented in Australia by *Nuttallochiton mirandus* which is recorded from deep water in the Australian Antarctic Territory. However, most of the members of this subfamily live in the northern Atlantic and East Pacific Oceans, and along the African coastline.

Ischnochitoninae (Fig. 3.34J). The sculpture of the tegmentum is generally radially arranged on the head valve, post-mucronal area of the tail valve and lateral areas of all the intermediate valves. The eaves are solid. The sutural laminae are separated by a jugal sinus, and the insertion teeth are usually sharp and not thickened at the edges. The insertion plates of intermediate valves may contain one or more slits. The girdle is covered with overlapping, usually striated, calcareous scales. Three genera, *Ischnochiton*, *Stenochiton* and *Lepidozona*, containing over 40 species occur in Australia. Thirty of these species are found along the southern Australian coastline (Pls 7.2, 7.4, 7.5). All of the southern Australian species and six tropical species are endemic. The genus *Stenochiton* is endemic to Australia.

Callistoplacinae (Fig. 3.34K). The sculpture of the tegmentum is heavily pronounced and radially arranged, and the eaves are solid. Incisions of the insertion plates generally correspond, in number and position, to radial ribs on the tegmentum of the anterior and tail valves. The insertion teeth are sometimes scalloped and generally thickened at edges, with a single insertion slit on each side of the intermediate valves. The girdle is naked or variously ornamented with imbricating scales or bristle-bearing pores. One genus, *Callistochiton*, containing eight species, occurs in Australia. Of the eight Australian species, two species (*Callistochiton antiquus* and *C. mawlei*), are found along the southern Australian coast, and the other six species (*C. granifer*, *C. generos*, *C. broomensis*, *C. clenchi*, *C. occiduus* and *C. augustensis*) have a northern Australian distribution. All species are endemic to Australia, with the exception of *C. granifer* which also occurs in New Caledonia (Kaas & Van Belle 1994). Names of two additional Australian species believed to belong to this genus, *Chiton coccus* and *Callistochiton recens*, are considered to be *nomina dubia* by Kaas & Van Belle (1994).

Dietary analyses of a number of ischnochitonid species in South Australia have shown a wide variety of feeding preferences in this group (Kangas & Shepherd 1984). Examples of herbivorous, omnivorous and carnivorous taxa have all been found. Some species are generalist feeders, whereas others are specialist feeders, such as *Ischnochiton torri*, which feeds predominantly on seagrass, and *Callochiton crocinus*, which feeds on the encrusting alga *Petroderma* (Kangas & Shepherd 1984). The complexity of intestinal looping increases with the amount of plant matter in the diet; carnivorous chiton species generally have a large stomach and a simple posterior intestine, whereas a complex multi-looped intestine occurs in exclusively herbivorous species (Saito & Okutani 1992; Cochran 1993). Although the morphological structure of the polyplacophoran digestive tract appears to be correlated primarily with diet, some interspecific variation in the arrangement of intestinal looping has been found in members of the subfamily Ischnochitoninae, which may be of taxonomic value at the species level (Cochran 1993).

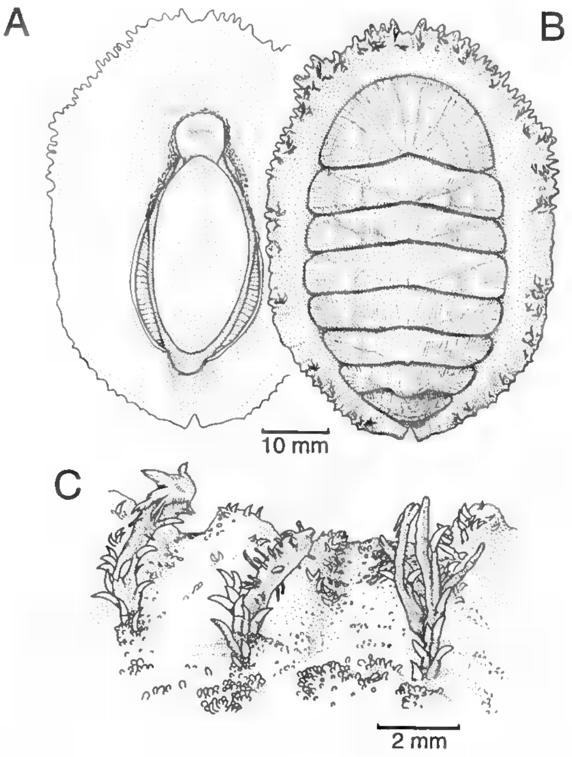


Figure 3.35 Family Schizochitonidae. *Loricella angasi*, external appearance. **A**, whole animal, ventral view, showing the head area; **B**, whole animal, dorsal view; **C**, detail of dorsal surface of girdle. [I. Grant]

The morphology of the ischnochitonid radula has been studied by several workers (Thiele 1893, 1909–1910, 1929; Kaas & Van Belle 1985b, 1987, 1990, 1994; Cochran 1993). The major lateral tooth is the most conspicuous and morphologically variable structure in the radula, and has unicuspid to tricuspid denticle caps. However, interspecific variation in the central and first lateral teeth has also been found in a large number of ischnochitonid radulae (Eernisse 1986; Bullock 1988b; Cochran 1993).

Other internal morphological structures of polyplacophorans have also been used as taxonomic characters. Interspecific variation has been found in the spatial relationship of the gonopore (reproductive opening) and nephridiopore (excretory opening) (Sakker 1982; Cochran 1993), and in chromosome number and morphology (Nishikawa & Ishida 1969; Kawai 1976; Vitturi, Rasotto & Farinella-Feruzza 1982; Cochran 1993). Recently, electrophoretic techniques have also been used to determine enzymatic variation between species within the Ischnochitonidae (Eernisse 1984; Cochran 1993). Other anatomical features such as the arrangement of the gills in the pallial groove (Plate 1897–1901; Iredale & Hull 1927; Kaas & Van Belle 1985a, 1985b, 1987, 1990, 1994; Saito & Okutani 1989) are probably of more use at higher levels of classification (for example, the familial level).

The reproductive biology of most members of the family is not well known, although studies of the reproductive cycles of several North American ischnochitonids have shown that most species spawn gametes (Grave 1922; Himmelman 1975, 1979; Jalbert, Larrivee & Himmelman 1982). However, several species brood their young in the pallial groove (Turner 1978; Pearse 1979; Penprase 1981; Strack 1987; Cochran 1993). Twenty-three of the 34 species of chitons that are known or suspected brooders, including all of the known brooding species in

Australia, belong to the family Ischnochitonidae (Cochran 1993). The sequence of developmental stages in brooding species is similar to that of groups which spawn. However, development proceeds inside a chorion within the pallial groove until the young hatch at either the trochophore stage of development, or when metamorphosis is completed.

Most ischnochitonids are found either underneath rocks, or on rocks either partially or wholly embedded in sand. One exception occurs in members of the genus *Stenochiton*, which inhabit the root-sheaths, stems and leaves of seagrasses along the southern Australian coastline. Many species occur intertidally or subtidally in shallow water, although a few, such as *Ischnochiton tateanus* and *Subterenochiton gabrieli*, are found to depths of over 50 m. Most species exhibit strongly photonegative behaviour. Some species move to the sides and upper surfaces of the rocks at night, whereas others retain their cryptic behaviour (Kangas & Shepherd 1984). The tegmentum of some ischnochitonids is brightly coloured and strikingly patterned, as seen in *Ischnochiton virgatus*, *I. smaragdinus*, *I. versicolor*, *I. elongatus* and *Callochiton crocinus*.

Ischnochitonids are among the most commonly encountered chitons on Australian shores. Species such as *Ischnochiton elongatus* (Fig. 3.34A), *I. australis*, *I. cariosus* and *I. versicolor* may be found in large numbers at various localities along the southern Australian coastline. The geographic range of others is restricted. For example, *Ischnochiton mawlei* is endemic to Tasmania, and *I. pilsbryi* and *I. crebristriatus* are restricted to the central South Australian coastline. Similarly, tropical species such as *I. luticolens* and *I. tindalei* also have a limited distribution along the Queensland coast. Other species have extensive geographic ranges, for example *I. elongatus*, *Callistochiton antiquus* and *Callochiton crocinus* occur along the southern Australian coastline from Western Australia to Queensland. *Callochiton crocinus* is recorded from New Zealand, and *I. adelaidensis* occurs from Queensland to Papua New Guinea.

Fossil chitons are represented mainly by worn and broken fragments of valves, and in the majority of specimens, the insertion plates and sutural laminae are missing. Consequently, the identification and classification of many fossil species is difficult, and synonymy has resulted (Iredale & Hull 1927; Cotton & Godfrey 1940). The family Ischnochitonidae has a fossil history dating back to the Palaeocene epoch of the Tertiary Period (Van Belle 1983). It is represented by fossils found in Tertiary deposits in southern Australia (Cotton & Godfrey 1940; Gowlett-Holmes & McHenry 1988b). Specimens of the genus *Callistochiton* which are closely related to living species, and species in the genera *Callochiton* and *Ischnochiton* have been found in Pliocene beds in Victoria (Ashby & Cotton 1939; Gowlett-Holmes & McHenry 1988b). Other material from these deposits that is thought represent this family includes eroded valves or juvenile specimens. Specimens referred to *Ischnochiton*, and *Callochiton* (as *Ocellochiton*, see O'Neill 1984b) have been found in Miocene beds of Victoria and Tasmania (Iredale & Hull 1927; Cotton & Godfrey 1940; Gowlett-Holmes & McHenry 1988b). The family is also represented in Eocene deposits from Muddy Creek near Hamilton, Victoria, although material is scarce, and the classification and identification of specimens has been based on poorly-preserved intermediate valves (Ashby & Torr 1901).

Family Schizochitonidae

Schizochitonids are medium-sized to large chitons up to 90 mm long, and elongate to broadly oval in shape (Figs 3.35A, B, 3.36A; Pl. 9.5). The girdle is scaly with spiculose tufts or hairs, and slit posteriorly (Figs 3.35, 3.36A). The most recent revision of Australian species is that of Iredale & Hull (1925a, 1927); for a more up-to-date generic placement and synonymy of species see Kaas & Van Belle (1980) and Kaas (1985, 1991). The family comprises the three extant genera, *Schizochiton*, *Lorica* and *Loricella*, and one fossil genus, *Oochiton*.

In this family the tegmentum has extrapigmentary ocelli, and the central and lateral areas are usually differentiated. The insertion plates and sutural laminae are well developed. In *Loricella* (Fig. 3.35B) the head valve is very large. The girdle is usually scaly, often with spiculose tufts and hairs, with a slit at the sinus in the tail valve (Fig. 3.35). The spicules and hairs are often worn off larger specimens and dried specimens. The gills are holobranchial.

In *Lorica volvox* (= *L. cimolia*) and *Loricella angasi* the diet is varied, but includes a large proportion of animal matter (Kangas & Shepherd 1984). The latter species eats amphipods which it traps by rapidly clamping down the previously raised anterior part of the girdle. No information is available on internal anatomy and reproduction for this family. Schizochitonids are found on and under rocks and rubble on reefs in shallow water and intertidally, often in areas of good water movement, usually not under rocks embedded in sand. Species of *Lorica* are usually found on reefs in medium to high energy areas.

All three extant genera are found in Australia, New Zealand, the central Pacific Ocean, Indo-Pacific area, Indian Ocean and the Red Sea. Four of the seven extant species are found in Australian

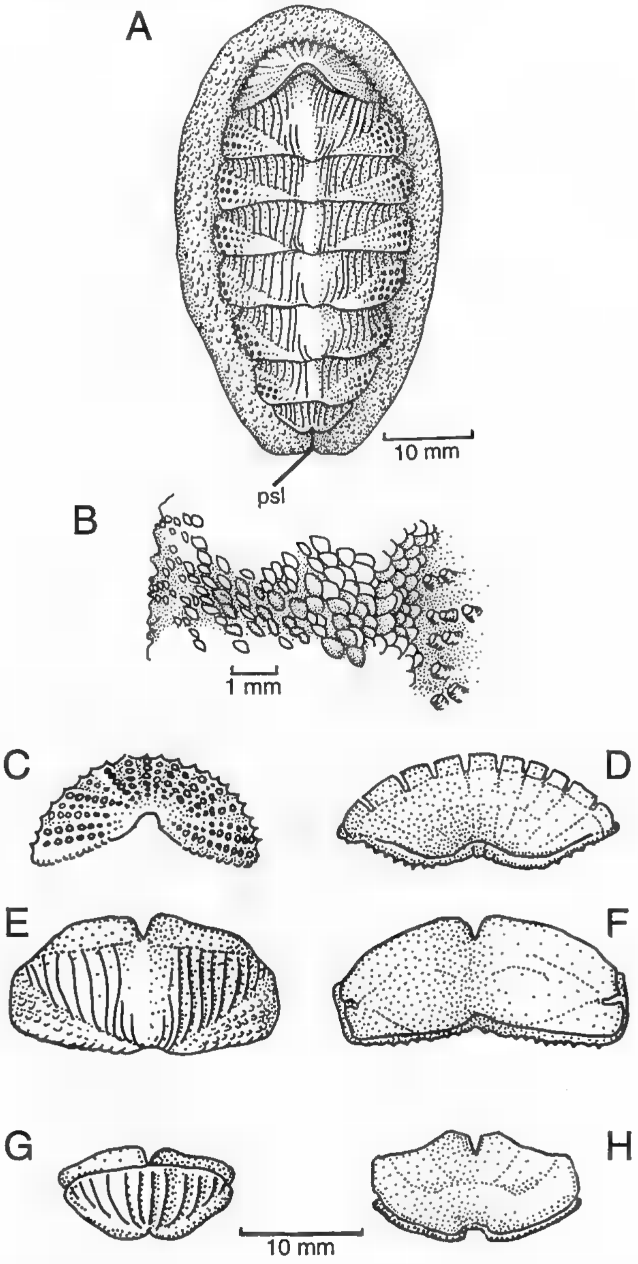


Figure 3.36 Family Schizochitonidae. *Lorica volvox*, external appearance and valves. A, whole animal, dorsal view, note the posterior slit; B, detail of dorsal surface of girdle; C, D, head valve; E, F, intermediate valve; G, H, tail valve. C, E, G, dorsal view of valves; D, F, H, ventral view of valves. psl, posterior slit. [I.Grant]

waters. *Lorica volvox* (Pl. 9.5) and *Loricella angasi* are widespread in southern Australian including Tasmania, and are endemic. *Loricella profundior* is a deep-water species found in the western Pacific, and recorded from off eastern Australia, and *Schizochiton incisus* is widespread, but is usually uncommon in the tropical Indo-Pacific area including Queensland and the Great Barrier Reef. Though schizochitonids have not been recorded from northern Western Australia, the Northern Territory, the Gulf of Carpentaria or Norfolk, Lord Howe or Christmas Islands they probably occur there, as they are known from all other Australian waters. The family is not known from the Subantarctic islands or Antarctica.

Fossil schizochitonids are recorded from the Miocene of Palau and the Marshall Islands and the Miocene and Pliocene of Australia (Van Belle 1981, 1983). Head, intermediate and tail valves of species of *Lorica* and *Loricella* were recorded from the Miocene (Eocene of Van Belle 1981) and Pliocene deposits of Muddy Creek, Victoria, and the Miocene deposits of Moorabool, Victoria, and Table Cape, Tasmania, by Ashby & Torr (1901), Hull (1910, 1915), Ashby (1921, 1925), Ashby & Cotton (1939) and Cotton & Godfrey (1940). The extinct genus *Oochiton* was described by Ashby (1929) from head, intermediate and tail valves from the Miocene deposits of Balcombe Bay, Victoria, and was recorded from Miocene deposits of Muddy Creek, Victoria, by Ashby & Cotton (1939).

Family Mopaliidae

The members of the family Mopaliidae are small to large chitons attaining up to 130 mm in length, oval in shape, and with the girdle variously ornamented (Fig. 3.37; Pl. 9.6). The most recent revision of this family is by Kaas & Van Belle (1994). The family is divided into three subfamilies, the Heterochitoninae, a group of fossil medium-sized to large chitons, the monotypic Katharininae, containing the one species, *Katharina tunicata* from the west coast of North America, and the Mopaliinae, a group of small to large chitons to 130 mm long, which contains all other extant species.

In the Mopaliinae, the tegmentum is variously sculptured with pustules and wrinkles and the central and lateral areas are usually differentiated. Sutural laminae and insertion plates are well developed, the latter not pectinate. The girdle bears various hairs, bristles and spines, but never has scales (Fig. 3.37B). The gills are holobranchial and abanal or adanal.

Kangas & Shepherd (1984) studied the feeding of the Australian species, *Plaxiphora (P.) albida*, a herbivore which feeds on filamentous algae, geniculate coralline algae and some crustose coralline algae. The Subantarctic species *P. (P.) aurata* feeds on green algal film, diatoms and encrusting coralline algae, showing a marked preference for the latter (Simpson 1976). The Californian species *Placiphorella velata* traps and eats small crustaceans under its large anterior girdle flap (McLean 1962) in a manner resembling that of the schizochitonid, *Loricella angasi*, which is morphologically similar (Ludbrook & Gowlett-Holmes 1989). Several species of the northern Pacific genus *Mopalia* are opportunistic grazing omnivores, and consume a variety of animal material, such as small molluscs, barnacles, bryozoans, hydroids and sponges, in addition to a variety of algae and diatoms (Barnawell 1960).

In the North American species *Mopalia muscosa*, the girdle hairs contain nerve fibres and are apparently sensory in function (Leise & Cloney 1982). In *Plaxiphora (P.) aurata*, both eggs and sperm are shed directly into the water (Simpson 1977), whereas the New Zealand species *P. (P.) australis* broods eggs and juvenile chitons in the pallial groove (Murdoch 1982).

The reproductive cycle of *Plaxiphora (P.) albida* in eastern Australia is annual and bimodal. Spawning occurs in spring from August to October and in autumn from February to April, and varies greatly among individuals (Sakker 1986, as *P. (P.) paeteliana* [= *P. (P.) albida*]). *Plaxiphora (P.) aurata* breeds annually on Macquarie Island (Simpson 1977), where spawning occurs from December to March, with a peak in January, although the males are in breeding condition from November to April. Post-spawning development is unknown in these species. The diploid chromosome complements of two species are 12 in the North American species *Katharina tunicata*, and 24 in *Placiphorella japonica* from Japan (Nakamura 1985).

Mopaliine chitons in Australian waters occur on rocky substrata in medium to high energy areas from the intertidal to shallow subtidal, often exposed at low tide. Most members of this subfamily in other areas are found under similar conditions, although the majority of species of the Northern Hemisphere genus *Placiphorella* are dredged from waters deeper than 100 m, and some are known from more than 1000 m. On Macquarie Island, *Plaxiphora (P.) aurata* is selectively preyed upon by the Kelp Gull (*Larus dominicanus*) in the intertidal zone (Simpson 1976).

The subfamily Mopaliinae contains five genera (Kaas & Van Belle 1994). Three of these, *Amicula*, *Mopalia* and *Placiphorella*, are found predominantly in the northern Pacific Ocean and Bering Sea; exceptions are a deep-water species from the northern Atlantic Ocean and a species from the northern Pacific coast of South America. The genus *Placiphorina* is currently known only from Bali, Indonesia. The remaining genus, *Plaxiphora*, contains three subgenera, *Plaxiphora sensu stricto*, *Fremblya* and *Mercatora*, and is predominantly circumpolar Antarctic in distribution, with individual species recorded from the northern Indian Ocean, Hawaii and Japan. Four species of the genus *Plaxiphora* are known from Australian waters, although northern records are very sparse

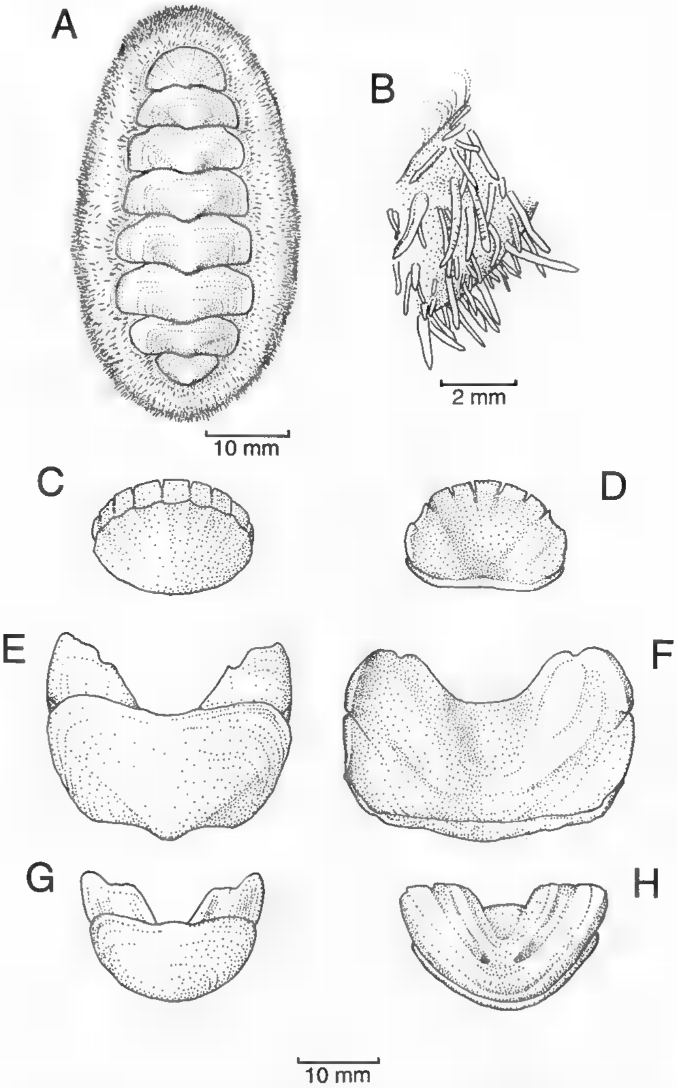


Figure 3.37 Family Mopaliidae, subfamily Mopaliinae. *Plaxiphora (Plaxiphora) albida*, external appearance and valves. A, whole animal, dorsal view; **B**, detail of dorsal surface of girdle; **C**, **D**, head valve; **E**, **F**, intermediate valve; **G**, **H**, tail valve. **C**, **E**, **G**, dorsal view of valves; **D**, **F**, **H**, ventral view of valves. [I. Grant]

and isolated. *Plaxiphora (Plaxiphora) albida* is common in temperate to subtropical Australian waters, and is endemic; *P. (P.) obscurella* is recorded from tropical Queensland and subtropical southern Western Australia, and also from New Caledonia. *Plaxiohora (Fremblya) matthewsi* has a similar distribution to *P. (P.) albida*, but is found in slightly deeper water. *Plaxiphora (Plaxiphora) aurata* is recorded from the Australian Subantarctic islands. The family is unknown from Norfolk, Lord Howe and Christmas Islands and the Antarctic mainland under Australian jurisdiction.

Fossil members of the Mopaliinae are recorded from the Pliocene and Pleistocene of North America and the Miocene of New Zealand (Van Belle 1981, 1983). Records of *Plaxiphora* from the Eocene of Australia (Van Belle 1981) are based on Ashby & Torr's (1901) descriptions of two species from Gellibrand, Victoria, which were based on Recent valves of the extant species *P. (P.) albida* (Gowlett-Holmes & McHenry 1988b). Members of the fossil subfamily Heterochitoninae are known only from the Jurassic of Europe.

Family Chitonidae

The members of this family are small to very large chitons, up to 200 mm long and are elongate to oval in shape (Pl. 8). The insertion plates are pectinate, and the tegmental sculpture and girdle ornamentation is variable. The family contains three subfamilies: the Chitoninae (Fig. 3.38), a group of small to very large chitons to 200 mm long, which occurs worldwide in temperate to tropical areas; the Acanthopleurinae (Fig. 3.39), a monogeneric group of large chitons up to 130 mm long, found mainly in tropical areas worldwide; and the Toniciinae (Fig. 3.40), a group of small to large chitons up to 70 mm long, found in temperate to tropical areas of the Indian and Pacific Oceans. All Australian acanthopleurines were documented by Ferreira (1986). The most recent reviews of members of the other two subfamilies were by Iredale & Hull (1926a, 1926b, 1927), but Kaas & Van Belle (1980) provided a more up-to-date generic placement and synonymy of species; see also Bullock (1988b, 1988c) for generic classifications of the Chitoninae.

In the subfamily Chitoninae, the tegmentum lacks extrapigmentary ocelli, and the tegmental sculpture varies from microgranulose to strongly grooved. The sutural laminae and insertion plates are well developed; the latter are pectinate. The girdle has closely packed, smooth or striated scales (Fig. 3.38B), and the gills are holobranchial.

The valves in the subfamily Acanthopleurinae are thick, heavy and beaked. The tegmental sculpture is coarsely granular to wrinkled, but it is usually destroyed by erosion in larger specimens. Extrapigmentary ocelli occur on the head valve, on the anterior part of the lateral areas of the intermediate valves and on the postmucronal area of the tail valve. The sutural laminae and insertion plates are well developed, the latter are strongly pectinate. The insertion teeth on the tail valve may be absent, often being replaced by a large transverse callus. The girdle is large and covered with a dense arrangement of spikes, spines or scales (Fig. 3.39B). The gills are holobranchial. The major lateral teeth of the radula bear discoid cusps.

In the subfamily Toniciinae the tegmentum is sculptured with nodules, pits and grooves, usually with striking colour patterns. Extrapigmentary ocelli are usually numerous and occur on all valves. The sutural laminae and insertion plates are well developed; the latter are pectinate. The girdle bears microscopic scales and spicules (Fig. 3.40B), and the gills are holobranchial.

Kangas & Shepherd (1984) studied the diet of four Australian chitonine species. *Rhyssoplax diaphora* is herbivorous, and feeds mainly on crustose coralline algae, whereas *Rhyssoplax calliozona*, *R. torriana* and *R. tricostalis* are omnivores, consuming sponges and bryozoans in addition to crustose coralline algae. The first three of these species have been observed feeding on top of boulders at night. On the Great Barrier Reef, the acanthopleurine *Acanthopleura gemmata* (Fig. 3.1) is an opportunistic grazing omnivore, which eats algal film, hydroids, nematodes and insect larvae and feeds at night (Thorne 1967). In Japan, *A. japonica* is also an opportunistic grazing omnivore, eating barnacles, gastropods and bivalves in addition to algae (Nishihama, Nojima & Kikuchi 1986). The Caribbean species, *A. granulata*, is an opportunistic algal grazer, and feeds mainly at night. Nothing is known about feeding in the subfamily Toniciinae.

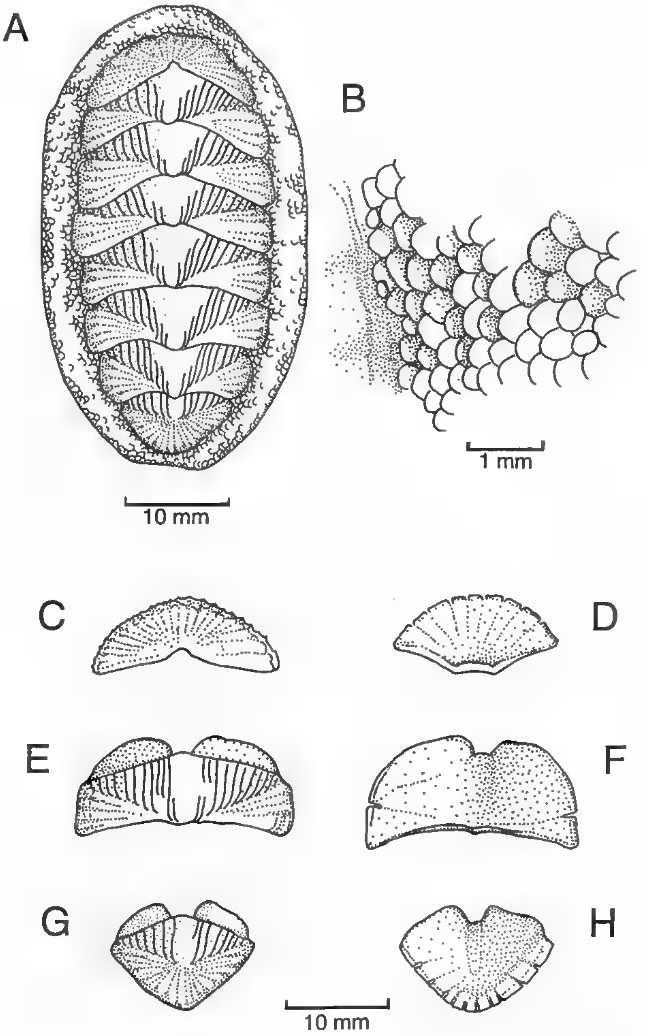


Figure 3.38 Family Chitonidae, subfamily Chitoninae. *Rhyssoplax calliozona*, external appearance. **A**, whole animal, dorsal view; **B**, detail of dorsal surface of girdle; **C**, **D**, head valve; **E**, **F**, intermediate valve; **G**, **H**, tail valve. **C**, **E**, **G**, dorsal view of valves; **D**, **F**, **H**, ventral view of valves. [I. Grant]

Although most chitonines are believed to be free-spawning, the South African *Radsia nigrovirescens* and the New Zealand species, *Chiton (C.) aorangi* and *C. (C.) torri*, brood their young to an advanced stage in the pallial groove (Smith 1966; Creese & O'Neil 1987). In *Sypharochiton pellisserpentis* in eastern Australia, the reproductive cycle is annual. The major spawning period occurs in spring from September to November and minor spawning in autumn from February to April; the reproductive cycles of males and females are closely synchronised. In this species there is a significant bias in the sex ratio to almost 2:1 in favour of males (Sakker 1986). In the Caribbean species, *Chiton (C.) tuberculatus*, individuals become reproductively mature at one year of age. Spawning takes place during the northern autumn, from October to early December and occurs at night, but not in phase with the moon or tides. The eggs are light green in colour and covered with short spines. They hatch within 24 hours, with a free-swimming stage of about three days before settlement and metamorphosis (Lewis 1960; Glynn 1970). The life span of chitonines is unknown, but is at least two years (Glynn 1970). The diploid chromosome number of the European species, *Rhyssoplax olivaceus*, is 26 (Vitturi 1982).

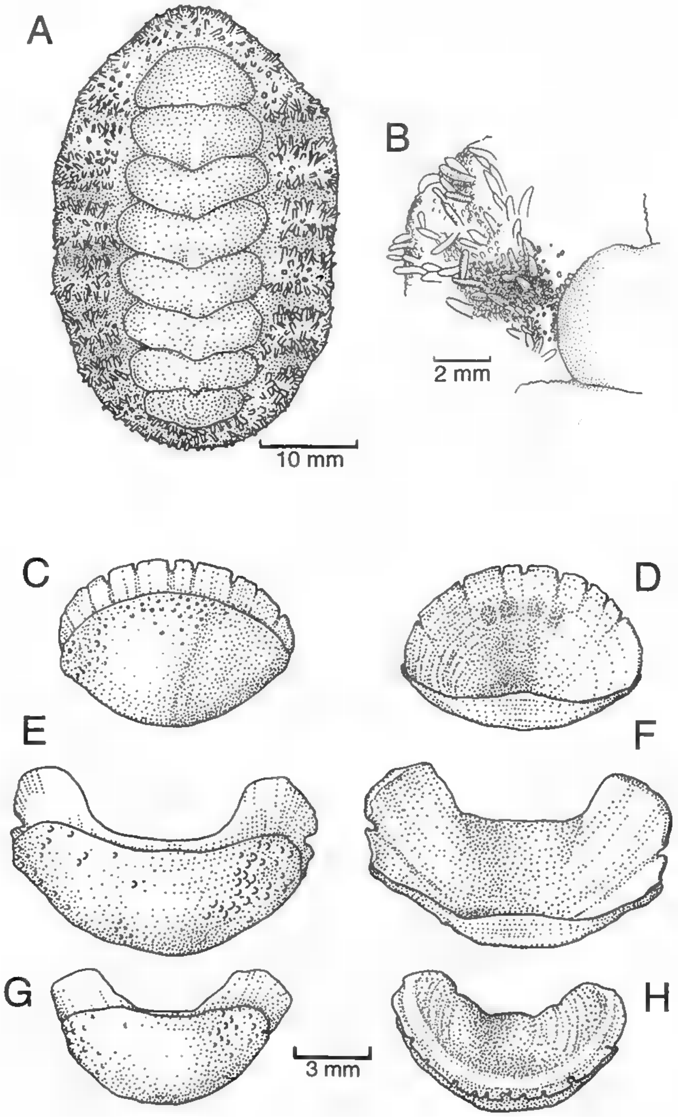


Figure 3.39 Family Chitonidae, subfamily Acanthopleurinae. *Acanthopleura gemmata*, external appearance and valves. **A**, whole animal, dorsal view; **B**, detail of dorsal surface of girdle; **C**, **D**, head valve; **E**, **F**, intermediate valve; **G**, **H**, tail valve. **C**, **E**, **G**, dorsal view of valves; **D**, **F**, **H**, ventral view of valves. [I.Grant]

On the Great Barrier Reef, *Acanthopleura gemmata* spawns at night in phase with the full moon from September to April. The eggs are black in colour and bear a covering of spines (Stephenson 1934). Off Perth, *A. hirtosa* spawns in autumn (Wells & Sellers 1987). In the Caribbean species, *A. granulata*, individuals become reproductively mature at one year of age. Spawning takes place in the northern autumn, from October to December, when the water temperature is at its highest, and occurs at night at the new and full phases of the moon. The eggs are light brown in colour and when laid form a lightly compacted mass held together by the interlocking spines of the outer covering of the eggs. Hatching occurs within 24 hours, releasing a free-swimming stage for one or two days before settlement and metamorphosis (Lewis 1960, Glynn 1970). Spawning in *A. spiniger* occurs in late September and early October in the Red Sea, usually in early evening, and individuals spawn for two to four successive nights. Individual females usually produce 50 000 to 65 000 eggs per night. The eggs are dark green, with a spiny covering and form a loose, dark mass when laid. They hatch about 12 hours after fertilisation, with a free-swimming stage of about four days before settlement and metamorphosis. The tail valve is not formed until 24 days after fertilisation (Soliman & Iskander 1982). The life span of acanthopleurines is unknown, but is at least two years (Glynn 1970; Wells & Sellers 1987). The diploid chromosome number of *Acanthopleura japonica* is 24 (Nakamura 1985).

In eastern Australia, the toniciine *Onithochiton quercinus* spawns annually in spring (October, November) and in late autumn (April, May), and the reproductive cycles of males and females are closely synchronised. In this species, the sex ratio is biased by almost 2:1 in favour of males (Sakker 1986). In New Zealand, brooding females of *O. neglectus* are found in all seasons except winter (June to August). The eggs are brooded for 12–15 days and then released as free-swimming trochophore larvae. Settlement usually occurs within 24 hours of release and is followed rapidly by complete metamorphosis (Creese 1986). The diploid chromosome number of *Onithochiton hirasei*, from Japan, is 24 (Nakamura 1985).

Chitonines are found on and under rocks, dead coral and rubble in shallow water and intertidally, including under rocks embedded in clean sands and on rock under a thin layer of sand. A few species are free-living in very coarse sands and gravel. Intertidally, animals are often in an exposed position. Boyle (1970) showed that the intertidal species *Sypharochiton pellisserpentis*, can decrease the effect of desiccation and conserve energy during exposure by forming aggregations, a behaviour that tends to reduce water loss and lower oxygen requirements (Horn 1982, 1985). This species moves and feeds at night or when submerged, as do most members of the subfamily. The Caribbean species *Chiton (C.) tuberculatus* and *C. (C.) stokesii*, from Panama, are known hosts of the boring mussel *Lithophaga aristata*, which can

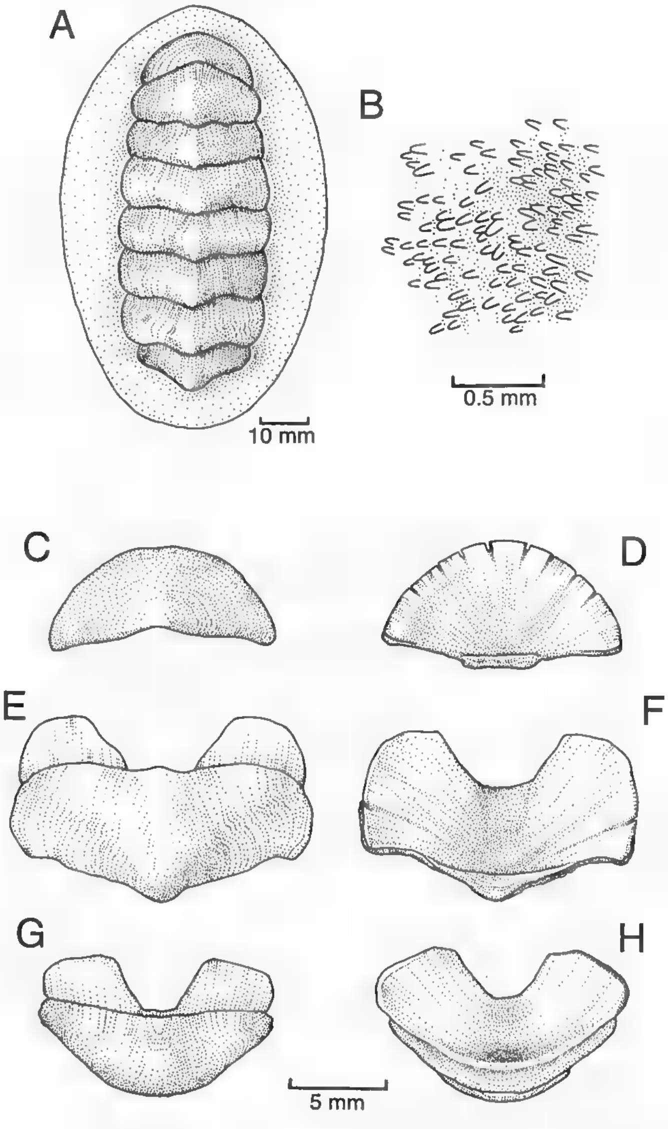


Figure 3.40 Family Chitonidae, subfamily Toniciinae. *Onithochiton quercinus*, external appearance and valves. **A**, whole animal, dorsal view; **B**, detail of dorsal surface of girdle; **C**, **D**, head valve; **E**, **F**, intermediate valve; **G**, **H**, tail valve. **C**, **E**, **G**, dorsal view of valves; **D**, **F**, **H**, ventral view of valves. [I. Grant]

seriously weaken the valves of the chiton (Bullock & Boss 1971). The commensal sphaeromid isopods, *Dynamenella perforata*, *Dynamenopsis dianae* and *Exosphaeroma* species have been recorded from the pallial groove of *C. (C.) tuberculatus* (Glynn 1968).

Acanthopleurine chitons are found on or under rocks in the intertidal zone, and are often exposed at low tide. Many species return to a homesite, which helps to reduce desiccation during exposure between tides (Glynn 1970; Nishihama *et al.* 1986). *Acanthopleura gemmata* in Queensland exhibits complex homing behaviour, and is capable of homing after displacement and after alterations to the substrata, apparently using topographical memory and chemical cues (Thorne 1967, 1968). According to Chelazzi *et al.* (1983), this species actively digs out its homesite with its radula and defends the homesite against intraspecific intruders. A commensal sphaeromid isopod *Dynamenella perforata* has been recorded from the pallial groove of *A. granulata* (Glynn 1968). The subfamily is of no economic importance.

Toniciine chitons live on and under rocks on reefs. *Onithochiton* species are often found in very shallow water and in association with encrusting calcareous red algae. *Tonicia (Lucilina)* species are often found on and under rocks buried in sand.

The generic classification of the subfamily Chitoninae is currently in a state of flux (for example, Bullock 1988b, 1988c); seven genera are recognised at present, among them *Chiton*, with four subgenera. The subfamily is found worldwide in temperate to tropical waters. Six genera are found in Australia; *Mucrosquama* and *Delicatoplax* (which includes only *D. translucens*), are endemic to eastern and southern Australia. *Sypharochiton pellisserpentis* is found only in eastern Australia and New Zealand and *S. funereus* is known only from Norfolk and Lord Howe Islands. *Chiton (Amaurochiton) glaucus*, the only member of the genus and subgenus found in Australia, is restricted to south-eastern Tasmania, where it was accidentally introduced from New Zealand in the early 1900s. The genus *Chiton* is mainly found on the Pacific and Atlantic coasts of the tropical Americas. The two other genera that occur in Australia, *Tegulaplax* and *Rhyssoplax*, both have Indo-Pacific distributions; most of the chitonines found in Australia are species of *Rhyssoplax* (Pls 8.2–8.5). Chitonine species are known from all Australian waters including Norfolk, Lord Howe and Christmas Islands, but records from northern Australia are sparse and isolated, and the tropical fauna of this subfamily may be expanded with further collecting. Most of the southern species are endemic. The subfamily is not known from the Subantarctic islands or Antarctica.

The subfamily Acanthopleurinae comprises the single genus *Acanthopleura*, which is found worldwide in tropical to subtropical areas. Of the 15 species currently recognised in *Acanthopleura*, seven are found in Australia. Three species, *A. spinosa* (Pl. 8.1), *A. gemmata* and *A. miles* are widespread Indo-Pacific species and four species, *A. arenosa*, *A. curtisiana*, *A. gaimardi* and *A. hirtosa*, are endemic to Australia. Acanthopleurines are recorded along all the western, northern and eastern coasts from Recherche Archipelago, Western Australia to Sydney, New South Wales, except the Gulf of Carpentaria, which probably represents a gap in collecting records rather than a genuine distribution gap as there are records from neighbouring waters. Members of this genus are often dominant in the intertidal fauna in tropical areas.

The subfamily Toniciinae comprises two genera, which are found throughout the Indian and Pacific Oceans in temperate and tropical waters and around the southern tip of South America. It is represented in Australia by the genera *Onithochiton* and *Tonicia (Lucilina)*; the nominate subgenus of *Tonicia* is absent from our waters. *Onithochiton quercius*, a common intertidal species, has a disjunct distribution with animals found in New South Wales, Queensland, southern Western Australia and Christmas Island. The southern *O. ashbyi* may prove to be a juvenile of another species, and *O. helenae* from Queensland is currently known from very few specimens. All currently recognised Australian *Onithochiton* species are endemic. The Indo-Pacific species, *Tonicia (Lucilina) fortilirata* and the highly variable *T. (L.) lamellosa* are widespread in tropical and subtropical Australian waters. All other Australian *Tonicia (Lucilina)* will probably prove to be synonymous with one of these two species. This subfamily is recorded from New South Wales north to Cape York, the Darwin area of the Northern Territory, Western Australia and South Australia. The lack of records from the Gulf of Carpentaria and most of the Northern Territory probably represents a lack of collecting effort rather than a genuine distribution gap, as toniciines are recorded from neighbouring areas. The lack of records from Victoria and Tasmania is probably genuine. No species are recorded from Norfolk and Lord Howe Islands or the Subantarctic islands and Antarctica.

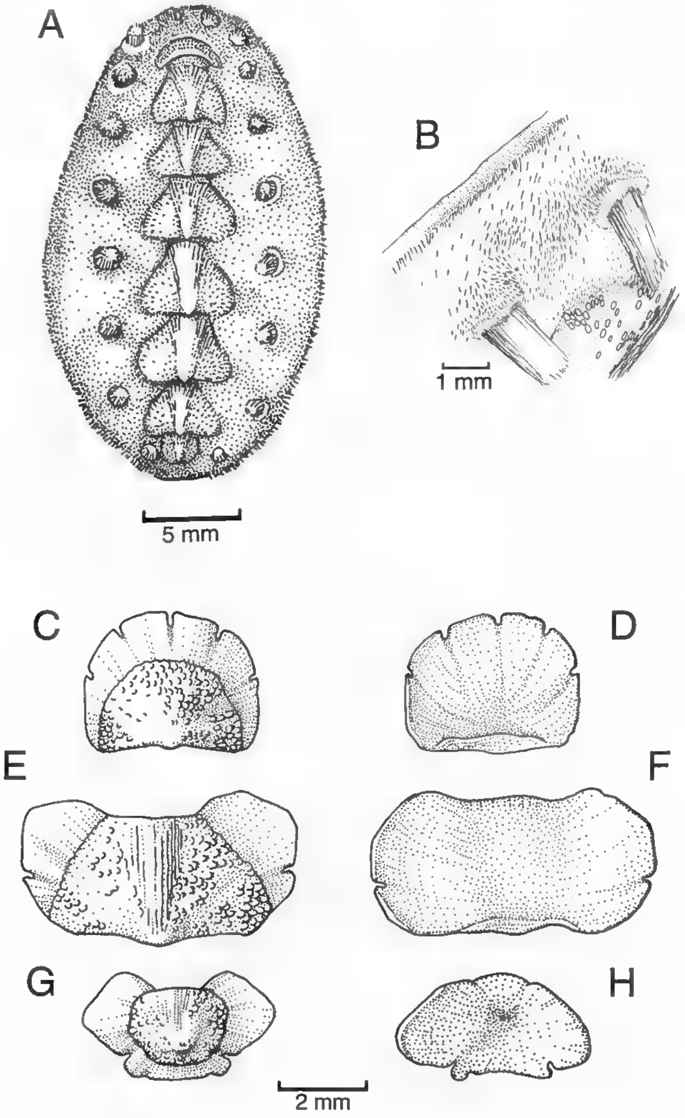


Figure 3.41 Family Acanthochitonidae. *Acanthochitona bednalli*, external appearance and valves. A, whole animal, dorsal view; B, detail of dorsal surface of girdle; C, D, head valve; E, F, intermediate valve; G, H, tail valve. C, E, G, dorsal view of valves; D, F, H, ventral view of valves. [I. Grant]

Fossil chitonines are recorded from the Carboniferous, Jurassic, Cretaceous, Eocene to Pliocene of Australia (Van Belle 1981, 1983). Intermediate valves of species of *Rhyssoplax* are recorded from Miocene beds at Table Cape, Tasmania (Ashby & Torr 1901), and the Pliocene level of a bore at Torrensville, South Australia (Ashby & Cotton 1936). Ashby & Cotton (1939) recorded a single tail valve of a species of the same genus from the Pliocene beds at Muddy Creek, Hamilton, Victoria.

The subfamily Acanthopleurinae is recorded as fossils from the Pleistocene of South America (Van Belle 1983; Ferreira 1986). There are no fossil records of this subfamily from Australia. The erosion of the tegmentum and girdle ornamentation can render identification of *Acanthopleura* specimens to species level very difficult, if not impossible, so effort should be made to collect smaller or more sheltered specimens with their sculpture intact.

Fossil toniciines are recorded from the Eocene, Miocene and Pliocene of Europe, the Miocene of Palau, the Miocene and Pliocene and Pleistocene of the Marshall Islands (Van Belle 1981, 1983). There are no fossil records of this group from Australia. According to O'Neill (1984a) there is considerable variation in morphology between juvenile and adult specimens of the New Zealand species, *Onithochiton neglectus*, which has given rise to a number of synonyms. Caution should be used when identifying juvenile chitons from any species in this subfamily.

Suborder ACANTHOCHITONINA

Chitons of this suborder have insertion plates present on all valves, the insertion plate of the head valve has at most five slits, and the teeth are smooth. The girdle is generally spiculose, never scaly. The tegmentum is often reduced, or occasionally absent.

The suborder comprises the families Acanthochitonidae and Cryptoplacidae.

Key to the families of the suborder Acanthochitonina

1(a) Body elongate oval; insertion plate of head valve mostly with five slits .... Acanthochitonidae
(b) Body vermiform; insertion plate of head valve with three slits, other valves having none ... Cryptoplacidae

Family Acanthochitonidae

The members of this family are small to very large chitons up to 360 mm long, and oval to elongate in shape (Fig. 3.41; Pl. 9.1). The tegmentum is sometimes reduced, and the girdle is fleshy and spiculose. The most recent revision of Australian species is that of Iredale & Hull (1925b, 1927), but Kaas & Van Belle (1980) and Gowlett-Holmes (1990, 1991) provide a more modern generic placement and synonymy of species. The family is divided into two subfamilies. The Acanthochitoninae are a group of small to very large chitons up to 150 mm long, represented worldwide. The Cryptochitoninae are a monotypic subfamily from the northern Pacific Ocean, represented only by *Cryptochiton stelleri*, which reaches 360 mm in length. The generic classification of the Acanthochitoninae is currently in a state of flux, with ten genera recognised at present, nine of which are extant.

In the Acanthochitoninae the valves are small to large, and always articulate (Fig. 3.41). The lateral and pleural areas of the tegmentum are not usually differentiated, and are sometimes reduced. The insertion plates and sutural laminae are well developed. The smooth to spiculose girdle has sutural tufts which are usually prominent. The gills are merobranchial and adanal or abanal. The major lateral teeth of the radula have tridentate caps.

The diploid chromosome numbers of *Acanthochitona communis* and *A. crinita*, both from Europe, and *A. defilippii* from Japan, are 24, 18 and 16, respectively (Kawai 1976; Vitturi 1982; Colombera & Tagliaferri 1983). Little is known of the feeding habits of members of this subfamily. Kangas & Shepherd (1984) recorded that the southern Australian species *Notoplax addenda* (as *N. speciosa*) feeds almost exclusively on sponges; *Cryptoconchus porosus*, of New Zealand, has been noted feeding on egg rings of gastropods, probably those of *Siphonaria* species (Mestayer 1920).

Eggs and sperm are shed directly into the water by *Cryptoconchus porosus* (Brewin 1942). Spawning occurs several times over the period late June to August, showing marked periodicity aligned with the new and full phases of the moon. Both males and females move to a position just below water level, head down, with the posterior region elevated to about 60° to spawn. The eggs are released in long gelatinous strings and are olive green to greenish yellow in colour. Post-spawning development is unknown. In this species, the olive green and orange girdle of males distinguishes them from females, in which the girdle is olive green and brown (Brewin 1942). The life spans of members of this subfamily are unknown.

Acanthochitonines are found on and under rocks, rubble and barnacles on reefs, including rocks embedded in sediments, on pebbles and shells in sands and some species are capable of free-living in coarse sands. *Acanthochitona bednalli* is sometimes found on the lower trunks and pneumatophores of mangroves (Milne 1966). Members of the genus *Notoplax* live in association with sponges upon which they feed, and *N. speciosa, N. addenda* and *N. glauerti* are often found in crypts within sponges. This subfamily is common in shallow waters and in the intertidal zone; some members of the genus *Notoplax* are known to occur deeper than 500 m.

Several species are known to host other invertebrates. One eastern Pacific species, *Acanthochitona hirundiniformis*, is a known host of the boring mussel *Lithophaga spatiosa*, which seriously weakens the valves of the chiton (Watters 1981). The parasitic mite *Halixodes chitonis* is recorded from the gills of the New Zealand species *Cryptochiton porosus* (Brucker 1897; Brucker & Trouessart 1900).

The Acanthochitoninae are recorded worldwide from tropical to polar regions. Members of six of the currently recognised genera *Acanthochitona*, *Notoplax*, *Leptoplax*, *Craspedochiton*, *Craspedoplax* and *Bassethullia* are recorded for Australia. The genus *Bassethullia* which is endemic to southern Australia contains three extant species, *B. glypta*, *B. matthewsi* (Pl. 9.1) and *B. porcina*, and the extinct, *B. propeporcina*. This subfamily has been recorded from all coasts of Australia. Records from northern Australia are few and isolated, but several species have been collected from northern Western Australia in recent years. *Acanthochitona approximans* is recorded from Norfolk and Lord Howe Islands, and *Notoplax leuconota* is recorded from Lord Howe Island. The subfamily is not known from the Subantarctic islands or the Antarctic coast under Australian jurisdiction, or from Christmas Island.

Fossil acanthochitonines are recorded from the Miocene of Africa and the Marshall Islands, the Miocene and Pliocene of Europe and Australia, and the Miocene, Pliocene and Pleistocene of New Zealand (Van Belle 1981, 1983). Intermediate valves of species of *Acanthochitona* have been recorded from the Miocene (Oligocene of Van Belle 1981; Ashby 1925) and Pliocene deposits at Muddy Creek, Victoria, by Ashby (1925) and Ashby & Cotton (1939), and from the Miocene deposits at Mornington, Victoria, by Ashby (1939). Intermediate valves of two species of *Notoplax* were recorded from the Pliocene level of bores at Torrensville and Parafield Gardens, South Australia (Ashby & Cotton 1936; Gowlett-Holmes 1992). The intermediate valves of a second acanthochitonid species from the same level of the latter bore were recorded by Gowlett-Holmes & McHenry (1988a), but its current generic position is uncertain. An intermediate valve of a species of the extinct genus *Afossochiton* was recorded from the Miocene

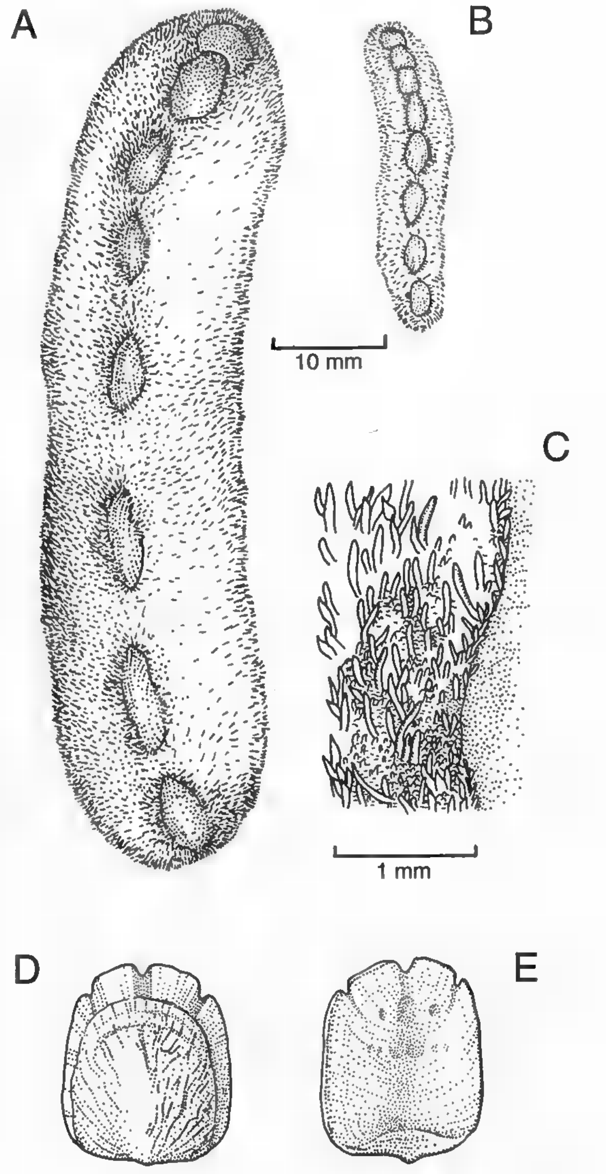


Figure 3.42 Family Cryptoplacidae. *Cryptoplax striata*, external appearance and valves. **A**, whole adult specimen, dorsal view; **B**, whole juvenile specimen, dorsal view, showing the differences in the spacing of the valves; **C**, detail of dorsal surface of girdle; **D**, **E**, head valve; **F**, **G**, intermediate valve; **H**, **I**, tail valve. **D**, **F**, **H**, dorsal view of valves; **E**, **G**, **I**, ventral view of valves. [I. Grant]

(Eocene of Ashby & Torr (1901)) deposits at Mornington, Victoria, by Ashby & Torr (1901). Ashby (1925) and Ashby & Cotton (1939) recorded the head, intermediate and tail valves of several species of the same genus from the Miocene (Oligocene of Ashby 1925) and Pliocene deposits of Muddy Creek, Victoria.

Family Cryptoplacidae

The members of this family are medium-sized to very large chitons up to 150 mm long. They are elongate, and vermiform in shape and have reduced valves with a fleshy and densely spiculose girdle (Fig. 3.42; Pls 9.2, 9.3). The valves are small and articulating in juveniles, but are usually separated in adults, at least posteriorly. The lateral and pleural areas of the tegmentum are not differentiated, and the insertion plates and the sutural laminae are well developed. The girdle has small sutural tufts which are prominent in live animals, but sometimes almost imperceptible in preserved specimens. The gills are merobranchial, and adanal or abanal.

Ashby (1923b) reviewed this family, but his work included a number of misidentifications. The most recent revision of Australian species is that of Iredale & Hull (1925b, 1927). The family contains the single genus *Cryptoplax*.

The southern Australian species, *Cryptoplax striata*, was recorded by Kangas & Shepherd (1984) as an opportunistic grazing omnivore, feeding on encrusting algae, drift seagrass and encrusting sponges. The valve sculpture, aesthete distribution and aesthete canal morphology in the eastern Australian *Cryptoplax mystica* are described by Currie (1989, 1992a). In the same species, unique sensory organs are found in pigmented cavities associated with aesthete canals. These sensory organs may function as photoreceptors or statocysts (Currie 1992b). No other information is available on internal anatomy or reproduction for this family.

These chitons are found in and under rocks, dead coral and rubble, often in holes and narrow crevices from which they rarely venture, on reefs in shallow water and in the intertidal zone. The small valves and the large, very flexible girdle enable individuals to conform themselves to the contours of their substratum.

The Cryptoplacidae are recorded from the tropical and temperate Indian and central western Pacific Oceans and the Red Sea. The widespread Indo-Pacific species *Cryptoplax burrowi* and *C. larvaeformis* are also found in tropical and subtropical Australian waters, the former species is also found on Christmas Island. Three endemic species occur in temperate Australian waters: *C. iredalei* and *C. striata* are widespread in southern Australia, and *C. mystica* is only known from New South Wales. A single endemic species, *C. royana*, is known from Lord Howe Island. Cryptoplacids are known from all Australian waters, except for the Northern Territory and the Gulf of Carpentaria, but since they are recorded from nearby waters, this family is almost certain to be present in these areas. The family is not known from Norfolk Island, the Subantarctic islands or Antarctica.

Fossil *Cryptoplax* are known from the Miocene of Europe, Borneo and Fiji and the Miocene and Pliocene of Australia (Van Belle 1981). Intermediate valves and one head valve of several *Cryptoplax* species have been recorded from the Miocene and Pliocene deposits at Muddy Creek, Victoria (Hall 1905; Ashby & Cotton 1939). Ashby (1940) recorded a head valve of a new species of *Cryptoplax* from the Pliocene level of a bore at Woodville, South Australia.

Measurements of species and characteristics based on preserved specimens of *Cryptoplax* should be used with caution, because these animals are easily distorted on preservation; also their shape and dimensions in life are quite variable. The degree of separation between the valves also varies with age and size, indicating caution in the use of this feature for distinguishing between species. It is preferable to use individuals of similar size for comparisons whenever possible.

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CLASS BIVALVIA

CHAPTER 4

DEFINITION AND GENERAL DESCRIPTION

The Bivalvia is a group of aquatic, typically bilaterally symmetrical, molluscs characterised by a laterally compressed body with an external bivalved shell (Figs 4.1A, 4.4; Pls 5, 10–16.4). Some species, however, such as those cemented by one valve to the substratum (for example, oysters) are not bilaterally symmetrical and a few (for example, *Entovalva* species) have an internal shell. The shell is either wholly or partly calcified and consists of left and right valves (Fig. 4.4). The valves are hinged dorsally, connected by a partially calcified elastic ligament and are held together by adductor muscles (one or two) which attach to their inner surfaces. The valves are opened by the ligament and closed by contraction of the adductor muscles.

Bivalve anatomy, illustrated in Figure 4.1B, diverges considerably from the basic molluscan plan. There is no head and no radula. The mantle lines each valve and in most species is attached some distance from the shell margin. The mantle lobes are joined dorsally and either joined or free ventrally. There is sometimes posterior fusion of the mantle margin to form inhalant and exhalant siphons. The spacious mantle cavity is latero-ventral, with left and right cavities extending upwards on each side of the visceral mass. Most bivalves have a pair of ctenidia suspended laterally in the mantle cavity. The gills may be greatly enlarged, lamellate and plicate.

The mouth and anus are located at opposite ends of the body and the gut is typically convoluted. A pair of ciliated labial palps connect the ctenidia and mouth, and direct food particles into it. The foot is extensible and either elongate or laterally compressed.

The nervous system is simple with fused cerebral and pleural ganglia, and visceral and pedal ganglia. As a head is lacking, there are no cephalic tentacles, but there are sensory tentacles and sometimes light-sensitive eye spots along the edges of the mantle lobes, particularly posteriorly and on the apices of the siphons.

Bivalves are either gonochoristic or consecutive or simultaneous hermaphrodites. Protandric hermaphroditism is common. Larval development is typically planktonic, the larvae being either planktotrophic or lecithotrophic, but direct development is not uncommon.

HISTORY OF DISCOVERY

The presence of arks, mussels, oysters and other bivalved molluscs in coastal middens is evidence that they have been exploited as a food resource in Australia since the earliest days of human colonisation many thousands of years ago (Bailey 1975; Stockton 1978). Like that of the Aborigines, the interest of the early European settlers and explorers in bivalves appears to have been mainly culinary. An early published reference to an Australian bivalve is that by Captain George Vancouver, commander of the ships H.M.S.S. *Discovery* and *Chatham* which passed along the south coast of Australia in 1791. In September and October of that year the ships entered King George Sound, which Vancouver named, and he wrote 'In our way out of the north-eastern harbour the boats grounded on a bank we had not before perceived; this was covered with oysters of a most delicious flavour on which we sumptuously regaled; and loading, in about half an hour, the boats for our friends on board, we commemorated the discovery by calling it Oyster Harbour'.

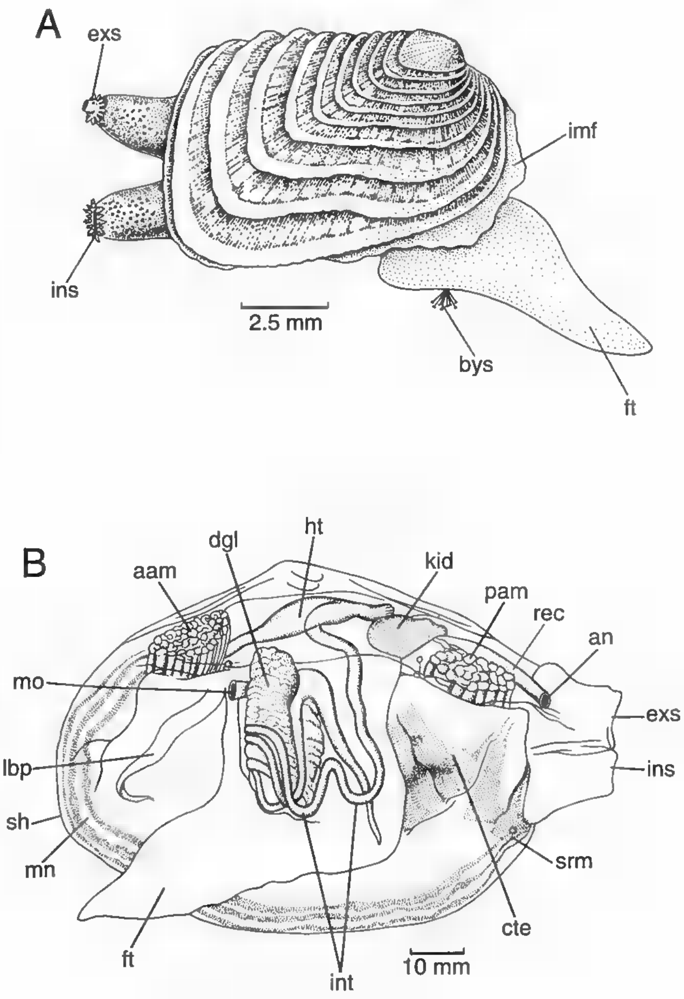

Figure 4.1 Typical bivalve features. A, external appearance: a live *Irus irus* (Veneridae), with foot and siphons extended. B, internal appearance: general anatomy based on the European *Mactra (Mactra) glauca* (Mactridae), left valve and mantle removed. **aam**, anterior adductor muscle; **an**, anus; **bys**, byssus; **cte**, ctenidium; **dgl**, digestive gland; **exs**, exhalant siphon; **ft**, foot; **ht**, heart; **imf**, inner mantle fold; **ins**, inhalant siphon; **int**, intestine; **kid**, kidney; **lbp**, labial palp; **mn**, mantle; **mo**, mouth; **pam**, posterior adductor muscle; **rec**, rectum; **sh**, shell; **srm**, siphonal retractor muscles. (A, after Morton 1985e; B, after Milne-Edwards in Fischer 1880–1887)
[A, R. Plant; B, S. Weidland]

The first scientific study of Australian bivalves began with the French Baudin Expedition of 1801–1803. That expedition's surviving zoologist, François Péron, collected many bivalves and other molluscs, most of them from King George Sound and Shark Bay in Western Australia. Regrettably, Péron did not live to describe his zoological collections although there are references to a few bivalves in his narrative. For example, he mentioned some remarkable shells he collected at Bernier Island (in Shark Bay) and wrote 'Of all the species of mussel known up to the present, one which I discovered is undoubtedly the most beautiful and splendid; deprived of its sea-coating, it reflected all the most vivid colours of the prism and of precious stones; it is radiant, if I may thus express it. I have described it under the name *Mytilus efflugens*'. This species is now known as *Septifer bilocularis*, named in 1758 by Linnaeus from material collected by Rumphius at Ambon.

Péron also described an oyster from Shark Bay, naming it *Ostrea sychophilla* (= *Saccostrea cuccullata*) and, like Vancouver, remarked on its palatability. He wrote 'However curious this oyster may be, its animal nevertheless was extremely delicate, and all opinions agreed in its flavour'.

Although Péron described few of his Australian specimens, much of his material was deposited in the Muséum National d'Histoire Naturelle in Paris and was used extensively by Lamarck in his monographs on invertebrate animals (Lamarck 1815–1822) in which many species and genera of bivalve were named. Lamarck cited the Baudin Expedition localities as 'Baie de Marins' (= Shark Bay), 'Port du George' (= King George Sound) or 'New Holland' (Western Australia).

Following the Baudin voyage at the beginning of the 19th Century, many European scientific expeditions collected bivalves and other molluscs in Australian waters. Notable among these were two more French expeditions, both with the naturalists J.-R.-C. Quoy and J.P. Gaimard aboard. The first was in 1817 under the command of Louis de Freycinet on the ships *Uranie* and *Physicienne* and the second in 1826–1829 on the *Astrolabe*, under the command of M.J. Dumont d'Urville. These expeditions collected extensively along the Australian coast and the published account of the voyages includes descriptions and illustrations of several bivalve species (Quoy & Gaimard 1830–1834).

Meanwhile, the English navigator Phillip Parker King had continued the hydrographic survey of the Australian coast begun by Flinders. With him were the naturalist Allan Cunningham and two officers, Bedwell and Roe, who were ardent shell collectors. They visited the southern and northern coasts of Western Australia during 1818 and the Northern Territory and Kimberley coasts in 1819–1820 on the *Mermaid* and again in 1821–1822 aboard the *Bathurst*. Shells, including some bivalves, collected during these epic voyages were later described by the English zoologist J.E. Gray (1827).

In the 1840s, the Royal Navy began detailed surveys of the Queensland coast with the ships *Fly* and *Rattlesnake*. These voyages resulted in large quantities of shells being collected, most of which found their way into the hands of the English collector Hugh Cuming. Many species from the Cuming collections, including bivalves, were named in journal articles and monographs by English authors such as H. & A. Adams, G.B. Sowerby and Lovell Reeve. Later, in 1874, the British oceanographic research ship *Challenger* spent 10 days in the Torres Strait, dredging in deep water. E.A. Smith (1885) published on the bivalve molluscs of that expedition.

The first local conchologist to publish material on Australian bivalves appears to have been George Angas of the Australian Museum. His writings were published mainly in the *Proceedings of the Zoological Society of London* during the 1860s and 1870s.

Sydney conchologist John Brazier (1874, 1879) described a collection he had made at the Percy Islands, Queensland, in 1871. He was also on the *Chevert* expedition which travelled up the Queensland coast in 1875 and he published a list of more than 600 molluscs, including bivalves, collected by that expedition (Brazier 1877). Although English, American and European scientists continued to describe Australian material, from this time on Australians began describing local species in local journals. Ralph Tate in Adelaide and J.E. Tenison Woods in Tasmania were prolific writers on the molluscs of south-eastern Australia during this period.

Australian Museum conchologist Charles Hedley wrote extensively on eastern Australian molluscs in the early 1900s, including bivalves taken during the *Thetis* Expedition off New South Wales (Hedley 1903) and on collecting expeditions to Mast Head Island (Hedley 1906) and the Hope Islands (Hedley 1909) in Queensland. His work included checklists of the molluscan faunas of Queensland (Hedley 1910), Western Australia (Hedley 1916) and New South Wales (Hedley 1918).

In South Australia, the medical practitioner, Joseph Verco published on southern Australian molluscs, and named many new bivalves in the *Transactions of the Royal Society of South Australia* between 1895 and 1918. Many of his species were based on material he had dredged from deep water. Meanwhile, his contemporary J.H. Gatliff wrote on the molluscs of Victoria in the *Proceedings of the Royal Society of Victoria* from 1907 to 1931. William L. May published illustrated checklists of Tasmanian shells (1921, 1923).

Undoubtedly, the most productive conchologist in the first half of the century, at least in terms of the number of taxa described, was Tom Iredale, Hedley's successor at the Australian Museum. Bibliographies of Iredale's work, including lists of the taxa he introduced, are given by McMichael & Whitley (1956) and Whitley (1972). Among his publications was a major work on bivalves from Queensland, mostly taken during the Great Barrier Reef Expedition (Iredale 1939). A second part of that study was never published, but the manuscript is preserved in the Australian Museum library.

In 1961, a major work devoted exclusively to South Australian bivalves was published by Bernard Cotton of the South Australian Museum. In the following year (1962), Hope Macpherson and Charles Gabriel (1962) of the National Museum of Victoria published a book on Victorian marine molluscs which included an account of the bivalves. Most recently, Kevin Lamprell and Thora Whitehead (1992) produced the first of two volumes on the *Bivalves of Australia* which is the first attempt to describe the marine bivalve fauna of the whole country.

Descriptions of components of the depauperate freshwater bivalve fauna of Australia are scattered through the literature. E.A. Smith (1882) published the first systematic account of the Australian freshwater molluscan fauna, including bivalve material. Iredale (1943) revised and added to the list. Freshwater mussels of Australia have been monographed twice, by Iredale (1934) and by McMichael & Hiscock (1958). B.J. Smith (1992) catalogued and updated the nomenclature of the non-marine bivalve fauna. The ecology and distribution of freshwater mussels in Australia has been described by Walker (1981). Atkins (1979) described the glochidium of *Hyridella drapeta*.

MORPHOLOGY AND PHYSIOLOGY

External Features and Shells

As primarily sedentary or sessile organisms, the Bivalvia have evolved consistent adaptive features that centre on their relative lack of motility. These adaptive features are reflected in the morphology of both the shell and the body.

The shell

In nearly all bivalves the shell protects the animal from the environment and from predators and acts as a site for muscle attachment. This calcium carbonate exoskeleton is composed of either aragonite or calcite or of both mineral morphs, and is

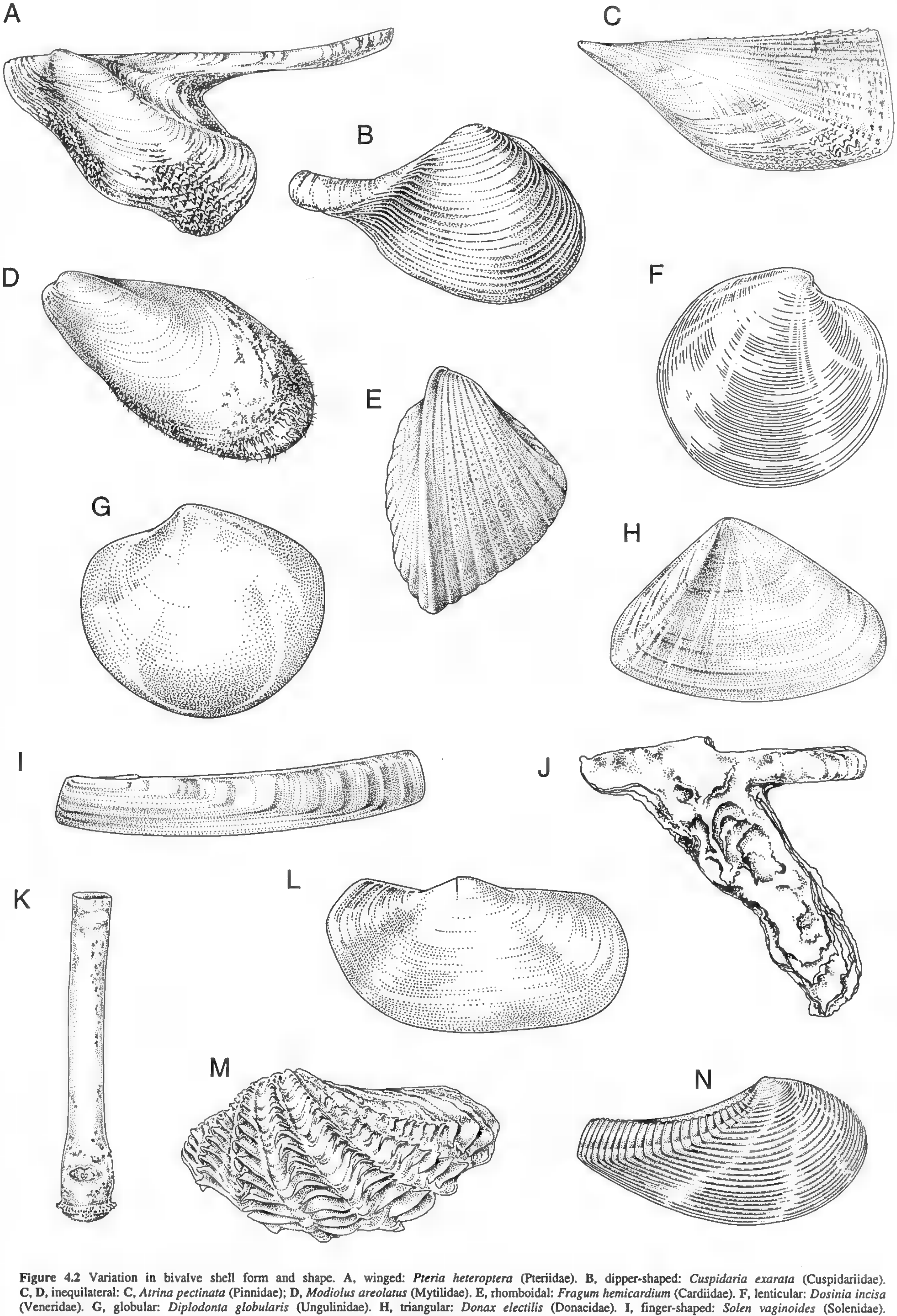

Figure 4.2 Variation in bivalve shell form and shape. A, winged: *Pteria heteroptera* (Pteriidae). B, dipper-shaped: *Cuspidaria exarata* (Cuspidariidae). C, D, inequilateral: C, *Atrina pectinata* (Pinnidae); D, *Modiolus areolatus* (Mytilidae). E, rhomboidal: *Fragum hemicardium* (Cardiidae). F, lenticular: *Dosinia incisa* (Veneridae). G, globular: *Diplodonta globularis* (Ungulinidae). H, triangular: *Donax electilis* (Donacidae). I, finger-shaped: *Solen vaginoides* (Solenidae). J, hammer-shaped: *Malleus meridianus* (Malleidae). K, tubular: *Brechites penis* (Clavagellidae). L, fragile: *Laternula recta* (Laternulidae). M, thick and heavy: *Tridacna maxima* (Tridacnidae). N, hatchet-shaped: *Nuculana ramsayii* (Nuculanidae). [R. Plant]

divided into separate layers (Fig. 4.7). The mineralised shell proper and its organic covering, the periostracum, are secreted by a thin underlying epithelial tissue, the mantle (Fig. 4.8).

Shell form

Bivalve shells are hinged dorsally and gape around the rest of the valve margin when the valves are open. Some species have a permanent posterior gape. The two valves are usually convex so that there is a space between them when they are closed. Each shell valve has a dorsal, beak-like umbo (Fig. 4.4) that represents the oldest part of the shell (the larval shell or prodissoconch). Umbones usually curve and point anteriorly and are termed prosogyrous. Those few bivalves in which the umbones are directed posteriorly are opisthogyrous; those directed perpendicular to the dorsal margin (or pointing directly at each other) are orthogyrous. When right and left valves are of equal size, the shell is equivalve. In some bivalves, such as many pteriomorphs, the valves are of unequal size and shape and are termed inequivalve. Scallops are typically equilateral (as in *Pecten* species) with the umbo located midway between the anteriormost and posteriormost portions of the shell. Conversely, most bivalves are at least somewhat inequilateral (for example, *Modiolus areolatus*, Fig. 4.2D), usually with the posterior region longer than the anterior.

An antero-ventral byssal notch or a ventral depression in the shell margin of some bivalves can indicate the emergence of a byssus by which the animal attaches itself to or in the substratum. Sexual dimorphism in shell form is rare in bivalves, but occurs in some unionids and carditids.

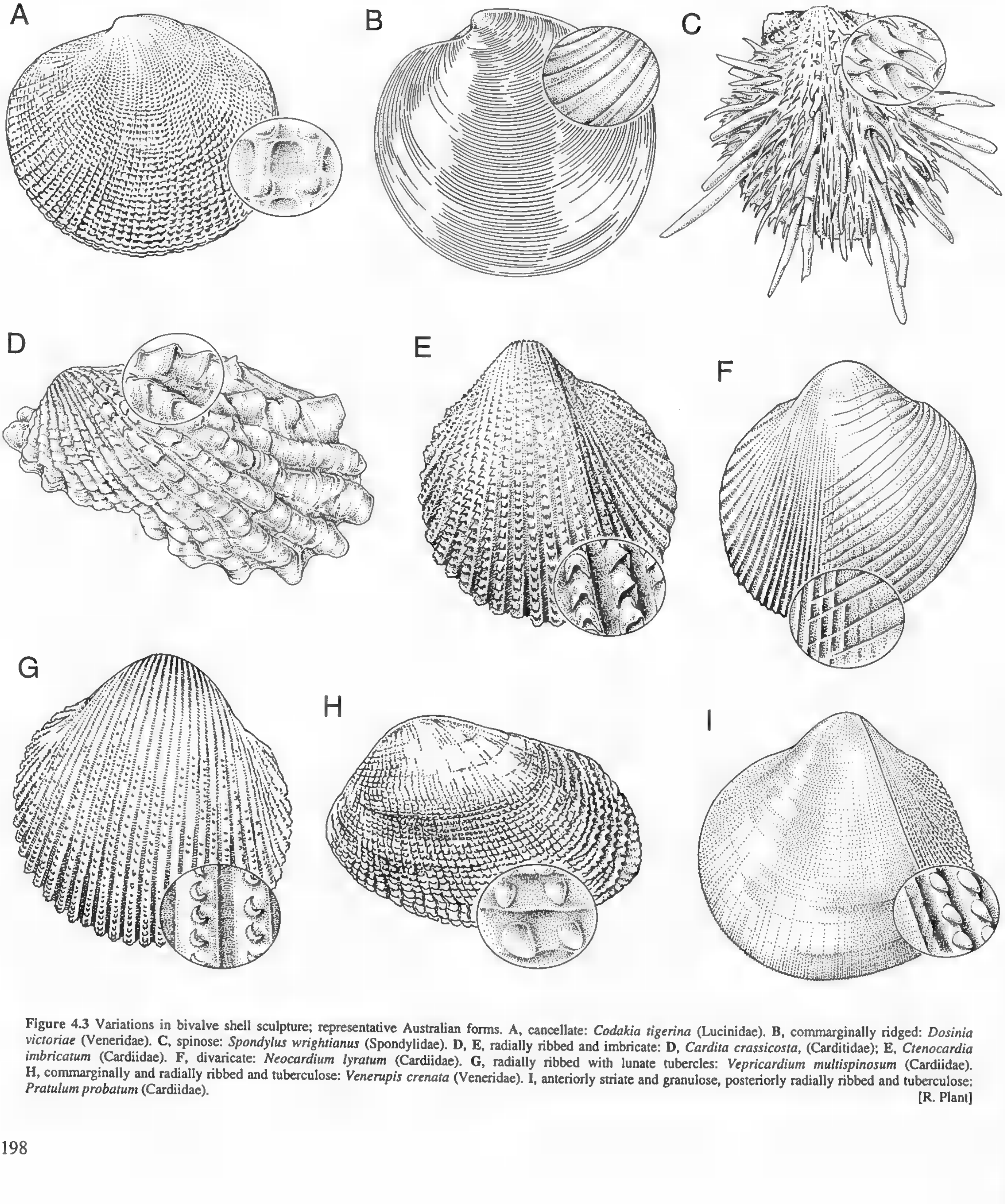

Figure 4.3 Variations in bivalve shell sculpture; representative Australian forms. **A**, cancellate: *Codakia tigerina* (Lucinidae). **B**, commarginally ridged: *Dosinia victoriae* (Veneridae). **C**, spinose: *Spondylus wrightianus* (Spondylidae). **D**, **E**, radially ribbed and imbricate: **D**, *Cardita crassicosta*, (Carditidae); **E**, *Ctenocardia imbricatum* (Cardiidae). **F**, divaricate: *Neocardium lyratum* (Cardiidae). **G**, radially ribbed with lunate tubercles: *Vepricardium multispinosum* (Cardiidae). **H**, commarginally and radially ribbed and tuberculose: *Venerupis crenata* (Veneridae). **I**, anteriorly striate and granulose, posteriorly radially ribbed and tuberculose: *Pratulum probatum* (Cardiidae).
[R. Plant]

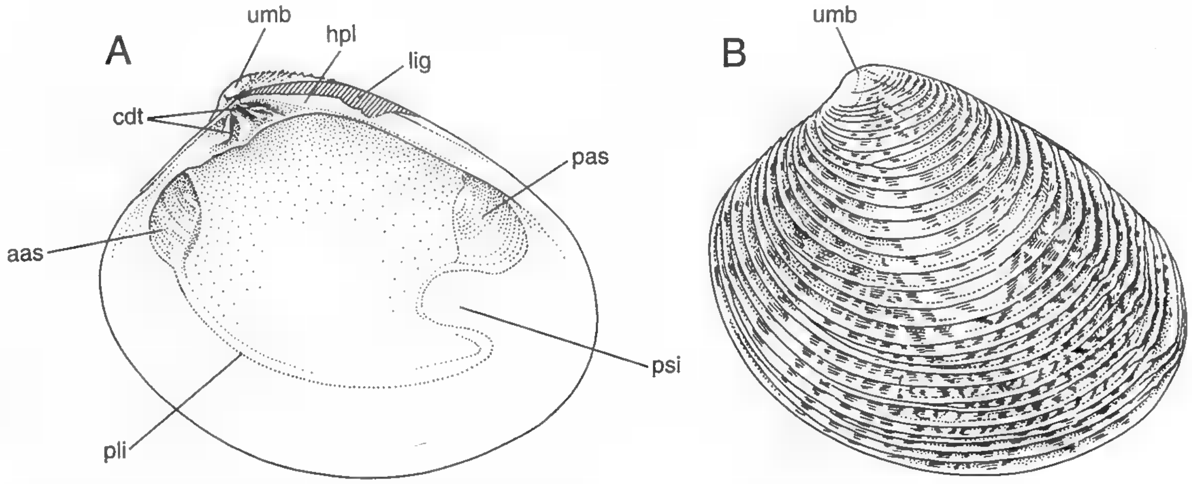

Figure 4.4 Bivalve shell morphology. *Katylesia scalarina* (Veneridae), equivalve, inequilateral shell: **A**, right valve interior; **B**, left valve exterior. **aas**, anterior adductor muscle scar; **cdt**, cardinal teeth; **hpl**, hinge plate; **lig**, ligament; **pas**, posterior adductor muscle scar; **pli**, pallial line; **psi**, pallial sinus; **umb**, umbo. [R. Plant]

Bivalve shells can be thick and heavy (*Tridacna maxima*, Fig. 4.2M) or thin and fragile (*Laternula recta*, Fig. 4.2L); strongly triangular (*Donax electilis*, Fig. 4.2H), globular (*Diplodonta globularis*, Fig. 4.2G), lenticular (*Dosinia incisa*, Fig. 4.2F), hatchet-shaped (*Nuculana ramsayii*, Fig. 4.2N), hammer-shaped (*Malleus meridianus*, Fig. 4.2J), finger-shaped (*Solen vaginoides*, Fig. 4.2I), minute and incorporated into a larger calcareous tube (*Brechites penis*, Fig. 4.2K), dipper-shaped (*Cuspidaria exarata*, Fig. 4.2B) or essentially reduced to small plates at the front end of an elongate tubular body (*Teredo navalis*). Some bivalve shells are highly irregular in form and vulnerable to environmental modification (for example, *Saccostrea cucculata*).

Shells range in size from the small *Condylocardia limaeformis*, measuring about 1 mm long, to the giant clam *Tridacna gigas*, which grows to over 1 m long and can weigh over 400 kg.

Beyond variation in general shell form, shell sculpture varies (Fig. 4.3) such that the valves may be covered with heavy and sometimes sharp calcareous spines (*Spondylus wrightianus*, Fig. 4.3G), short and small radially arranged granules (*Poromya illevis*), strong commarginal lamellae (*Callanaitis disjecta*) or radial ribs or both (*Venerupis crenata*, Fig. 4.3H), or raised fluted scales (*Cardita crassicostata*, Fig. 4.3D). Some have a coat of filamentous periostracal strands (for example, *Trichomya hirsutus*).

Shells of bivalves can be informative of the type of habitat they live (or lived) in and whether there have been short or long term environmental perturbations. Such intraspecific variation and diversity is well documented and manifests as macrostructural variations in external appearance. For example, among the ostreids, individuals that grow in fast-moving waters have shells that are thin and elongate whereas those in slow-moving waters are short and rounded. Ortmann (1920) documented the strong correlation between environment and shell shape in freshwater unionids. Variation in shell shape has been documented for *Alathyria jacksoni*, a hyriid of south-eastern Australian rivers (Balla & Walker 1991). In these freshwater mussels, the change in shell shape again appears to be related to water velocity (see also Chapter 1 Molluscs of Inland Waters and Fig. 1.67). Balla & Walker (1991) related the change in shell morphology to the stabilisation efficiency of this infaunal bivalve. Little, however, is known of the functional significance of environmentally induced shell variation.

Muscle scars

The shell interior may be marked by various scars that indicate the positions of muscle attachments (Fig. 4.4A). In particular, adductor muscle scars, either anterior and posterior or central (as in some pteriomorphs) reveal the size and location of these muscles. Terms used in description of the musculature of the body are also used to describe the muscle scars. When the anterior and posterior adductor muscles and their scars are of approximately equal size the shell is said to be isomyarian (= homomyarian) (Fig. 4.10A). When they are significantly unequal the shell is heteromyarian (= anisomyarian) (Fig. 4.11). When there is only one adductor, *i.e.* the anterior adductor is lacking, the shell is monomyarian.

The pallial line is a thin incised scar representing the attachment for the mantle retractor muscles. In siphonate bivalves, there is typically a posterior sinus in the pallial line where siphonal retractor muscles attach (Fig. 4.4A). The depth and width of the pallial sinus indicates the size of the siphons and so the depth to which the bivalve can burrow into the substratum. Other scars, such as byssal protractor and retractor muscle scars, may also be present and provide evidence of the musculature and life style of the bivalve.

Ligament

Although the hinge teeth effectively prevent misalignment of the valves, the elastic ligament, with adductors relaxed, abducts the valves (Fig. 4.5). The ligament is thus involved with opening the valves to allow water flow and all concomitant functions. Additionally, Trueman (1964) suggested that the ligament allows the valves to stabilise the shell in its burrow by pushing the valves against the surrounding sediment.

Like hinge dentition, the ligament has been utilised in taxonomic and phylogenetic studies of the Bivalvia (Figs 4.5, 4.6, 4.10, 4.11). The ligament frequently has two components, an internal fibrous and an external nonfibrous or lamellar ligament. Ligament position and structure is variable among the Bivalvia and a number of descriptive terms are in use. Ligaments that extend both anterior and posterior of the umbones, placing them in a central position, are said to be amphidetic. Ligaments located posterior to the umbones are called opisthodetic (Fig. 4.4A). An alivincular ligament is flat and located between the umbones with the nonfibrous layer extending beyond the margins of the internal fibrous layer or resilifer, as in ostreids. Ligaments that are parivincular, as in some tellinids, are cylindrical and stand proud of the posterior dorsal margin of the hinge line.

Yonge (1978a) suggested that the amphidetic ligament form may be the most primitive among living bivalves. The ancestral ligament would have been two-layered, but covered additionally by an external periostracal layer. These three layers would thus correspond to the primitive three-layered condition of the shell, that is, periostracum plus outer and inner mineralised shell layers. However, Waller (1978) has shown that the non-fibrous, outer ligament is not hypertrophied periostracum. Based on an extensive survey of all Recent bivalve families and the extensive palaeontological interpretations of Pojeta (1978) and Runnegar (1983), Waller (1990) concluded that the primitive ligament was opisthodetic.

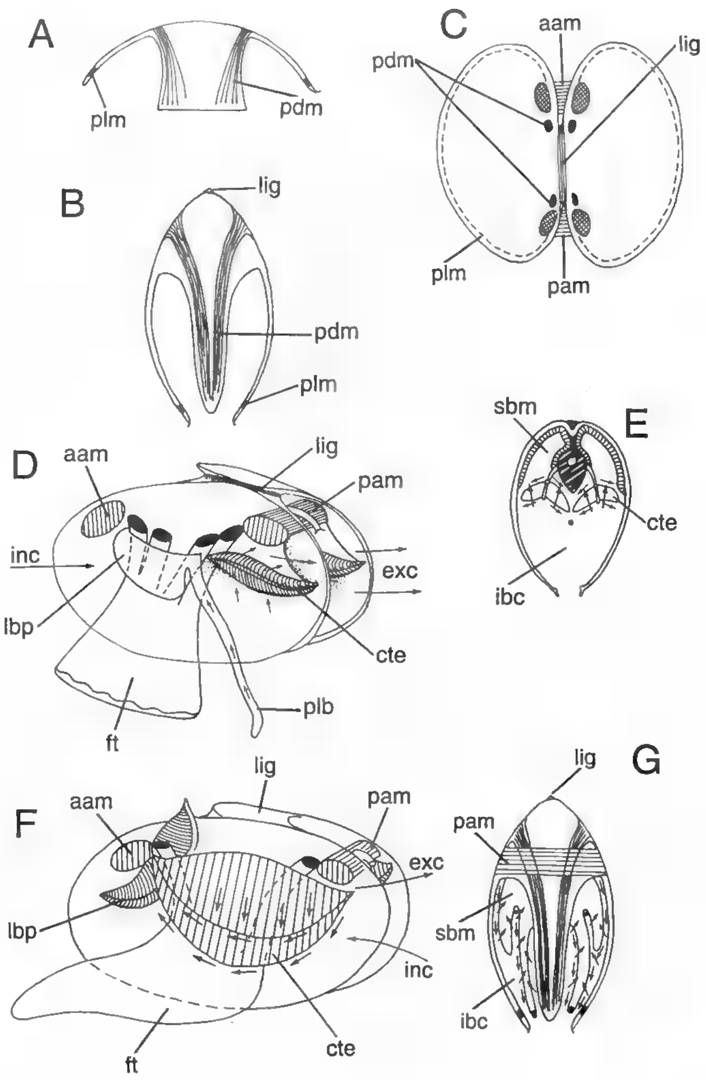

Figure 4.5 Evolution in bivalve form. **A**, **B**, before and after lateral compression and the development of the ligament. **C**, after compression, viewed from above showing the cross-fusion of pallial muscles at each end to form the adductors. **D**, **E**, schematic representations of a protobranch bivalve: **D**, left side; **E**, transverse section through the ctenidia. **F**, **G**, schematic representations of a lamellibranch bivalve: **F**, left side; **G**, transverse section through the ctenidia. **aam**, anterior adductor muscle; **cte**, ctenidium; **exc**, exhalant current; **ft**, foot; **ibc**, infrabranchial chamber; **inc**, inhalant current; **lbp**, labial palp; **lig**, ligament; **pam**, posterior adductor muscle; **plb**, palp proboscis; **plm**, pallial muscles; **pdm**, pedal retractor muscle; **sbm**, suprabranchial chamber. Arrows indicate direction of ciliary currents. (A–C, after Allen 1985; D, E, after Morton, J.E. & Yonge 1964; F, G, after various sources) [B. Morton]

The ligament may be partially calcified, often with fine aragonitic needles supporting the polymerised organic structure (tanned glycoprotein) (Gregoire 1972; Marsh, Hamilton & Saas 1978).

The ligament may sit in a hollowed out depression in the hinge plate known as the resilifer, located internally just beneath the umbo. A spoon-shaped, projecting resilifer (for example in the mactrids) is termed a chondrophore. This structure has been found to show tidal and seasonal growth lines in *Mya arenaria* (Cerrato, Wallace & Lightfoot 1991) and, when present, could prove a useful tool in assessing life histories. The ligament may have an associated lithodesma, a small calcareous plate or ossicle. In shells of the Anomalodesmata, a lithodesma effectively divides the ligament into two compressive units assuring adequate abductive thrust of an otherwise wide ligament (Yonge & Morton 1980; Prezant & Carriker 1983).

Hinge dentition

The inner dorsal region of bivalve shells may contain a hinge plate bearing teeth, with corresponding sockets on the opposite valve, that prevent misalignment of the valves upon closure (Fig. 4.6). Dentition varies from absent, that is edentulous as in some Anomalodesmata, to heavily toothed (as in some Heterodonta). The hinge is considered to be conservative and its characters are used extensively in taxonomic and phylogenetic studies of the class. Bivalve hinge dentition can be categorised according to the size, form and position of the teeth.

Nuculoids and arcoids have taxodont dentition with numerous straight, or chevron-shaped teeth, arranged regularly in a row along the hinge plate (Fig. 4.6F, G). A triangular resilifer often forms a gap or recess at the centre of the hinge (below the umbo) between the anterior and posterior series of taxodont teeth. Usually the teeth are oblique, not perpendicular to the dorsal margin. The taxodont hinge type arose early in the evolution of the Bivalvia, apparently twice. The primary taxodont hinge of the nuculoids is sometimes referred to as ctenodont. Evolution of a taxodont hinge in the Arcoidea is believed to be a secondary development and the arcoid hinge is referred to as pseudoctenodont.

Another type of hinge dentition, actinodont, is seen in some early Palaeozoic fossil bivalves. The teeth radiate from the umbones, the outer ones being longer and lying close to the dorsal shell margin.

Pachydont hinge dentition is found only in the extinct hippuritid bivalves: the teeth correspond in position to the cardinals of heterodontids but they are large, massive and usually rounded.

Some mytilids, among the pteriomorphs, have a dysodont dentition with a few small, simple and seemingly ineffective teeth below the terminal or subterminal umbones (Fig. 4.6H).

Large, subequal teeth symmetrically placed on each side of a central ligament pit form an isodont dentition, as in the Placunidae, Spondylidae and Plicatulidae (Fig. 4.6I).

The large subclass Heterodonta takes its name from its characteristic heterodont hinge dentition (Fig. 4.6C–E) with inclined cardinal or central teeth below the umbo and usually with elongate lateral teeth on each side. The cardinal teeth are perpendicular to the hinge plate. The details of this arrangement are varied among the diverse species in the group. Typically, there are either two or three cardinals, one or two anterior laterals and one or two posterior laterals in each valve, but some of these teeth may be reduced or lacking. Lateral teeth are lacking in representatives of some heterodont families. When present, posterior laterals lie behind the ligament. In many species one of the cardinal teeth in each valve is bifid.

Schizodont dentition is a term of questionable taxonomic value (see Cox 1969). It was introduced for the type of dentition seen in representatives of the Trigonioidea in which there are a few strong teeth radiating from below the umbones, the central tooth of the left valve being broad and bifid (Fig. 4.6A). However, some bivalve taxonomists now regard this condition as merely a variation on the heterodont hinge type.

Members of the Myoida have desmodont dentition in which the teeth are either reduced or absent and accessory ridges may replace the teeth along the hinge line.

There have been several attempts to provide notation systems and formulae to describe heterodont hinge dentition. Steinmann (1903) designated each tooth with a numeral and each socket by a 0, so that a formula could be given for each valve indicating either the presence or absence of teeth. This system does not distinguish between cardinals and laterals, or between prominent and rudimentary teeth. A system proposed by Dall (1913) labelled lateral teeth separately, added a symbol for the resilifer, and recorded rudimentary teeth in parentheses. Neither the Steinmann nor the Dall version has been widely used by bivalve taxonomists. Boyd & Newell (1969), however, proposed a modified version which they applied to the Crassatelloidea.

Bernard (1895, 1896a, 1896b, 1896c, 1898) and Munier-Chalmas (1895) devised a hinge notation formula based on observations of the ontogenetic development of heterodont teeth. Hinge teeth develop from lamellae on the hinge of post-larval shells. There are usually two anterior lamellae in the right valve, and a single anterior lamella in the left valve fitting between them. Another lamella may be developed as a marginal rim on the left valve. These anterior lamellae give rise to the anterior lateral teeth and the cardinal teeth. Similar posterior lamellae may be present that can give rise to posterior lateral teeth. The post-larval lamellae are designated by Roman numerals. Numbering from the ventral side upwards, those of the right valve are designated I and III (and sometimes V). Those of the left valve are designated II and IV (and sometimes VI).

The distal parts of the lamellae form the lateral teeth which are labelled A for the anterior laterals and P for the posterior laterals. Thus, when the full series of laterals is present in the right valve they are designated as AI, AIII, PI and PIII. The left laterals are designated AII, AIV, P II and P IV.

Cardinal teeth develop from the proximal ends of the anterior lamellae as swellings which eventually detach. They are designated by Arabic numerals corresponding to the Roman numerals designating the lamellae from which they are formed. Lamella I in the right valve forms only a single cardinal which is designated as 1, but Lamella III may bend to form two cardinals designated as 3a and 3b. Similarly, the proximal ends of Lamellae II and IV of the left valve may each form two cardinals which are designated as 2a and 2b, and 4a and 4b.

The teeth of the right valve have odd numbers and those of the left valve have even numbers. The formula for a whole bivalve shell is given with the numbers for each valve in series, beginning at the anterior end, one above the other, separated by a line. The numbers for cardinal teeth are positioned opposite a space on the other side of the line representing the corresponding socket of the other valve. If any tooth is rudimentary, it is given in brackets. The hinge formula of a hypothetical shell with all possible teeth present but with the posterior laterals rudimentary would be given as follows:

Right valve: AI AIII 1 3a 3b (PI) (PIII)

Left valve: AII AIV 2a 2b 4a 4b (PII) (PIV)

Such a shell with a complete suite of possible teeth does not exist. In particular, the full suite of cardinal teeth is never developed.

On the basis of ontogenetic studies, Bernard distinguished two main types of heterodont dentition, although there are many variations of both types. The lucinoid type has only two cardinal teeth in each valve, numbered 3a and 3b (right valve) and 2 and 4b (left valve). This dentition type is found in the Lucinoidea, Cardioidea, Carditoidea and Crassatelloidea. In the corbiculoidean (= cyrenoid) type there are usually three cardinal teeth in each valve, numbered 3a, 1 and 3b (right valve), and 2a, 2b and 4b (left valve). (Note that Lamella III of the right valve bends over the cardinal formed from Lamella I which occupies the position immediately below the umbo. This type of dentition is seen in the Corbiculoidea and Veneroidea; Fig. 4.6C).

It is not possible to determine the correct hinge formulae for the majority of bivalves because the ontogenetic origins of the teeth seen in adult shells are rarely known. Boyd & Newell (1969) have disputed the homologies of the cardinal teeth designated by Bernard. Nevertheless, when the ontogenetic development of the hinge teeth is known and homologies can be established the formulae may be useful in taxonomic and phylogenetic studies.

The periostracum

The organic periostracum covers the exterior of bivalve shells. It may be thick, as in arcoids and some mytiloids, or thin, as in ostreids. The periostracum may inhibit calcareous shell dissolution in acidic waters, inhibit settlement of fouling organisms, act as a template for shell deposition, enclose the mantle cavity, stabilise the bivalve in shifting sediments, and confer camouflage and defence (Kennedy, Taylor & Hall 1969; Bottjer & Carter 1980). Periostracal structures are categorised by Bottjer & Carter (1980) by their irregular surfaces, homogeneous and patterned structures, adventitious structures, and vacuolation.

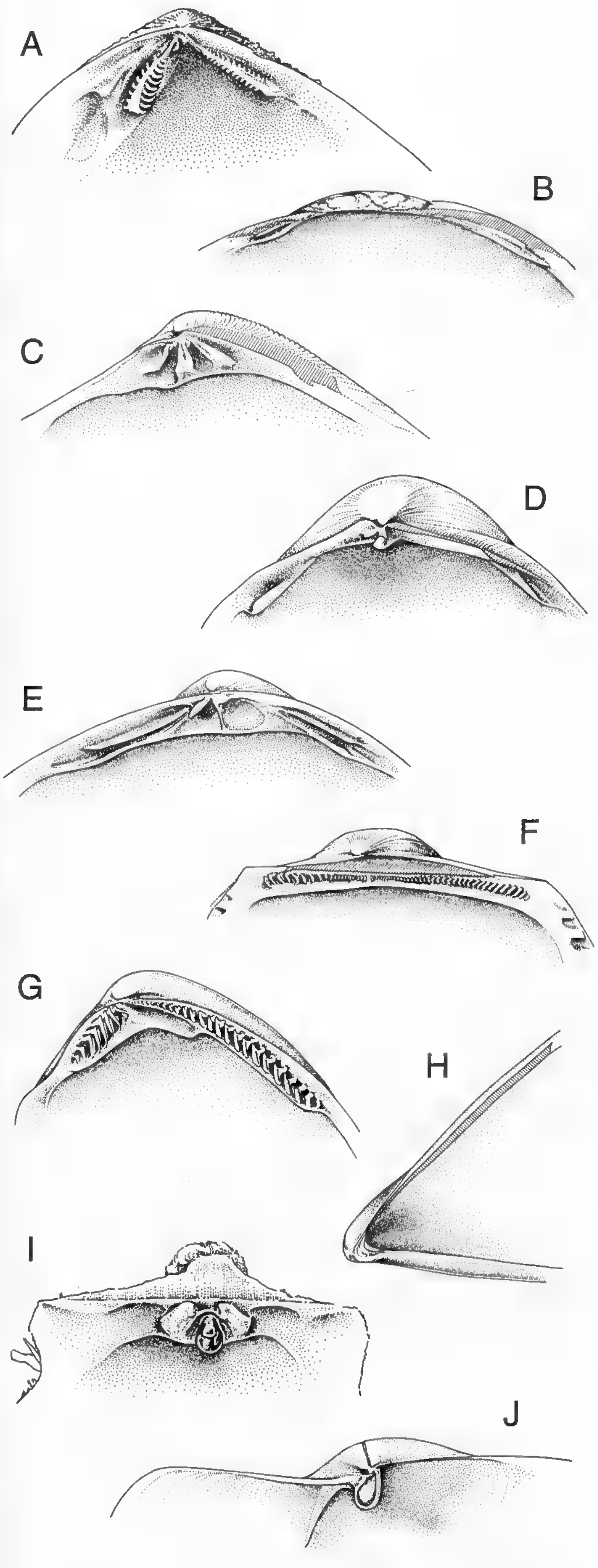

Figure 4.6 Bivalve hinge plates show important variation that can be used in phylogenetic and taxonomic studies. These hinges represent a variety of tooth systems found in heterodont bivalves. **A**, **B**, schizodont: **A**, *Neotrigonia margaritacea* (Trigoniidae); **B**, *Velesunio ambiguus* (Hyriidae). **C**–**E**, heterodont: **C**, *Katylesia scalarina* (Veneridae); **D**, *Fulvia* sp. (Cardiidae); **E**, *Mactra eximia* (Mactridae). **F**, **G**, taxodont: **F**, *Andara crebricostata* (Arcidae); **G**, *Nucula superba* (Nuculidae). **H**, dysodont: *Mytilus planulatus* (Mytilidae). **I**, isodont: *Spondylus wrightianus* (Spondylidae). **J**, desmodont: *Laternula constricta* (Laternulidae). [R. Plant]

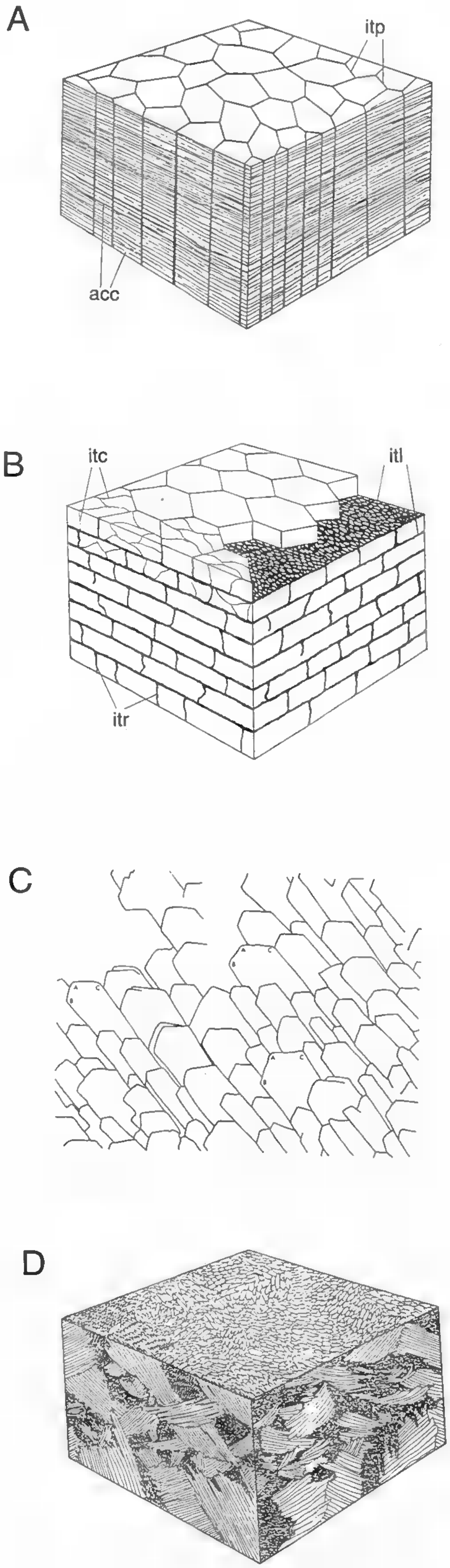

Figure 4.7 Bivalve shell microstructure variation. **A**, prismatic layer from an ostreid bivalve. **B**, nacreous layers in a lyonsiid; the tablets can accrue as sheet nacre or lenticular nacre. **C**, foliated calcite layer in an ostreid. **D**, complex crossed-lamellar layer in a corbiculid. **acc**, accretion lines; **itc**, intracrystalline organic matrix; **itl**, interlamellar organic matrix; **itp**, interprismatic conchiolin walls; **itr**, intercrystalline organic matrix. (A, C, after Carriker, Palmer & Prezant 1980; B, after Prezant 1981; D, after Prezant & Tan Tiu 1986) [R. Plant]

Shell composition and microstructure

The molluscan shell is composed of a calcium carbonate mineral component either deposited on or embedded within an organic matrix. The latter, comprising less than 10% of any shell, is composed mainly of glycoproteins. Aragonite and calcite form various microstructural layers in the Bivalvia. Because shell microstructure offers such a wealth of information on molluscan evolution, ecology and behaviour, and because shells offer ideal models for biomineralisation and calcification studies, we have available a large resource of published information on the fine structure of the bivalve exoskeleton (for a recent and extensive listing, see Carter 1990). Although external shell form can be modified environmentally, shell microstructure is more conservative.

Microstructurally, the bivalve shell has undergone significant radiation. Definitions, distributions within bivalve taxa, and representative micrographs of bivalve shell microstructural types are given in Carter (1990). The most primitive shell type, found in many palaeotaxodonts and palaeoheterodonts, has a prismato-nacreous microstructure. In this shell type (Fig. 4.7A), a prismatic layer composed of either calcitic or aragonitic prisms of variable thickness underlies the periostracum. This, in turn, is underlain by a nacreous or mother-of-pearl layer that forms the inner shell surface. The prisms, often polygonal in cross section, are arranged perpendicular to the shell surface and the flat nacreous tablets lie in the same plane as the shell surface. Various types of prismatic layers can be discerned including simple, fibrous, composite and spherulitic prismatic layers. These are outlined by Watabe (1988). A specialised simple prismatic layer, the myostracum, forms the distinct shell structure involved in muscle attachment. As such, myostracum underlies most muscle attachment areas of the shell and is revealed surficially as the muscle scars of the shell interior surface.

The nacreous layer, always of aragonite, forms the lustrous, iridescent inner surface of many mollusc shells and is of similar composition to pearl. Nacre may be deposited as either polygonal or round tablets that merge with growth within and upon the organic matrix (Fig. 4.7B). Variations in nacre formation are also outlined in Watabe (1988). Nacre is typical not only of the primitive palaeotaxodonts, but also occurs in many pteriomorphs, palaeoheterodonts, anomalodesmatans, and some heterodonts (for example, the Hiatelloidea) (see Uozumi & Suzuki 1981). Most typically, nacre grows as thin, flat sheets (sheet nacre), tall pyramidal columns (columnar nacre), or elongate stacked tablets (row stack nacre), although Prezant (1981) described 'ring nacre', in which newly forming nacreous tablets grow along the margins of mature tablets in some Anomalodesmata.

In many Pteriomorphia, a foliated calcite layer is present that is composed of flat, elongate laths or blades that resemble roofing shingles (Fig. 4.7C; Watabe, Sharp & Wilburn 1958). Most heterodonts, and thus most bivalves, have shells with some crossed-lamellar microstructure (for example, Fig. 4.7D). Again, there are variations on the theme of rectangular lamellae, rods, or blades, interdigitating or crossing each other. Small third order lamellae, essentially elongate crystals, compose the larger second order lamellae, which in turn compose the still larger first order lamellae. The latter, often rectangular in form, are deposited parallel with the shell surface. Many pteriomorphs have first order lamels arranged either concentric to or parallel to the shell edge with alternating blocks arranged obliquely to each other. Complex crossed-lamellar microstructures can have first order lamellae arranged in cones that lie perpendicular to the shell surface. A spiral crossed-lamellar structure has been described for the freshwater heterodont *Corbicula* (Prezant & Tan Tiu 1986) and may be present in other taxa. Most heterodonts have a complex crossed-lamellar layer, often found below a foliated calcitic layer.

Small spherules of aragonite may compose a distinct homogeneous layer, found in the Protobranchia, some Heterodonta and some Anomalodesmata. A homogeneous layer *sensu stricto* is composed of small spherules whereas a granular homogeneous

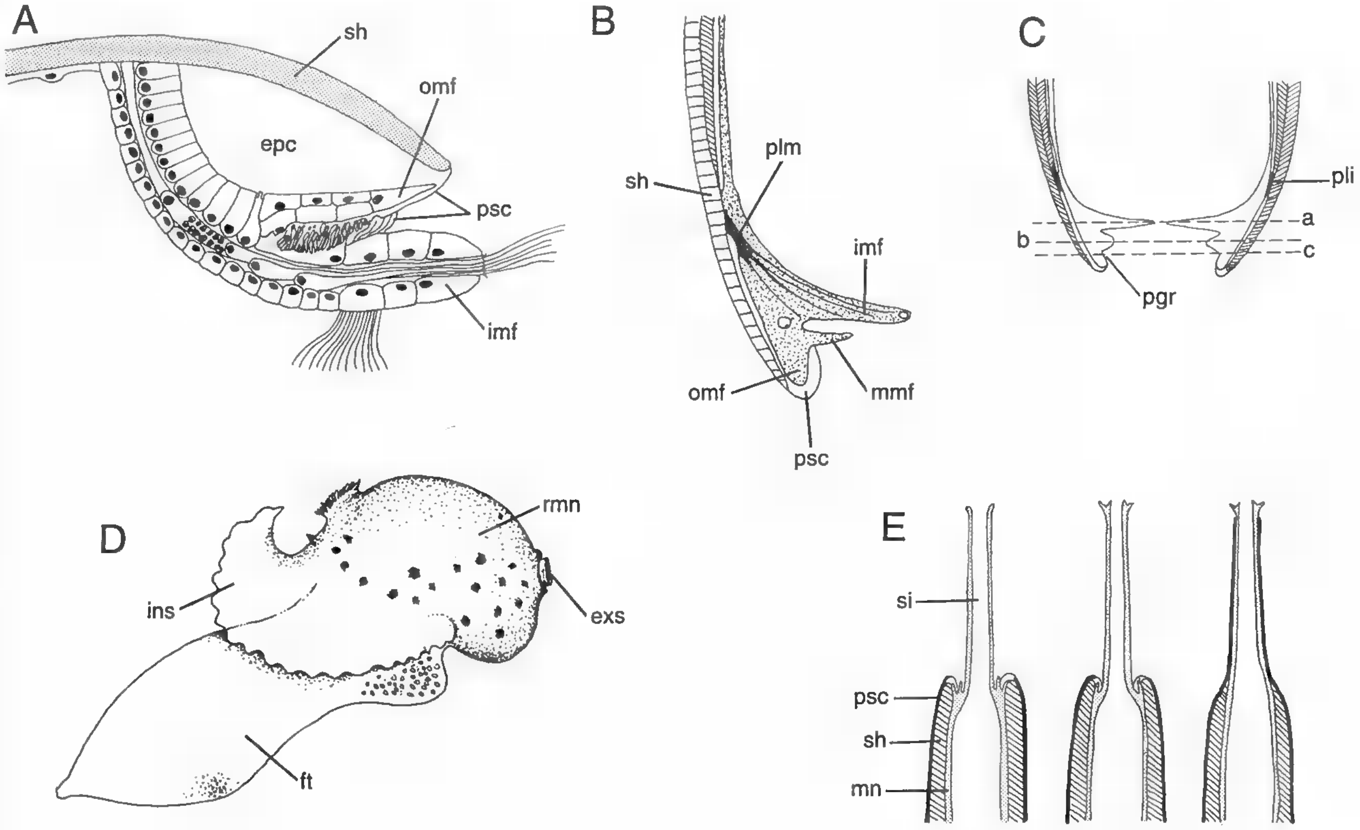

Figure 4.8 The bivalve mantle. **A**, a transverse section through the mantle margin of the pediveliger of *Ostrea edulis* (Ostreidae); note the absence of a middle mantle fold. **B**, a transverse section through the adult bivalve mantle margin showing the basic features and three folds of the mantle. **C**, the mantle margins of a typical bivalve showing the possibility for left and right union of inner folds (a), inner surface of middle fold (b) and outer surface of middle fold (c). **D**, *Chlamydoconcha orcutti* (Chlamydoconchidae) with the mantle reflected, enclosing a much reduced shell. **E**, diagrammatic cross sections of mantle and shell showing the three basic siphonal types in the Bivalvia; from left to right, fusion progressively involves inner folds (Type A); inner surface of middle folds (Type B); outer surface of middle folds and thus periostracal grooves (Type C). **epc**, extra-pallial cavity; **exs**, exhalant siphon; **ft**, foot; **imf**, inner mantle fold; **ins**, inhalant siphon; **mmf**, middle mantle fold; **mn**, mantle; **omf**, outer mantle fold; **pgr**, periostracal groove; **pli**, pallial line; **plm**, pallial retractor muscle; **psc**, periostracum; **rmn**, reflected mantle; **sh**, shell; **si**, siphon. (A, after Waller 1981; B, E, after various sources; C, after Yonge 1957; D, after Morton 1981b) [B. Morton]

layer is composed of larger granules. Larval shells, composed of prodissoconchs I and II, are always aragonitic and often appear homogeneous in microstructure.

Some accessory shell layers are also evident. Hamilton (1969) described the mosaicostracum, a thin calcareous layer that could bind the periostracum to the prismatic or outer shell layer in pteriomorphs (Carriker 1979) and other bivalves. Carriker & Palmer (1979) described the ligostracum as another thin calcified layer that binds the ligament to the shell.

Although shell microstructure is conservative for the most part, there are reports of significant alterations in basic microstructural form induced by environmental shifts (see Tan Tiu & Prezant 1987, 1989a; Prezant, Tan Tiu & Chalermwat 1988 for reports on *Corbicula* and *Geukensia*). A general discussion can be found in Carter (1980).

Colour pigments and pigmentation

On first sight most bivalves appear rather bland in terms of colouration. There are, however, numerous remarkably coloured bivalves that may also have radiating, chevron, or zigzag patterns. The pectinids, in particular, often show bright red, yellow and orange colouration. These are porphyrin based pigments that are probably loosely bound in the shell and are readily soluble in acid (Nuttall 1969). Not all pigments are so easily dispersed. Some are bound tightly in the organic matrix of the shell. The purple pigment that can be found in the internal shell layer of corbiculids and venerids cannot be extracted through the use of acids or organic solvents. Pigment in molluscan shells, if not serving an obvious defensive function as camouflage (which would be unlikely for infaunal bivalves), is assumed to be a metabolic waste product stored within the shell (Comfort 1951), but there is little published information on this.

Mantle and Body Cavities

The true bivalve coelom comprises little more than the pericardium containing the median ventricle and lateral auricles which receive blood from the efferent vessels of the ctenidia. A pair of coelomoducts (renal organs or kidneys) open into the pericardium by renopericardial ducts and externally into the suprabranchial chamber by way of renal ducts. Closely associated with these are the single or paired ducts from the gonads. The rest of the body cavity is a haemocoel formed by the enlargement of venous blood spaces.

The shell valves and underlying mantle (Fig. 4.8), however, enclose a mantle cavity that bathes the body in a fluid approximating the external medium. Extensive mantle fusion, particularly in deeply burrowing taxa, more effectively separates pallial fluids from the external environment, water exchange being limited to the pedal gape anteriorly and the two siphonal orifices posteriorly. Mantle cavity and body cavities are therefore separate, the former protectively facilitating respiratory gas exchange and suspension-feeding, the latter, of reduced dimensions and comprising coelom and a bathing haemocoel.

The greatly enlarged and enveloping bivalve mantle cavity is divided by the ctenidia into lower (infrabranchial) and upper (suprabranchial) chambers, thereby separating incurrent (inhalant) from excurrent (exhalant) flows (Fig. 4.5D–G). Water and contained filterable food enters the inhalant aperture to the infrabranchial chamber. It passes through the ctenidia where material is filtered from it. The supernatant water is expelled from the suprabranchial chamber via the exhalant aperture.

Dorsally, the mantle secretes the ligament uniting the two valves (Fig. 4.5B, C). Elsewhere, however, the left and right mantle lobes are either free or united to varying degrees, more clearly delineating apertures of the mantle cavity. Each mantle lobe marginally comprises inner (muscular), middle (sensory) and outer (secretory) folds (Fig. 4.8A–C; Yonge 1957, 1982). The latter secretes shell (outer surface) and periostracum (inner surface).

The most primitive condition is where mantle lobes are not fused (except dorsally). Such a condition is best seen in members of the Arcoidea and in *Neotrigonia* (Trigonioidea) where separation of the exhalant from the inhalant siphon and the inhalant siphon from the pedal gape is effected by simple apposition of the mantle margins (Morton 1987a).

In other groups, fusion of the lobes physically separates and defines the orifices identified above. The simplest fusion is of the inner folds (Type A). More complex fusions involve the inner (Type B) and outer (Type C) surfaces of the middle folds and the inner surfaces of the outer folds (Type D) (Yonge 1982). Such specialised fusions have some phylogenetic value in that they broadly characterise each subclass. Functionally, the fusions make the processes of feeding and burrowing more efficient and extensive fusions are more typical of deep-burrowing groups. A fourth pallial aperture between the inhalant siphon and the pedal gape is found in members of the Solenoidea, Mactroidea and some representatives of the Anomalodesmata (Yonge 1948; Morton 1981a). The three basic siphonal types are illustrated in Figure 4.8E.

Primitively, water entered the mantle cavity anteriorly and posteriorly, but was always discharged posteriorly, confining the animals to the sediment surface. Extant bivalves of this form are the nuculoids and arcoids, although the condition also persists in a few heterodonts, for example, in the Lucinoidea and Galeommatoidea. Restriction of the inhalant stream to the posterior, to lie alongside the exhalant stream, removed the requirement for surface-dwelling, allowed deep-burrowing and eventually the colonisation of hard surfaces. This latter lifestyle is also associated with the retention of the larval byssus into adulthood (Yonge 1962) and with the progressive evolution of the bivalve ctenidium and extent of pallial fusions (Stanley 1970).

Musculature and Locomotion

The bivalved shell is primitively equivalve and dimyarian, that is the valves are cross-connected by two adductor muscles located antero-dorsally and postero-dorsally (Fig. 4.9B). Terms relating to the relative sizes of the muscle scars on the inner surfaces of the shell valves, as described in an earlier section, are also used for the musculature itself (Fig. 4.9A, B).

The adductor muscles close the shell valves, typically sealing the margins; when they relax, the elastic primary ligament opens the valves. The opening thrust of the ligament is therefore antagonistically regulated by the muscles, permitting variation in the degree of opening and closure and the speed with which such processes occur. Each adductor muscle is divided into two components – slow and quick. The slow component, comprising smooth muscle fibres, is responsible for the sustained, economical, closure of the valves. The quick muscle, comprising striated muscle fibres, is responsible for the rapid phasic adductions that effect larger changes in mantle cavity volume and thus the pumping of water into and out of the mantle cavity.

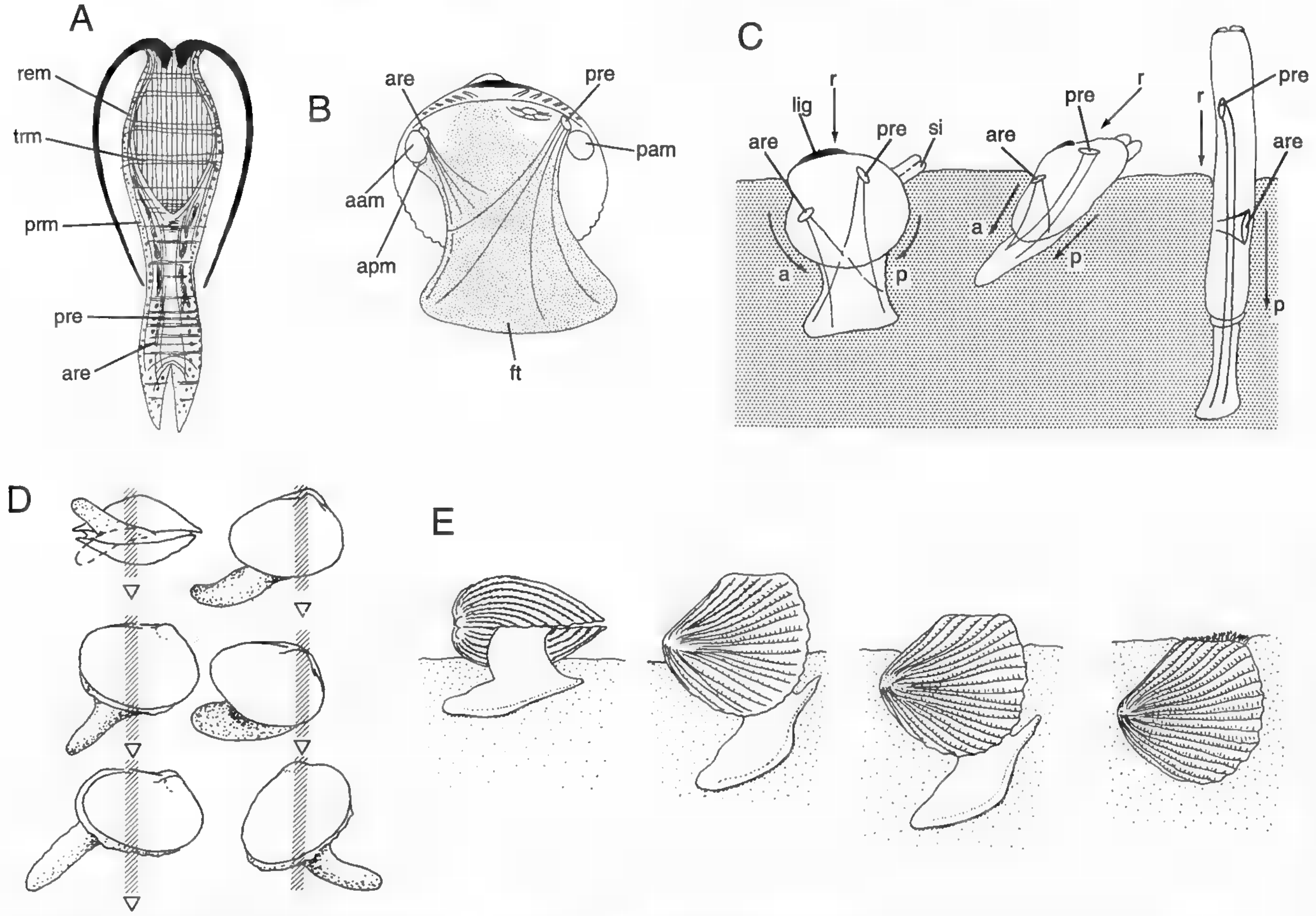

Figure 4.9 Burrowing in bivalves. **A, B**, generalised diagrams of a bivalve to show the principal musculature used in digging: **A**, transverse section; **B**, lateral view. **C**, a comparison of burrowing in species of *Mercenaria* (Veneridae), *Donax* (Donacidae) and *Ensis* (Pharidae), showing in each the left valve, ligament, siphons, and anterior and posterior retractor muscles. Movement brought about by these (a, and p, respectively) and with the resultant direction (R) of movement of the shell into the sand is indicated. **D**, stages in the surface locomotion of a leptonid bivalve: the foot is extended (left sequence of 3) and the shell then pulled forward (right sequence of 3). **E**, four stage sequence of burrowing in *Neotrigonia gemma* (Trigoniidae). **aam**, anterior adductor muscle; **apm**, anterior protractor muscle; **are**, anterior retractor muscle; **ft**, foot; **lig**, ligament; **pam**, posterior adductor muscle; **pre**, posterior retractor muscle; **prm**, protractor muscle; **rem**, retractor muscle; **si**, siphons; **trm**, transverse muscles. (A–C, E, after various sources; D, after Gage 1968)

[B. Morton]

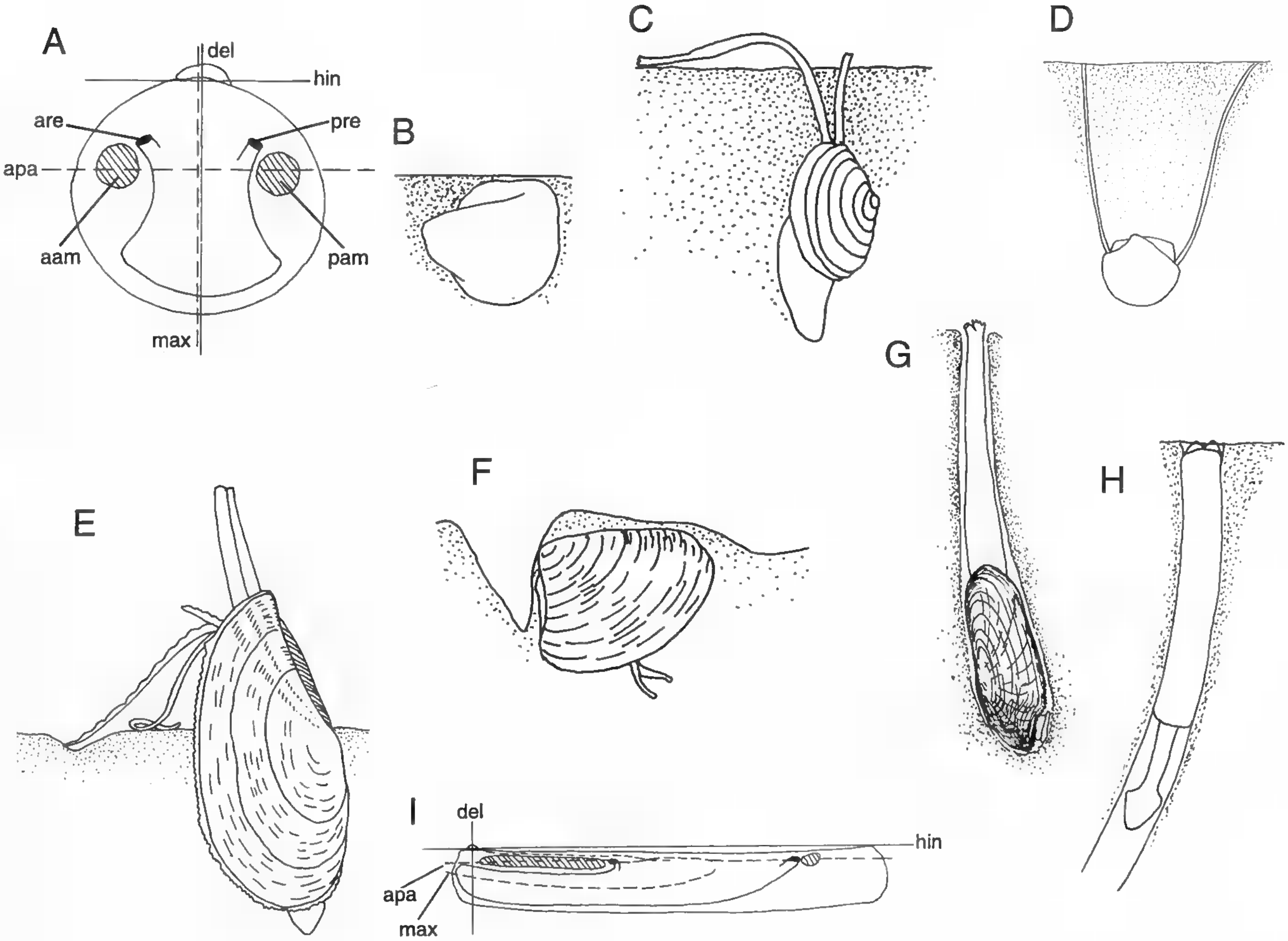

Figure 4.10 The relationship between bivalve body and shell as indicated by the anterior-posterior and median axes of the body and the hinge and demarcation lines of the mantle/shell. **A–G**, isomyarian (= homomyarian): **A**, generalised condition; **B**, *Americardia*; **C**, *Tellina* (Tellinidae); **D**, *Phacoides* (Lucinidae); **E**, *Yoldia* (Yoldiidae); **F**, *Nucula* (Nuculidae); **G**, *Barnea* (Pholadidae). **H**, **I**, posteriorly elongate bivalve: **H**, generalised condition; **I**, *Ensis* (Pharidae). **aam**, anterior adductor muscle; **apa**, anterior-posterior axis; **are**, anterior retractor muscle; **del**, demarcation line of the mantle/shell; **hin**, hinge line; **max**, median axis of the body and the hinge; **pam**, posterior adductor muscle; **pre**, posterior retractor muscle. (A, I, after Allen 1985; B, H, after various sources; C–G, after Cox 1969) [B. Morton]

A number of variations upon this basic theme occur and are of phylogenetic importance, although convergence in form has resulted in some lineages having essentially similar body plans and thus musculature. The simplest modification is the reduction of the anterior adductor relative to the posterior adductor (anisomyarian). The most characteristic and numerous anteriorly anisomyarian bivalves, not only in Australia but elsewhere, are members of the Mytiloidea, for example, *Xenostrobus* (Wilson 1967), although other groups in which this arrangement occurs are the Trapeziidae (*Fluviolanatus*) (Morton 1982a), Cyamioidea (Ponder 1971) and Dreissenoidea (Yonge & Campbell 1968). There are only one or two examples of anisomyarian bivalves with a reduced posterior adductor, for example, *Chlamydoconcha orcutti* from the west coast of North America (Morton 1981b), and Australian representatives of the Clavagelloidea, for example, *Brechites* (Morton 1984a).

Yonge (1962) has demonstrated that the assumption of the anisomyarian form results from the paedomorphic retention of the larval byssus into adult life, permitting colonisation of hard substrata, typically in river estuaries and on rocky shores. With anterior reduction, there is concomitant posterior enlargement so that a triangular shell form developed, typically also ventrally flattened, is created permitting stability on ecologically more dynamic habitats. The ultimate consequence of anterior reduction is loss of the anterior adductor to create a monomyarian form. In such a situation, the posterior muscle is enlarged yet further and during ontogeny migrates to occupy a more central position between the valves. This process is also related in phylogeny to the retention of the byssus, and the subsequent reorganisation of the body around the posterior adductor, permitting residence within narrow crevices as in members of the Isognomonidae. The shell valves also assume a more circular form. Examples of monomyarian bivalves are: members of the Anomioidea (Yonge 1977) which, unusually, are byssally attached through a notch in the lower valve; the Ostreidae, Chamidae and Cleidothaeridae (Yonge 1979) all cemented by the cup-shaped lower valve; the Pectinoidea, some of which are cemented, for example *Hemipecten forbesianus* (Yonge 1981), whereas others are mobile swimmers, for example, *Amusium pleuronectes* (Morton 1980a) or are bysally attached.

The bivalve foot is extended by the pumping of blood into its capacious haemocoel. Its fine movements are regulated not only by blood volume, but also by the interactive contractions of the various components of the pedal musculature. Surrounding the haemocoel are concentric rings of circular, oblique and longitudinal muscle fibres that direct pedal extension and permit mobility.

In typical burrowing, isomyarian bivalves (Fig. 4.10A–G), a series of other muscles is responsible for movement of the foot (Fig. 4.9). These muscles always include, internal to each adductor, anterior and posterior pedal retractors. In some lineages, notably the superfamilies of the Protobranchia and diverse superfamilies of other groups, for example, Unionoidea, Trigonioidea and Arcoidea, there are also posterior pedal elevators and protractors. Each set of paired muscles attaches to the shell and sends fibres down into the foot. They are responsible for the contraction of the foot within the mantle cavity and also for locomotion.

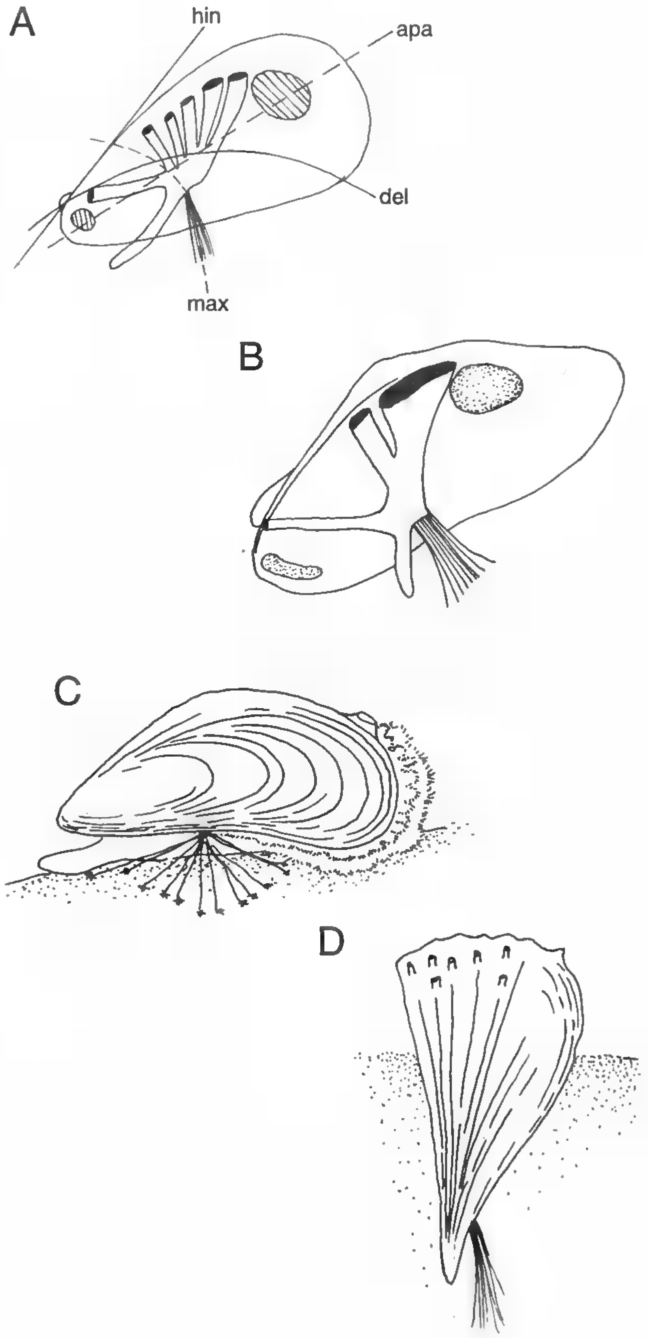

Figure **4.11** Bivalve body form, continued. Heteromyarian bivalves: A, generalised condition; B, *Modiolus* (Mytilidae); C, *Mytilus* (Mytilidae); D, *Pinna* (Pinnidae). **apa**, anterior-posterior axis; **del**, demarcation line of the mantle/shell; **hin**, hinge line; **max**, median axis of the body and the hinge. (A, after Allen 1985; B–D, after Cox 1969) [B. Morton]

The mantle margin unites with the inner surface of the shell along the pallial line by attachment of the left and right pallial retractor muscles. From this point the pallial retractors radiate into the mantle edges and, acting antagonistically with the haemocoelic blood, are responsible for mantle expansion and retraction. Members of the Tellinoidea are characterised by a cruciform muscle in the mantle margin, anterior to the base of the inhalant siphon (Fig. 8.26; Frenkiel 1979).

The posteriorly directed siphons, when present, are of varying length according to habit. The siphons are retracted by enlarged pallial retractors, now termed siphonal retractors. The size of these retractors varies according to siphon length. Their point of attachment is marked by the pallial sinus. For burrowing bivalves, the extent of the sinus gives an indication of the depth in the sediment at which the animal lives (Fig. 4.10C–E, G). In surface-dwelling species, with no need for long siphons, the sinus is either short or absent.

Unlike most other molluscan groups, the Bivalvia is characterised by a typically inanimate life style, residence within the substratum obviating the need for wide-ranging movements. Except for cemented forms, all bivalves can move, although it is likely that the passive, suspension-feeding, life style only rarely necessitates this. For the majority, locomotion is by the single, medially aligned foot, but involves the coordinated actions of most of the musculature (Fig. 4.9).

In burrowing groups, locomotion is downwards when protection is required. If the animal is somehow removed from its burrow, re-burrowing is necessary, and a well-defined sequence of events is followed (Fig. 4.9C, E). The foot is greatly extended from between the parted shell valves. Taking a grip on the substratum, typically by dilation of the tip, the pedal retractors pull the shell downwards. This is typically also correlated with a sharp adduction of the shell valves, forcing mantle fluids out of the pedal gape and thereby helping to fluidise the surrounding sediment so that movement through it is made more efficient.

An approximately similar situation is seen in the epibyssate Mytiloidea. If the mussel requires a change of position or is dislodged, the attaching byssal threads are broken and shed. The foot again extends forwards but secures itself to the substratum by a plantar surface. Pedal retraction, aided by adduction, creates lift and pulls the bivalve forward. Surface locomotion of this kind, irrespective of eventual adult form and habitat, is essential for the post-metamorphosed juvenile seeking a site suitable for adult occupation. The stages in locomotion at the sediment surface by a leptonid bivalve are shown in Figure 4.9D.

So effective are the burrowing activities of some bivalve species, for example, species of *Solemya* (Reid 1980) and *Solen* (Stanley 1970), that when removed from the sediment they swim, although this is probably of no value to the animal in its natural habitat. Other reported swimmers are species of *Lima*, which typically live enmeshed in a loose byssal nest inside a deep coral or rock crevice. Disturbed, such animals may dramatically adduct the shell valves, row with their long tentacles (Fig. 4.24C) and by directing a jet of mantle fluids, make jerky swimming movements (Gilmour 1967).

Free-living members of the monomyarian Pectinoidea, however, can and do swim. In these bivalves, the enlarged, centrally located, posterior adductor muscle, with a large quick component, can rapidly and frequently adduct to force water out of the mantle cavity in a form of jet propulsion. The mantle margin is developed into a muscular curtain or velum which permits escape of the water at only two points, in front of and behind the shell auricles. The powerfully produced jets of water effect lift from the sediment and, once the animal is water-borne, provide the propulsive force to keep it moving in a forward direction, although the animal is actually swimming backwards. In less specialised scallops, for example, species of *Chlamys*, swimming is inefficient, jerky and triggered only by contact with a predator. In *Amusium*, however, the shell is highly modified to form an aerofoil, with a smooth friction-alleviating external shell surface (but with internal ribbing for strength). In such a bivalve, swimming events cover long distances and there is the suggestion (Morton 1980a) with some supporting evidence, that swimming may be part of seasonally regulated breeding movements.

Feeding and Digestion

Within the Bivalvia, the mechanisms of feeding and digestion are relatively consistent, with some variations reflecting the adaptive radiations within the class (see Figs 4.12–4.14).

The primitive bivalve was almost certainly a deposit-feeder and in the extant representatives of the Nuculoida, this method of feeding is still employed. The leaf-like ctenidia principally serve a respiratory function and feeding is by palp proboscides that collect surface detritus for transport to the mouth (Fig. 4.10E). In the Solemyidae, direct absorption occurs, the gut being reduced to minute proportions in some species and absent in others (Reid 1980).

Similarly, the more primitive representatives of other groups, for example, the Galeommatoidea, feed on detritus and have a primitive flow-through mechanism of anteriorly arranged inhalant current and posteriorly directed exhalant current, which confines such animals to the sediment-water interface. In addition, the Solemyidae and Lucinidae have symbiotic, chemoautotrophic bacteria within bacteriocytes in the gills which play a role in nutrition through the oxidation of sulphur that is prevalent in the reducing environments of the muds they inhabit (Reid & Brand 1986; Reid 1990).

The great majority of the remaining bivalves, however, feed upon the rich soup of plant detritus, bacteria and algal cells that characterises the immediate surface of the sediment or clouds the water of more open marine and freshwater systems. To capitalise upon this, the gills, initially serving a respiratory gas exchange function only, have been enlarged and moved from the primitively posterior position (as in *Nuculana*), to lie lateral to the body as two pairs of deep folds, dividing infrabranchial from suprabranchial chambers (Fig. 4.5E, G). In this position the ctenidia form a filtering structure of large surface area (Fig. 4.12B). Each ctenidium comprises inner and outer demibranchs and each demibranch has descending and ascending lamellae.

Water enters the mantle cavity through the inhalant stream (anteriorly located in more primitive groups; Fig. 4.5D). The current is created by specialised lateral cilia on the sides of each filament (Fig. 4.12C–E), augmented by the pumping motions of the adductor muscles closing the valves. On passage of the water through the ctenidia, fine particles of potential food are sieved out by stiff, bristle-like, latero- or eulatero-frontal cilia (Fig. 4.12E) and flicked onto the surface of the filament where frontal cilia transport the material either downwards or upwards to ciliated

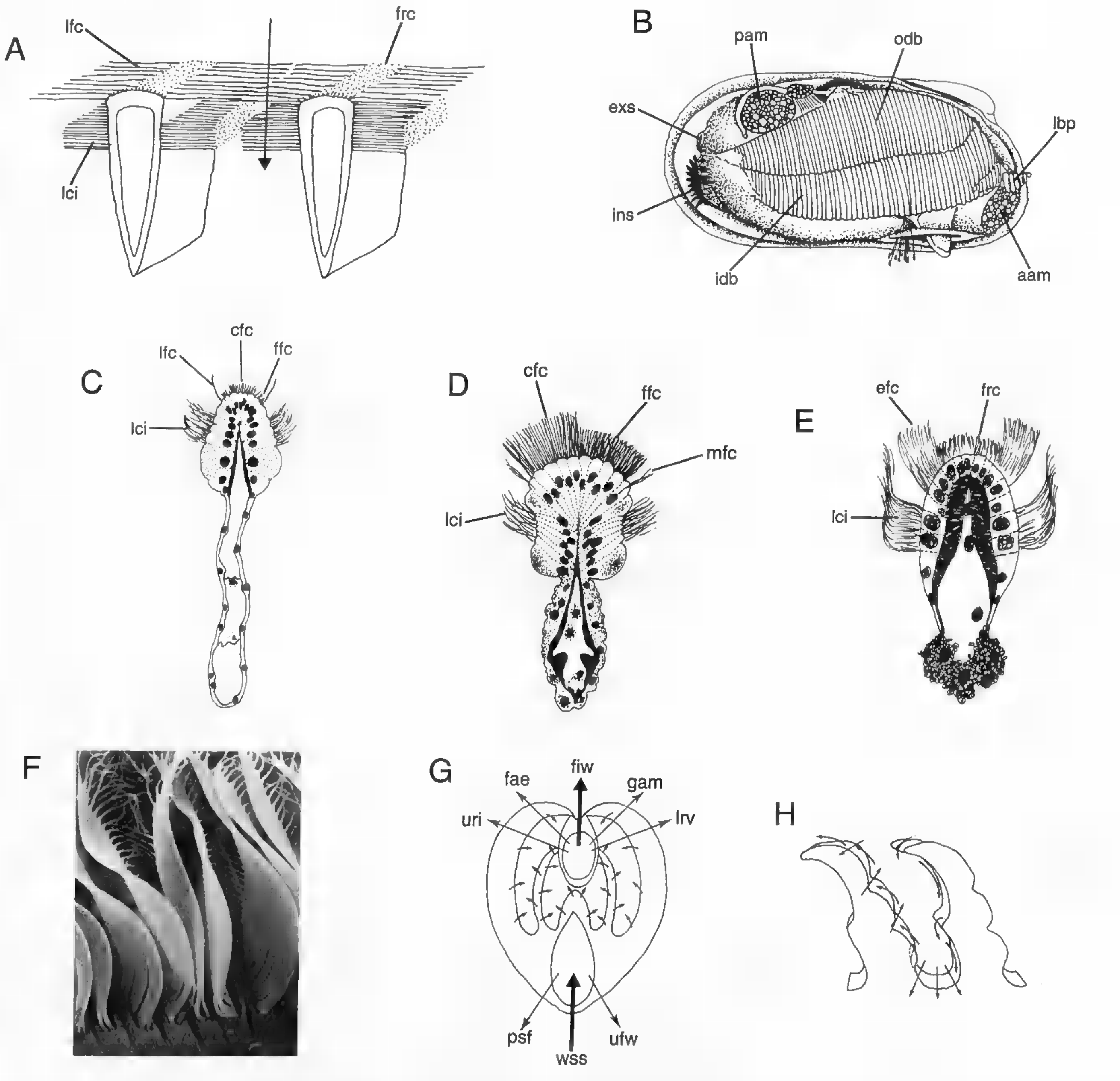

Figure 4.12 Feeding in bivalves. A, a schematic illustration of two gill filaments and the important ciliary blocks. B, *Fluviolanatus subtorta* (Trapeziidae), lateral view, showing the great extent of the ctenidia. C, D, E, transverse sections through ctenidial filaments of *Trisidos* (Arcidae), *Enigmonia* (Anomiidae) and *Montacutona* (Galeommatidae), respectively, showing the various arrangements of ciliary tracts. F, eulatero-frontal cilia of *Venus* sp. (Veneridae). G, a generalised bivalve showing components of inhalant and exhalant waters. H, a transverse section through two labial palp ridges of *Yoldia* sp. (Yoldiidae), showing the complex arrangement of ciliary acceptance, rejection and resorting currents. **aam**, anterior adductor muscle; **cfc**, coarse frontal cilia; **efc**, eulatero-frontal cilia; **exs**, exhalant siphon; **fae**, faeces; **ffc**, fine frontal cilia; **fiw**, filtered water; **frc**, frontal cilia; **gam**, gametes; **idb**, inner demibranch; **ins**, inhalant siphon; **lbp**, labial palps; **lci**, lateral cilia; **lfc**, latero-frontal cilia; **lrv**, larvae; **mfc**, micro-lateral frontal cilia; **odb**, outer demibranch; **pam**, posterior adductor muscle; **psf**, pseudofaeces; **ufw**, unfiltered water; **uri**, urine; **wss**, water and suspended solids. Arrows indicate direction of current. (A–E, G, H, after various sources; F, reproduced with permission of The Royal Society of London)
[B. Morton]

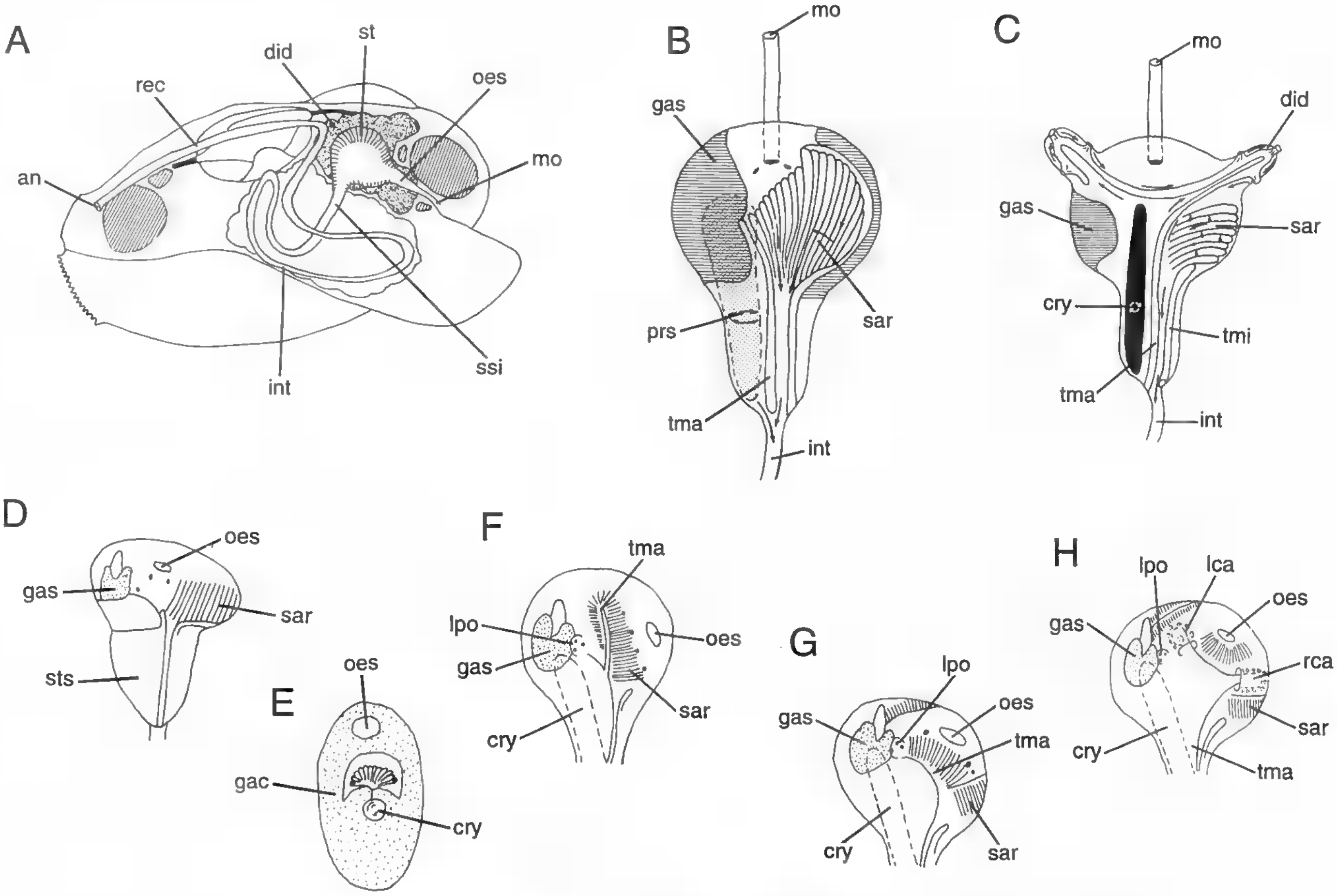

Figure 4.13 Bivalve digestion. A, the digestive system, lateral view. B, protobranch stomach. C, lamellibranch stomach. D–H, stomach types: D, Gastroproteia; E, Gastrodeuteia; F, Gastrotiteia; G, Gastrotetartika; H, Gastropempta. **an**, anus; **cry**, crystalline style; **did**, digestive diverticula; **gac**, gastric cuticle; **gas**, gastric shield; **gd**, gonad; **int**, intestine; **lca**, left caecum; **lpo**, left pouch; **mo**, mouth; **oes**, oesophagus; **prs**, protostyle; **rca**, right caecum; **rec**, rectum; **sar**, sorting area; **ssi**, portion of intestine housing style sac; **st**, stomach; **sts**, style sac; **tma**, major typhlosole; **tmi**, minor typhlosole. (A, after Cox 1969; B, C, after Owen 1966; D–H, after Purchon 1987a)
[B. Morton]

grooves (Fig. 4.12A). In the dorsal grooves, particles are always transported to the mouth, but in more primitive lineages within the Protobranchia and Pteriomorphia, for example, the Arcoidea and Pterioidea, the ventral marginal food grooves transport material away from the mouth for rejection posteriorly. In the more typical lamellibranch bivalve, however, particle transport within the grooves is, both dorsally and ventrally, towards the mouth.

Grades of ctenidial organisation occur in the Bivalvia; the main types were described by Pelseneer (1889), Ridewood (1903) and Atkins (1936, 1937a, 1937b, 1937c, 1938a, 1938b, 1938c). In her series of papers, Atkins described in great detail the ctenidia of a wide range of species, including their ciliation, food grooves and directions of ciliary beat. She classified the variations and discussed their distribution within the class. The gill types she designated are often used by taxonomists and morphologists to describe bivalves.

The primitive leaf-like ctenidia of the nuculoids and solemyoids are known as the protobranch type, from which the name of the order is derived. The highly modified, septate gill of the carnivorous Cuspidarioidea and Poromyoidea is known as the septibranch type. Lamellibranch bivalves have broad, strongly ciliated, lamellate ctenidia with a sorting function. Large, more or less symmetrical, W-shaped ctenidia in which the filaments are loosely connected by ciliary junctions are called filibranch (many pteriomorphs). Others with the filaments more intimately united are known as either pseudolamellibranch (other pteriomorphs and palaeoheterodonts) or eulamellibranch (heterodonts and some anomalodesmatans). In the Heterodonta and Anomalodesmata, refinement of gill structure is associated with enhanced mantle fusions permitting colonisation of habitats deep in the substratum and increasing feeding efficiency. In those bivalves in which the mantle margins are little fused and life styles above sediment level are adopted, the ctenidia may be plicate (or deeply folded) to increase surface area, although plication can also occur in a range of other burrowing species.

In virtually all bivalves, food material is sorted finally on the paired labial palps lying to left and right of the mouth (Fig. 4.1B). Each triangular palp comprises a series of ridges and grooves, aligned at right angles to the oral grooves between them. On the grooves and in the depths of the channels between them is a complex array of ciliated tracts that effect (a) acceptance, (b) rejection and (c) re-sorting of material passed to them from the ctenidia (Fig. 4.12H). Accepted material is passed to the mouth. Rejected material passes backwards and is accumulated by ciliated tracts on the visceral mass and mantle to be consolidated into a pseudofaecal bolus which is ejected from the inhalant siphon periodically by rapid adduction of the shell valves.

The lips of the mouth are typically simple flaps but in the Limoidea and Pectinoidea they are fused to varying degrees of intimacy, related to the need by these monomyarian bivalves to prevent food material from being flushed out of the mouth by powerful rejectory currents located nearby. This is especially important in the swimming Pectinoidea (Gilmour 1964). Stasek (1963) recognised three categories of ctenidial-palp association related to the degree of contact between the ctenidia and palps, that is, whether they are separate and connected by an oral groove or whether the ends of the ctenidia are located between the palp surfaces and with a grade of intermediate connection between.

The bivalve digestive system is characterised by a complex stomach and associated structures, but bivalves have an otherwise simple alimentary tract lacking oesophageal salivary glands (Fig. 4.13). Bivalve stomachs have been described in detail by Graham (1949), Owen (1956), Purchon (1956, 1957, 1958, 1960, 1987a), Reid (1965) and Dinamani (1967). Purchon (1987a) reviewed the literature on stomach structure throughout the class. The stomach, like the ctenidia, is characterised by grades of organisation generally characteristic for each subclass (Fig. 4.13B–H).

Morton (1983a) has reviewed digestion in the Bivalvia. Digestion principally occurs in two phases: extracellular digestion occurs in the stomach, and intracellular digestion is restricted to the digestive diverticula opening laterally from the stomach. Because of the uniform diet of small particles, broad generalisations can be made about stomach structure and function. Movement of material in the stomach is by cilia and even at this late stage, further selection of material takes place on the complex array of ciliated sorting areas (Fig. 4.13D–H). Rejected material is passed, in an intestinal groove, flanking the right side of a typhlosole, directly to the midgut for discharge in the faecal string.

The principal organ of extracellular digestion is the uniquely molluscan crystalline style, projecting into the stomach from the midgut (in the more primitive Nuculanidae, for example Fig. 4.13B) or from a side sac united with the midgut or from a sac separate from the midgut (the more specialised condition; Fig. 4.13C–H). The style, projecting into the stomach from its sac, is rotated by cilia against a gastric shield lining the postero-dorsal wall of the stomach. Its dissolution releases enzymes into the stomach, breaking down mucoid-bound food strings and effecting primary extracellular digestion. Such material is transferred in a fluid suspension into large caecal embayments in the stomach wall and thence via a duct system to the digestive diverticula (Fig. 4.14).

The digestive tubules (Fig. 4.14C, D) are organs of intracellular digestion and absorption. They are generally thought to comprise two cell types, digestive cells and crypt cells (Fig. 4.14C–E), although the latter may actually be a number of cells with diverse functions, of which the replacement of exhausted digestive cell types and the formation of new tubules are especially important. The breakdown of digestive cells at the end of a digestive phase results in the formation of fragmentation spherules that in the stomach may release excess enzymes to facilitate crystalline style dissolution. In the Nuculidae, crypt cells are also thought to secrete enzymes aiding extracellular digestion in the stomach (Owen 1956).

Dissolution of the style, stomach pH and coordinated cytological changes in the digestive tubules all suggest that the processes of feeding and digestion in the Bivalvia are rhythmic and coordinated by the arrival of food in the stomach at the beginning of a new phase of feeding correlated, for example, with the rise of the tide (Morton 1983a). There is evidence from freshwater and sublittoral species that they have a circadian feeding and digestive rhythm, for example, *Tridacna* (Morton 1978a), *Pecten* and *Lithophaga* (Salanki 1968).

Members of the typically deep-water anomalodesmatan families Parilimyidae, Verticordiidae, Cuspidariidae and Poromyidae are exceptions to the microphagous life style described above. Species of these families are predatory, typically upon crustaceans and polychaetes (Morton 1978b). Prey capture is by a raptorial inhalant siphon (Fig. 4.24E) and in their various representatives there is a trend towards the reduction and muscularisation of the ctenidium into a septum (as in the Cuspidariidae and Poromyidae) (Yonge 1928). The palps are also muscular and help stuff food into the mouth. The stomach is developed into a crushing gizzard, with the crystalline style reduced and the digestive diverticula responsible for the production of powerful proteases (Reid 1978).

Two other families, the Teredinidae and Tridacnidae, have interesting variations upon the established pattern of digestion. The teredines (shipworms) feed on filtered food and upon the wood fragments eroded from their tunnel heading. This is achieved in specialised digestive tubules (Morton 1978b) with the cooperation of symbiotic cellulolytic bacteria housed in oesophageal pouches (Popham & Dickson 1973). The Tridacnidae are suspension-feeders, but also possess zooxanthellae in the greatly expanded siphons and other regions of the mantle which are exposed to light. These are culled from the siphons by amoebocytes, digested and their photosynthetic breakdown products used by the giant clams (Yonge 1980). Probably all bivalves are capable of direct absorption of dissolved organic matter (DOM).

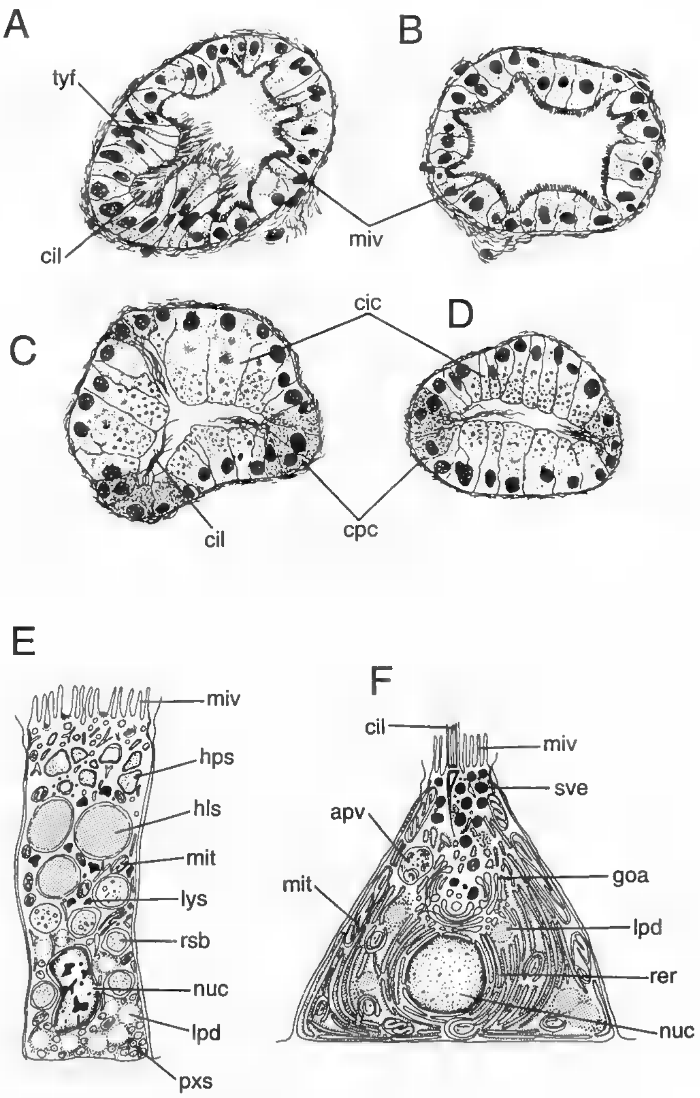

Figure 4.14 Bivalve digestion. **A–D**, digestive diverticula, transverse sections: **A**, primary duct; **B**, secondary duct; **C**, **D**, digestive tubules. **E**, **F**, stylised drawings of median sections of cells: **E**, a digestive cell; **F**, basiphilic cell. **apv**, autophagic vesicle; **cic**, digestive cell; **cil**, cilia; **cpc**, crypt cell; **goa**, golgi apparatus; **hls**, heterolysosome; **hps**, heterophagosome; **lpd**, lipid; **lys**, lysosome; **mit**, mitochondrion; **miv**, microvilli; **nuc**, nucleus; **pxs**, peroxisome; **rer**, rough endoplasmic reticulum; **rsb**, residual body; **sve**, secretory vesicle; **tyf**, flare of typhlosole. (After various sources) [B. Morton]

The Protobranchia are deposit-feeders, perhaps representing more closely the primitive bivalve condition. The Heterodonta have largely adopted a burrowing and suspension-feeding mode of life collecting the rich soup of surface detritus, although many Tellinoidea are deposit-feeders. The Pteriomorphia are largely epibyssate colonists of hard substrata, lack the extensive pallial fusions required by the burrowing heterodonts and myoideans, and have typically large, filibranch and plicate ctenidia. They exploit the suspended material of the water column. The extant Anomalodesmata are highly specialised remnants of an ancient pholadomyoidean stock, and one group has radiated in the deep seas to become predators, a remarkable attestation to the potential of adaptation and the plasticity of the bivalve plan.

Circulatory System

In bivalves, as in other animals, the circulatory system enables substances to be transported between the environment and metabolising cells deep within the body (Fig. 4.15A). It also facilitates cell to cell interactions mediated by humoral factors, and the dispersal of phagocytic amoebocytes and haemoglutinins involved in immune defence.

The heart consists of two auricles attached laterally to a single, median ventricle, all of which are enclosed within the pericardium (Fig. 4.15B). In most species, the ventricle is loosely wrapped around the rectum, which passes through the pericardial cavity (Fig. 4.15B, C), although this is not so in some protobranchs, for example, *Nucula*, and eulamellibranchs, for example, *Ostrea*.

The heart is myogenic and beats spontaneously. It exhibits features of both heterometric and homeometric autoregulatory control in that increased intracardiac pressures have positive inotropic and chronotropic effects. However, extrinsic nervous control exerts an over-riding cardio-regulatory effect *in vivo*. Both inhibitory and excitatory nerve fibres innervate the myocardium. Neurotransmitters involved in the mediation of nervous activity include acetylcholine, serotonin and opioid peptides.

From the ventricle, blood passes to the tissues via anterior and posterior aortae (Fig. 4.15A) although there is considerable variation on this basic scheme. For example, in some filibranchs (for example, *Mytilus*), only an anterior aorta is present, while in some deep burrowers, the posterior aorta is modified to form a bulb. The latter probably serves as a safety device preventing backflow of blood into the ventricle when aortic pressure is raised during sudden siphonal contraction.

From the aortae, the blood enters the extensive haemocoelic spaces within the tissues then returns to the heart by way of either the ctenidia or the kidney (Fig. 4.15A). The venous blood, largely from the large pedal sinus in the foot, passes through Keber's valve into a median sinus. From here it passes laterally in a plexus of fine vessels around the kidney and is collected into the afferent branchial vessels which run longitudinally along the bases of the ctenidia. After passing through the ctenidia, blood is collected by the longitudinal efferent vessels and returned to the auricles. Blood from the pallial sinuses is also collected laterally and passes to the auricles (Brand 1972). Such a system is classified as 'open' in contrast to a 'closed' system in which vessels conduct blood through capillary beds.

Circulation times have been calculated for only a few species. In a species of *Noetia* the value was 10 minutes at 25°C and 30 minutes at 50°C. Maximum systolic blood pressures are in the range of 2.7–130 mm of water. Taking this information into account it appears that although the circulatory system is 'open', peripheral resistance to blood flow is higher and circulation times are much slower than in many 'closed' systems. Movements associated, for example, with burrowing may temporarily impede blood flow to various regions, notably the foot. Apparently valve-like structures in the efferent pedal blood vessel prevent backflow as the muscle mass of the foot contracts.

The blood (which constitutes 40 to 60% of fresh tissue weight) serves not only as a transport medium but also as a hydrostatic skeleton against which muscles can contract during locomotion. Furthermore, redistribution of blood from one tissue to another serves a useful role in siphon extension. Typically the bivalve blood contains no respiratory pigments. The exception to this is the members of the Arcoidea, which typically and primitively inhabit anaerobic muds.

The blood cells are leucocytes. Two general types occur, a hyaline leucocyte ('leucocyte') and a granular leucocyte ('granulocyte'). Such cells show extreme variations in size, but the average cell count for all circulating leucocytes in *Tapes semidecussata* was 1650 ± 180 mm^{-3} (Cheney 1971). Phagocytic transport of a wide range of natural and artificial substances has been observed in bivalves and in *Tridacna* it appears that amoebocytes transport and digest senescent algal zooxanthellae cells, eventually either releasing them into the gut or the greatly enlarged kidneys. Yonge (1926) first ascribed digestive properties to the amoebocytes of the oyster *Ostrea edulis*.

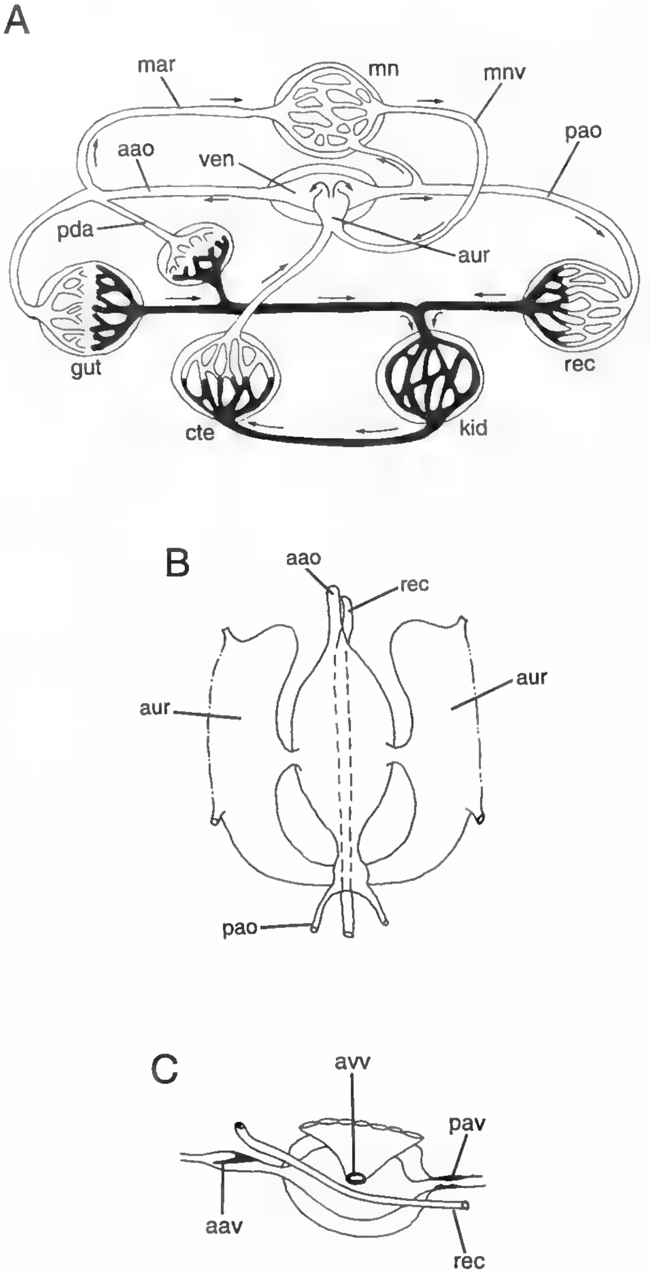

Figure 4.15 The bivalve circulatory system. **A**, a generalised system (oxygenated blood clear; deoxygenated blood black). **B**, the heart of *Laevicardium* (Cardiidae), viewed from above. **C**, the position of the circulatory valves. **aao**, anterior aorta; **aav**, anterior aortic valve; **aur**, auricle; **avv**, auriculo-ventricular valve; **cte**, ctenidium; **gut**, gut; **kid**, kidney; **mar**, anterior mantle vein; **mn**, mantle; **mnv**, mantle vein; **pao**, posterior aorta; **pav**, posterior aortic valve; **pda**, pedal artery; **rec**, rectum; **ven**, ventricle. Arrows indicate direction of flow. (A, after Cox 1969; B, C, after various sources) [B. Morton]

Excretion

Ammonia is the principle end product of amino acid metabolism. It is highly toxic and therefore must be rapidly eliminated from the tissues. In bivalves this presents little problem as ammonia is highly soluble and can be excreted directly into the surrounding aqueous environment. A more potent influence on the development of bivalve excretory systems has been the need to achieve effective ionic and osmotic regulation in diverse habitats with salinities ranging from that of seawater to freshwater.

The excretory system comprises the heart, the pericardial coelom and a pair of conducting tubes leading from the renopericardial apertures to the 'nephridiopores' opening into the suprabranchial chamber. The terms 'kidney', 'nephridium' and 'coelomoduct' are all widely used to refer to these conducting tubes. Pericardial glands (Keber's gland) occur as lappets either on the auricles of the heart or as pouches on the pericardial wall itself, either inside or outside the pericardial space. In reviewing the distribution of the glands, White (1942) concluded that they are of no phylogenetic significance. Similarly, their role as either the site of ultrafiltration and/or as organs of secretion is debated. Evidence for the latter function is small (Strohl 1924). Evidence for the former stems from the researches of Picken (1937) and Potts (1954) who respectively estimated the filtration rate at 0.2 and 0.03 ml/g wet tissue weight/hour. Injected (Kowalevsky 1889–1890) and ingested (Morton 1969) fine particles of dye and colloidal graphite accumulate in the cells of the pericardial gland.

Mangum & Johansen (1975) believed that ultrafiltration takes place across either the walls of the pericardium or the auricles, which are rich in podocytes, whereas the ventricular wall has none (Pirie & George 1979; Hawkins, Howse & Sarphie 1980). Four main factors affect the rate of filtrate formation: (a) intracardiac hydrostatic pressure; (b) pericardial hydrostatic pressure; (c) haemolymph colloid osmotic pressure; (d) pericardial filtrate colloid osmotic pressure (Depledge 1985). Providing the sum of the forces tending to force fluid through the heart wall – (a) and (d), is greater than that of the opposing forces – (b) and (c), filtration takes place.

Florey & Cahill (1977) and Jones & Peggs (1983) have shown that the osmotic pressure inside and outside the heart is the same and that intracardiac pressure exceeds pericardial pressure. Tiffany (1972) has shown that fluid filtration may proceed even at low systolic pressures of 20–40 mm of water. Pierce (1971) and Fyhn & Costlow (1975) have shown that haemolymph and pericardial fluid show a high degree of similarity in terms of Na^+, Ca^{2+}, Mg^{2+} and Cl^- except that protein concentration is reduced and blood cells are rare in pericardial fluid. Such evidence is in accord with the hypothesis that pericardial fluid is produced by filtration of haemolymph across the heart wall (Martin & Harrison 1966) and Florey & Cahill (1977) state 'there is as yet no convincing argument against this filtration hypothesis; in fact, our new pressure measurements (on a number of bivalves), supports it'. Probably, as determined histologically by White (1942), ultrafiltration takes place either across the podocyte-rich walls of the pericardium or the atria.

Filtrate composition is, however, also modified during passage through the kidney, the first half of which is glandular and involved in the selective uptake of ions and nutrients. The second half of the kidney constitutes a bladder from which the urine is eventually voided via the nephridiopore. In the Protobranchia these distinct areas cannot be recognised, the kidney appearing glandular throughout. The system appears to be highly effective. For example, freshwater bivalves excrete large volumes of urine which is very hypotonic (compared to the body fluids).

Some of the cells in the kidneys contain spherical concretions (nephroliths) ranging in size from 1–60 µm. They are composed largely of calcium phosphate with lesser amounts of metals such as iron, chromium, copper and nickel. They may constitute part of a detoxification mechanism as their composition appears to reflect contamination levels in the external environment (Reid & Brand 1985).

Of particular interest is the excretory system of the giant clam, *Tridacna*, which accounts for 10% of the animal's tissue weight (Yonge 1980). Morton (1978a) suggested that the final breakdown of zooxanthellae might occur in the coelomoducts. Disputed by Trench, Wethey & Porter (1981) this view has been partially substantiated by Reid, Fankboner & Brand (1984) who demonstrated that substances which could be derived from zooxanthellae (such as high levels of oxalate, magnesium and sulphur), occur in the kidneys. Proteolytic activity has also been demonstrated in the kidneys.

The bivalve excretory system has thus been implicated in the removal of nitrogenous waste, ionic and osmotic regulation, detoxification of metals and uptake of nutrients. However, quantitative evaluation of these functions is lacking.

Respiration

In most metazoans, uptake of oxygen for aerobic metabolism occurs across a specialised respiratory structure (gill or lung). Oxygen is then transported in the blood throughout the cardiovascular system where it is exchanged in the tissues for carbon dioxide. Usually, a respiratory pigment increases the oxygen carrying capacity of the blood. Bivalves diverge significantly from this basic scheme.

Typically, bivalves have one pair of ctenidia. In septibranchs the mantle cavity is highly vascularised. In protobranchs the ctenidia are located posteriorly and play little or no role in food collection (Fig. 4.5D). In all other lamellibranchs the laterally displaced ctenidia are greatly enlarged and filter fine food particles from the inhalant water (Figs 4.5F, G, 4.12A–G). It thus appears that the ctenidia serve a dual role.

Bayne (1971) showed that during progressive hypoxia, *Mytilus edulis* was able to regulate oxygen uptake by dramatically increasing ventilation rate (elevated ventilation/perfusion ratio). There is, however, now a considerable body of evidence to support the view that under normal circumstances the ctenidia are of limited importance in gas exchange in bivalves. For example, Famme & Kofoed (1980) showed that oxygen uptake in *Mytilus edulis* takes place across the entire, undifferentiated, surface of the body. Famme (1981) went on to demonstrate that artificial perfusion of the tissues at different rates does not affect oxygen consumption. This evidence indicates that neither loading of the blood with oxygen in the gills nor the subsequent transport of oxygen to the tissues, is necessary for normal aerobic metabolism. Similarly, ligation of the anterior aorta in *Modiolus demissus* only reduced oxygen uptake by 10–15% (Booth & Mangum 1978). Further corroborative evidence is that respiratory pigments are usually not present in bivalve blood. Consequently, the oxygen carrying capacity of the blood is very low, as is oxygen utilisation (2.5 to 12%; Ghiretti 1966).

If the cardiovascular system and ctenidia were important for regulation of oxygen uptake one might expect perfusion and ventilation to vary simultaneously. In *Ostrea edulis*, filtration rate (= ventilation rate) and heart rate do increase together (Walne 1972) although not proportionally (a 300% increase in ventilation rate is associated with a 17% increase in heart rate). Most studies, however, have shown that ventilation and perfusion rates vary independently. In *Mya*, for example, heart rate increased with increasing temperature but ventilation rate was unchanged (Lowe & Trueman 1972). Starvation of *Mytilus* led to a reduction in heart rate, ventilation rate and oxygen consumption. A resumption of feeding was associated with an increase in ventilation rate and oxygen uptake while heart rate was initially unchanged (Thompson & Bayne 1972; Coleman 1974).

It should be noted that bivalves are found in a wide range of salinities and therefore are exposed to environments with different degrees of oxygenation characteristics. Freshwater contains approximately 25% more oxygen per unit volume than seawater within the normal environmental temperature range. Superimposed on this is the special situation which arises during aerial exposure. Most littoral marine bivalves adduct their valves in air. Periodic valve adduction also occurs during submergence (Salanki 1964; Morton 1969, 1970). During such closures (either in air of water) both bradycardia and suppression of oxygen consumption are exhibited (Bayne, Thompson & Widdows 1976; Depledge 1985). These responses are identical to those that occur during hypoxia and the animals are known to be heavily reliant on anaerobic metabolism during such periods (Dugal 1939). Heart rate increases several minutes before shell opening in *Isognomon alatus* and *Arctica islandica* (Trueman & Lowe 1971; Taylor 1976), perhaps in order to fill the ctenidia with blood ready for the resumption of filtration.

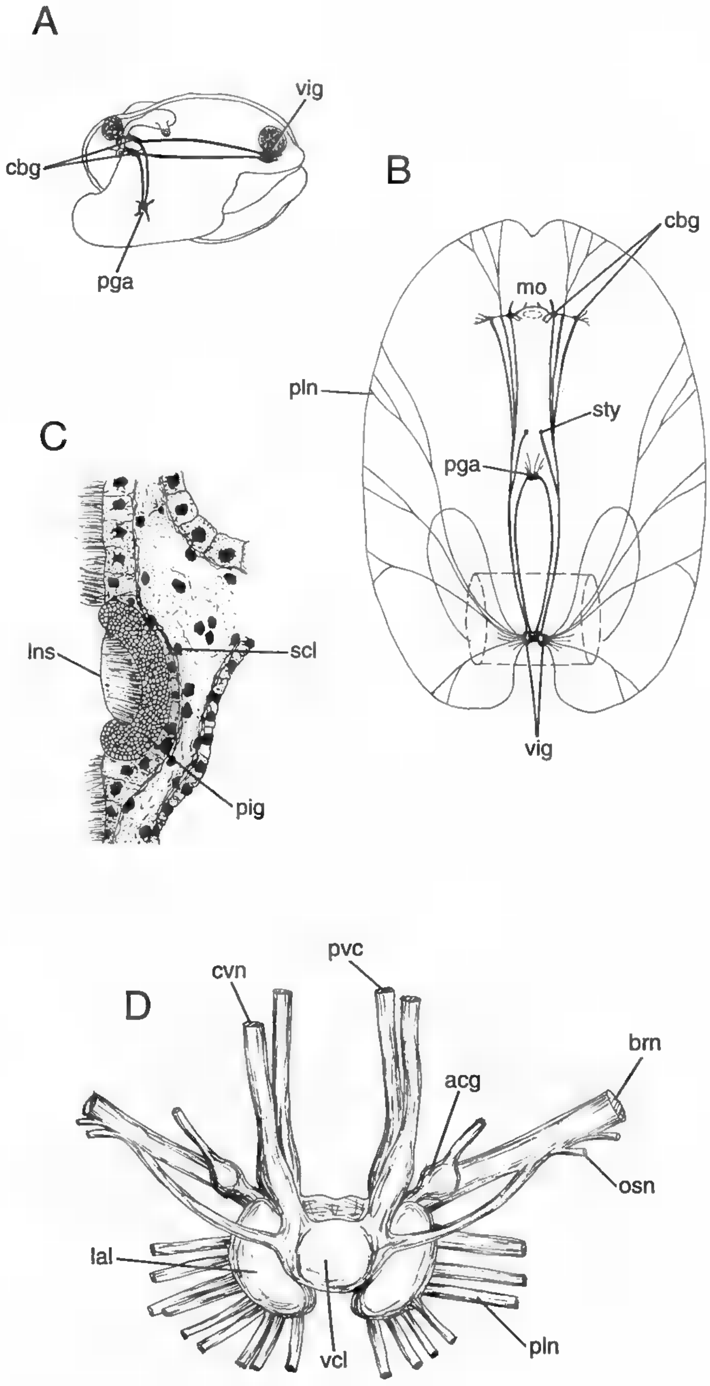

Figure 4.16 The bivalve nervous system. **A**, a generalised nervous system, seen from the side. **B**, the nervous system of *Spondylus* (Spondylidae). **C**, a transverse section through the cephalic eye of *Philobrya* sp. (Philobryidae). **D**, the visceral ganglia of *Spondylus* sp. **acg**, accessory ganglion; **brn**, branchial nerve; **cbg**, cerebral ganglia; **cvn**, cerebrovisceral nerve; **lal**, lateral lobe; **lns**, lens; **mo**, mouth; **osn**, osphradial nerve; **pga**, pedal ganglia; **pig**, pigment cells; **pln**, pallial nerves; **pvc**, pedovisceral connective; **scl**, sensory cells; **sty**, statocyst; **vcl**, ventro-central lobe; **vig**, visceral ganglia. (A, after Cox 1969; B–D, after various sources)
[B. Morton]

Intertidal bivalves are able to maintain oxygen uptake and aerobic metabolism in air although usually at reduced rates compared with those in seawater (McMahon & Williams 1984). This is achieved through gaped valves and exposure of the mantle edges (Lent 1968; Coleman 1973) or via open siphons (Boyden 1972). These methods, which are expensive in terms of water loss, are only effective for relatively short periods, such as are encountered during the tidal cycle. Freshwater bivalves may experience more prolonged exposure to air. These species are often thin-shelled, for example, the Unionoidea, allowing direct oxygen uptake through the valves (Dietz 1974). In the Sphaeriidae the problem is solved by pyramidal cells extending through punctae in the calcareous portion of the shell to lie beneath the periostracum, thereby facilitating gaseous exchange, again through closed valves (Collins 1967; McMahon & Williams 1984).

Finally, mention was made above of the absence of respiratory pigments from the blood of most bivalves, but there are exceptions. In the primitive taxodont families, Arcidae and Glycymerididae, haemoglobin occurs widely as an oxygen carrier in red blood cells (Booth & Mangum 1978). Intracellular haemoglobin does not occur in more highly evolved lamellibranchs, though in a few species haemoglobin is found in an extracellular form. Recently Kraus & Colacino (1986) have demonstrated the presence of an oxygen-binding haemoglobin localised in the nerves of *Tellina alternata* which can continue unloading oxygen for 30 minutes in hypoxic conditions. Neural excitability can therefore be sustained under such circumstances.

Sense Organs and Nervous System

The bivalve nervous system comprises three pairs of ganglia (Fig. 4.16A, B). The fused cerebral and pleural ganglia are supra-oesophageal and united by a circumoesophageal commissure. Beneath the posterior adductor lie the visceral ganglia which are connected to the cerebral ganglia by the cerebro-visceral connectives passing through the digestive gland and ventral to the pericardium. The pedal ganglia are embedded in the visceral mass, a little dorsal to the muscular foot. They are connected to the cerebral ganglia by the cerebropedal connectives. The cerebral ganglia innervate the labial palps, anterior musculature and the anterior mantle. The visceral ganglia innervate the ctenidia, heart, posterior mantle and siphons (Fig. 4.16D). Anterior and posterior pallial nerves unite to form the circum-pallial nerves. The cerebral ganglia also receive impulses from a pair of statoliths located near the pedal ganglia (Fig. 4.18F).

Commensurate with the sessile life style, the bivalves lack a head and, in the majority, cephalic functions are limited to the handling of potential food by the labial palps and lips of the mouth. Adult cephalic eyes (Fig. 4.16C) appear to be restricted to members of the Pteriomorphia, for example, *Mytilus*, *Avicula*, *Malleus*, and *Arca* (Pelseneer 1899). They are little more than pigment-lined cups filled with a crystalline material, located on the axial face of the first gill filament at the base. Innervated from the cerebral ganglia and comprising pigment and ciliated sensory cells, they can have little role in photoreception (Rosen, Stasek & Hermans 1978).

For the majority of bivalves, sensory perception of the external world is from the posterior where siphons sample the water above. Yonge (1957, 1982) showed that the bivalve mantle margin could be divided into three folds; inner muscular, middle sensory and outer secretory (Fig. 4.8B). Exceptions to this generalisation occur: the folds may be duplicated and in representatives of the Arcoida (for example, *Arca*, *Barbatia*, *Glycymeris*) photophores and ommatidium-like eyes develop on such a sub-fold of the outer fold – beneath the periostracum (Waller 1980; Morton 1987c). Conversely, species of the Cardioidea, including the giant clams (Tridacnidae) have eyes on the inner folds (Stasek 1966; Barber & Wright 1969).

The mantle edge of all bivalves is tactile both on its general surface and more particularly on the array of tentacles and papillae that typically arise from the edge of the inner and middle folds and are especially abundant around the tips of the siphons where they form a sensory screen for the inhalant water (Fig. 4.18A–C). They also develop, but less frequently, across the exhalant orifice. There is only one remarkable exception to the above plan. An alternative system has evolved in *Pholadomya candida* (Pholadomyoidea), in which the siphon tips lack tentacles. Instead, a forked tentacle is developed on the posterior edge of the visceral mass and projects within the inhalant siphon. This opisthopodium receives nerves from the pedal ganglia and, it is believed, samples the inhalant flow for velocity, constituents or both (Morton 1980b).

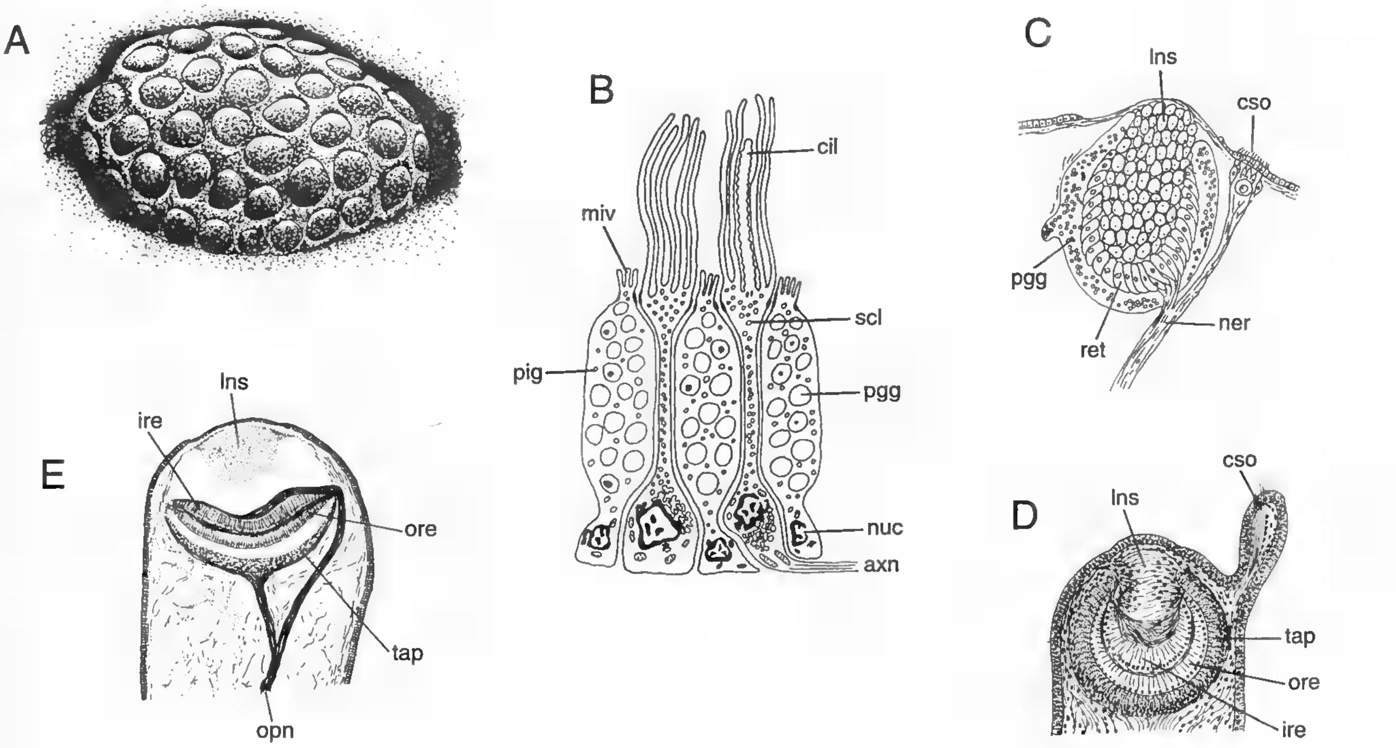

Figure 4.17 Pallial eyes. **A**, a surface view of the multi-faceted arcoid compound eye. **B**, part of the retina of the arcoid compound eye showing the arrangement of sensory and pigment cells. **C–E**, sections through pallial eyes: **C**, *Tridacna* sp. (Tridacnidae); **D**, *Laternula truncata* (Laternulidae); **E**, *Pecten* sp. (Pectinidae). **axn**, axon; **cil**, cilia; **cso**, ciliary sense organ; **ire**, inner retina; **lns**, lens; **miv**, microvilli; **ner**, nerve; **nuc**, nucleus; **opn**, optic nerve; **ore**, outer retina; **pgg**, pigment granule; **pig**, pigment cell; **ret**, retina; **scl**, sensory cell; **tap**, tapetum. (A–C, E, after various sources; D, after Adal & Morton 1973) [B. Morton]

An organ which perhaps is accessory to the siphonal tentacles in monitoring water quality is the osphradium that lies just anterior to the visceral ganglia (Fig. 4.18D, E). It is innervated from an accessory ganglion on each branchial nerve just in front of where it arises from the visceral ganglia (Kraemer 1981).

Photoreceptors of a wide range of complexity often occur on the mantle margin. Almost all bivalves, even if eyeless, respond to sharp changes in light intensity – the shadow reflex – by contraction of the siphons, pallial retraction and adduction. Light sensitive nerves, in the absence of eyespots, have been considered to be receptors. These may be sensory axons or a photosensitive region of the pallial nerve itself (Charles 1966).

True pallial eyes exhibit a range of forms (Fig. 4.17). In the Arcoida, numerous photophores and eyes with a structure similar to that of the cephalic eyes (Waller 1980) adorn the posterior mantle (Fig. 4.17A, B). Such eyes are developed on the outer fold and thus perceive light fluctuations through the shell and periostracum as in *Enigmonia* (Anomioidea) (Bourne 1907). In the Cardioidea (for example, *Cardium edule*, Barber & Wright 1969), each eye has a thin cornea, a large multicellular lens, which is oval with its long axis parallel to the optic axis, and a single layer of columnar cells constituting the retina. The retina is of the inverse type, the nervous supply from the tentacular nerve to the sensory cells passing between lens and retina.

In the Limidae, the pallial eyes are simple cups composed of alternating sensory and pigment cells. The retina is not inverted, the optic nerve fibres collecting together outside the cup.

In the Spondylidae and Pectinidae (Barber, Evans & Land 1967), complex pallial eyes occur in virtually all shallow-water genera including *Pecten*, *Chlamys*, *Amusium*. A thin cornea overlies a multicellular lens (Fig. 4.17E). Beneath this is a double retina, each composed of sensory and interstitial cells. Both retinas are of the inverse type, the optic fibres passing between lens and retina. Below the retina is a light reflecting layer or tapetum derived from the underlying cellular pigment layer. The tapetum reflects light back through the retina thereby increasing the sensitivity of the eye. The sensory cells of the *Pecten* retina comprise concentrically laminate stalks of cilia with a 9 + 0 filament pattern characteristic of nonmotile cilia with a suspected sensory function.

Presence of complex eyes in the Pectinoidea was thought to be associated with the adoption of swimming by representatives of this superfamily (Yonge 1953). However, an eye of fundamentally similar structure was described for *Laternula truncata* (Anomalodesmata; Fig. 4.17D) by Morton (1973a) and Adal & Morton (1973). This bivalve is a passive burrower, the eyes detecting changes in light intensity and causing siphonal tentacles to flick sand over the siphons camouflaging them.

Associated with the eyes of *Cardium* and *Laternula* species are ciliated sub-tentacles, possibly assisting in orientation. Tentacles of essentially similar construction are present in many anomalodesmatans, but are most specialised in the deep-water septibranch predators where they respond to the vibrations of swimming crustacean prey by orientating the raptorial inhalant siphon and effecting capture (for example, *Cuspidaria* and *Cardiomya*, Fig. 4.22E; Reid & Reid 1974; Reid & Crosby 1980). Accessory siphonal ganglia occur in cuspidariids and coordinate the complex messages received from the sense organs.

Proprioreceptors coordinate muscular activities, which are especially important in burrowing and tunnelling, whereas chemoreceptors taste food, permitting a bivalve to respond positively or negatively to food quality (as well as volume and size) and to other chemicals, for example those in inhaled sperm (Nelson & Allison 1940), which coordinate gamete release for external fertilisation.

An important orientation mechanism is provided by the paired statocysts, which lie just above the pedal ganglia (Fig. 4.19F), but are innervated from the cerebro-pleural ganglia. Each comprises a spherical or oval sac, lined with cilia and has either a single statolith or numerous statoconia, or both (Fig. 4.19G). Differential stimulation of the cilia, by the statolith, results in relay of messages regarding orientation and is especially important in the larva, but also has wide significance for adult burrowing bivalves.

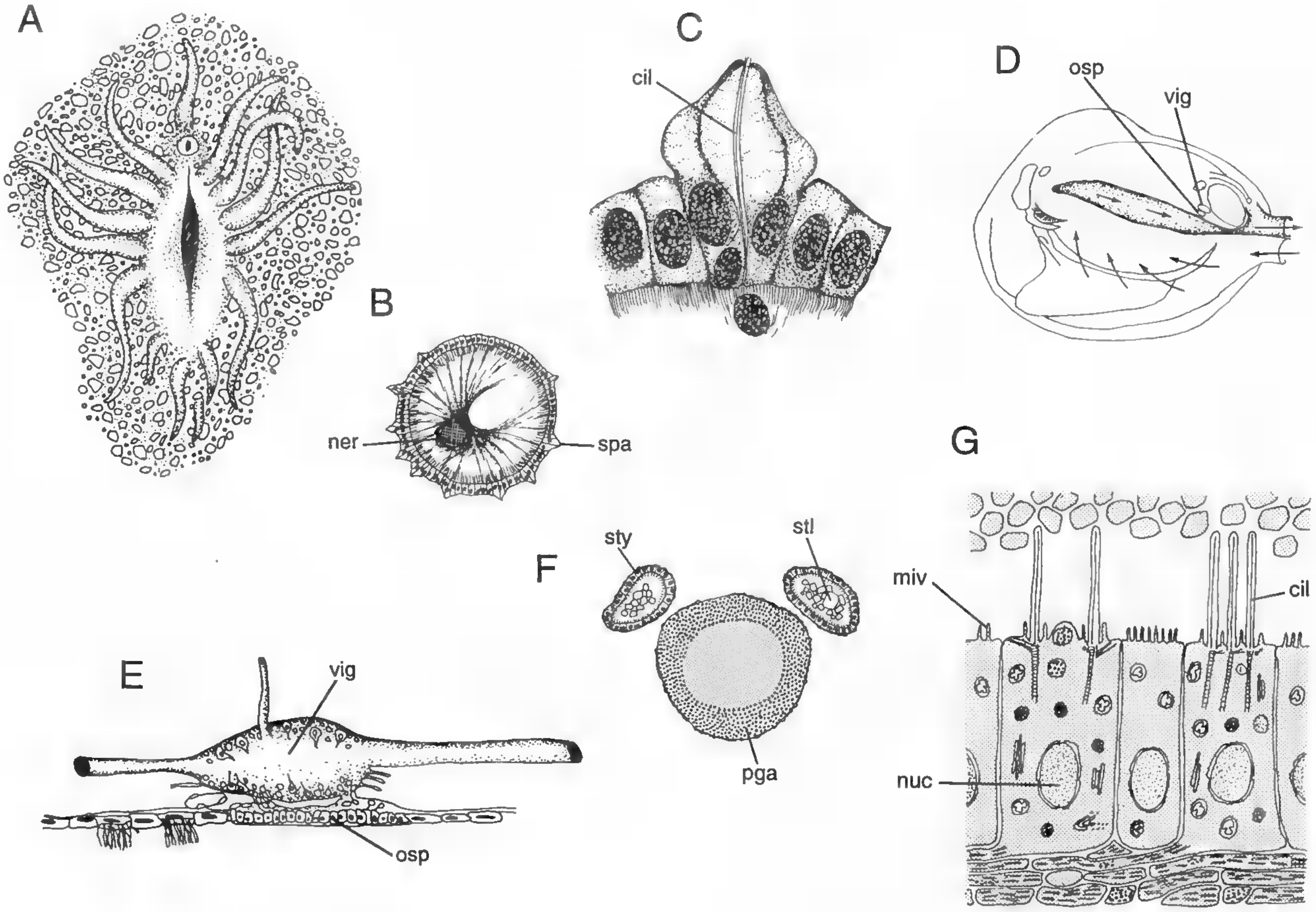

Figure 4.18 Bivalve sense organs. **A–C**, *Poromya* sp. (Poromyidae): A, siphonal tentacles; **B**, transverse section through the siphonal tentacle, showing sensory papilla; **C**, detail of sensory papilla. **D**, diagrammatic representation of a bivalve, showing the position of the osphradium. **E**, the osphradial cells below the visceral ganglia. **F**, the statocysts located close to the pedal ganglia. **G**, statoliths and sensory cilia in the statocyst wall of *Pecten* sp. (Pectinidae). **cil**, cilia; **miv**, microvilli; **ner**, nerve; **nuc**, nucleus; **osp**, osphradium; **pga**, pedal ganglia; **spa**, sensory papilla; **stl**, statolith(s); **sty**, statocyst; **vig**, visceral ganglia. (A–C, after Morton 1981c; D, after original source; E, after Kraemer 1981; F, after Morton 1985a; G, after Cragg & Nott 1977) [B. Morton]

Cragg & Nott (1977) reviewed statocyst structure in the Bivalvia and came to the general conclusion that a single statolith is characteristic of the Protobranchia and Heterodonta whereas the majority of the Pteriomorphia have a statocyst with several statoconia. Investigating the structure of the anomalodesmatan statocyst, Morton (1985a) demonstrated a wide range of form, with highly specialised statocysts occurring in the burrowing, pedal gape-feeding *Pholadomya* and the predatory cuspidariids. Statocyst structure possibly has some phylogenetic significance, but if so, information is as yet insufficient to support any hypotheses.

Reproduction

Throughout their life, the great majority of bivalves are either male or female and thus are unisexual, dioecious or gonochoristic. Representatives of some families, however, produce sperm and eggs and are ambisexual, monoecious or hermaphroditic.

The paired gonads open into the suprabranchial chamber at a gonopore (Fig. 4.1B), either close to the nephridiopore or united with it in a common urino-genital aperture, the latter condition usually being considered the more primitive. There is usually little or no way of determining the sex of a bivalve without opening it. Only in the protandric *Xylophaga* species have secondary sexual characters in the form of seminal vesicles in the male phase been described (Purchon 1941).

The posteriorly separated ctenidial axis of the similarly protandric galeommatoidean *Montacutona compacta* acts as a storage organ for sperm, again in the male phase (Morton 1980c). Females can sometimes be identified by their swollen shell in those species that brood fertilised eggs within the ctenidia, for example, species of the freshwater Unionoidea (Anderson & Ingham 1978). This, however, is not true of other brooding species, for example, representatives of the freshwater Corbiculoidea (Britton & Morton 1980) nor of the unionid *Anodonta woodiana* in Hong Kong (Dudgeon & Morton 1983).

In dioecious species, there is usually an approximately equal division of the sexes, though females may predominate in older age classes, for example, in *Corbicula fluminalis* (Morton 1982b). Often, however, about 5% of *C. fluminalis* are functional hermaphrodites, the adaptive significance of this possibly being to ensure some degree of reproductive success in the event of exaggerated mortality of one or other of the sexes.

Some groups of bivalves have adopted hermaphroditism as a reproductive strategy. These include virtually all representatives of the Anomalodesmata, Galeommatoidea, Pectinoidea, Teredinidae, Ostreidae and Sphaeriidae. The expression of sexuality, however, even among these hermaphrodites varies and Coe (1943) has erected four categories of hermaphroditism: simultaneous, consecutive, rhythmical consecutive and alternative. Linked to hermaphroditism, is brooding of fertilised eggs in the suprabranchial or infrabranchial chambers. The linkage is not obligatory, however, so that for example, the alternative hermaphrodites *Crassostrea virginica* and *C. gigas* do not brood. Conversely, the dioecious unionid *Anodonta woodiana* broods (Dudgeon & Morton 1983).

The best examples of simultaneous hermaphrodites are representatives of the Anomalodesmata. Both sexes mature simultaneously with the chance, therefore, of almost certain self fertilisation. This reproductive strategy allows anomalodesmatans to occupy highly specialised habitats. Close examination of some apparently simultaneous hermaphrodites reveals a tendency towards protogyny in a few species, but a more prevalent trend towards protandry, for example, *Pisidium* (Morton 1986). This may sometimes be because of selective sexual mortality, but in representatives of some important groups, for example, *Sphaerium*, *Musculium* and *Pisidium* (Corbiculoidea) (Morton 1985b, 1986), male gametes ripen ahead of female gametes. Such a situation is also typical of some pectinoideans, for example, *Pecten* and *Chlamys*, but is most clearly expressed in the typically commensal Galeommatoidea and the wood-boring Teredinidae. In both groups this has led to an extreme expression of consecutive hermaphroditism, whereby a male changes into a female. The resulting sexual dimorphism in a number of galeommatoideans, for example, in species of *Chlamydoconcha* (Morton 1981b) and in *Zachsia zenkewitschi*, a teredinid occurring in seagrass rhizomes (Yakovlev & Malakhov 1985), has created the extreme phenomenon of dwarf males. *Zachsia* dwarf males inhabit lateral pallial pouches just anterior to the siphons of a female. In species of *Montacuta* (Deroux 1960; Jenner & McCrary 1968) males are retained within the mantle tissue of the female. In the galeommatids *Ephippodonta* and *Chlamydoconcha* (Morton 1976, 1981b), dwarf males live in pouches in the reflected mantle folds of a female. Whether or not such individuals, upon death of the female, undergo a sex change themselves and develop into adult females is unknown.

A variation on the above theme is rhythmical consecutive hermaphroditism – best known for the oyster *Ostrea edulis* – with annual changes of sex undertaken by each individual. Alternative hermaphroditism in which sex change is erratic occurs as a further variant of this strategy in the non-incubatory oysters of the genus *Crassostrea*.

Except for the Anomalodesmata (simultaneous hermaphrodites) and highly specialised commensal galeommatoideans, the various expressions of hermaphroditism are not rigidly adhered to by all individuals of a species. Thus, just as populations of otherwise typically dioecious species usually have a small percentage of hermaphrodites, so populations of otherwise typical hermaphrodites often contain a few dioecious individuals, for example, in *Corbicula fluminea* (Morton 1983b).

Sex determination is related to the relative speed of development of the expressions of maleness and femaleness and is genotypically controlled. It is, however, becoming increasingly obvious that individual variation in shell size, form and colour is one expression of phenotypic variation that can also be manifested in the expression of sexuality. Except in those highly specialised anomalodesmatans and galeommatoideans noted above, we now know that most species occupy a range of habitats and that within such a range, variations in sexual expression exist. This was first recognised by Coe (1945) for *Tivela stultorum* which is almost invariably unisexual in San Diego and hermaphroditic elsewhere along the Pacific coast. Most up-to-date evidence for variation in sexual expression comes from research on the freshwater *Corbicula fluminea* which is predominantly dioecious in lentic waters and predominantly hermaphroditic in lotic waters (Morton 1983b). Shell polymorphism is also reflected in sexual expression, light morphs being predominantly female, dark morphs predominantly hermaphroditic (Britton & Morton 1986).

Reproductive strategy and variations in sexual expression adapt each species to its particular habitat, ensuring reproductive success. Because each major group of bivalves has adopted its own broad ecological category, broad phylogenetic trends also find expression in sexual strategies. The Anomalodesmata are all simultaneous hermaphrodites. The freshwater Palaeoheterodonta are dioecious with subsequent brooding of eggs and a parasitic larval stage. In the sea, the great majority of the Pteriomorphia and Heterodonta are dioecious and non-brooding, with specialised examples of hermaphroditism resulting from, or facilitating, exploitation of specialised niches as in the Galeommatoidea.

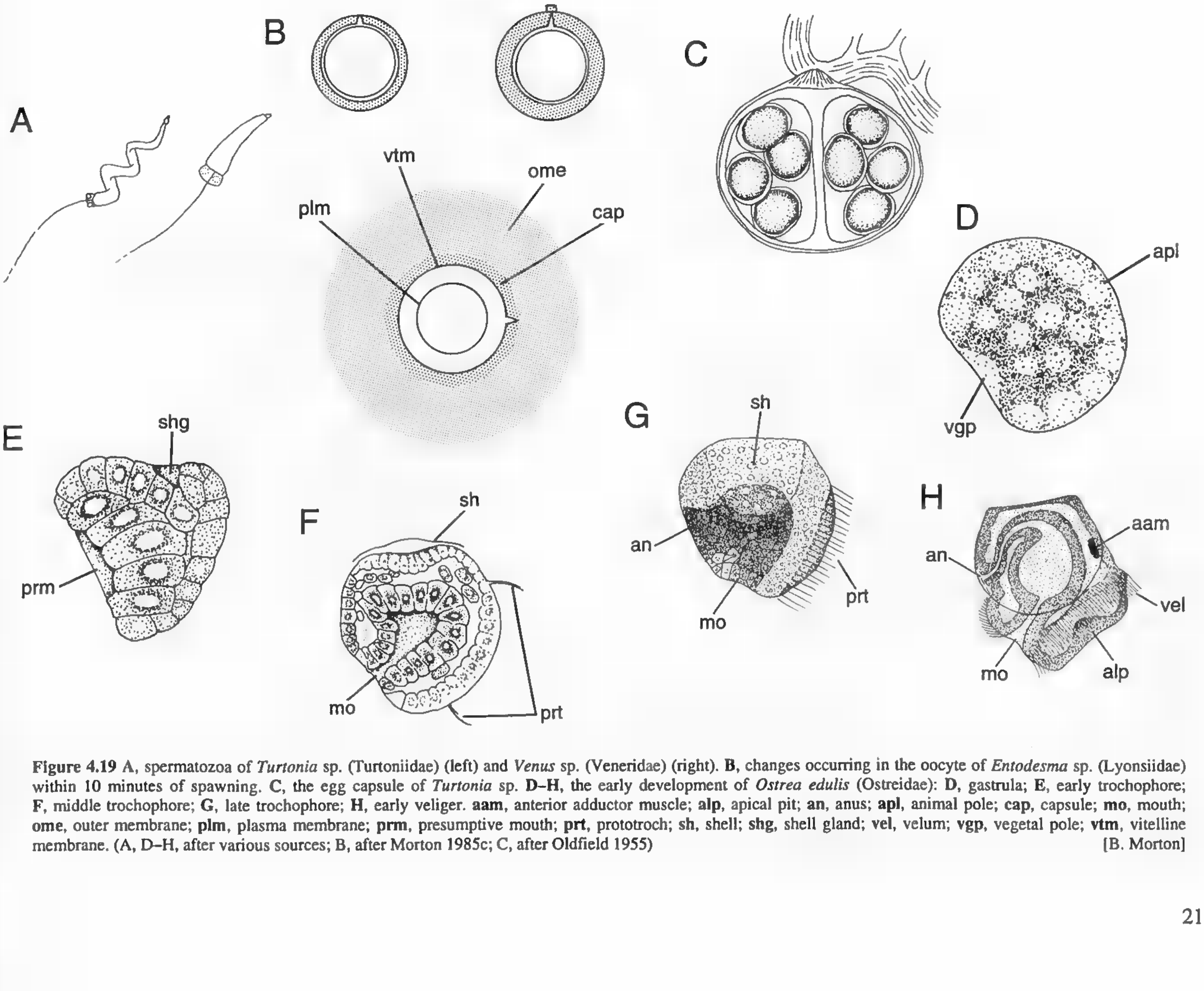

Figure 4.19 A, spermatozoa of *Turtonia* sp. (Turtoniidae) (left) and *Venus* sp. (Veneridae) (right). **B**, changes occurring in the oocyte of *Entodesma* sp. (Lyonsiidae) within 10 minutes of spawning. **C**, the egg capsule of *Turtonia* sp. **D–H**, the early development of *Ostrea edulis* (Ostreidae): **D**, gastrula; **E**, early trochophore; **F**, middle trochophore; **G**, late trochophore; **H**, early veliger. **aam**, anterior adductor muscle; **alp**, apical pit; **an**, anus; **apl**, animal pole; **cap**, capsule; **mo**, mouth; **ome**, outer membrane; **plm**, plasma membrane; **prm**, presumptive mouth; **prt**, prototroch; **sh**, shell; **shg**, shell gland; **vel**, velum; **vgp**, vegetal pole; **vtm**, vitelline membrane. (A, D–H, after various sources; B, after Morton 1985c; C, after Oldfield 1955) [B. Morton]

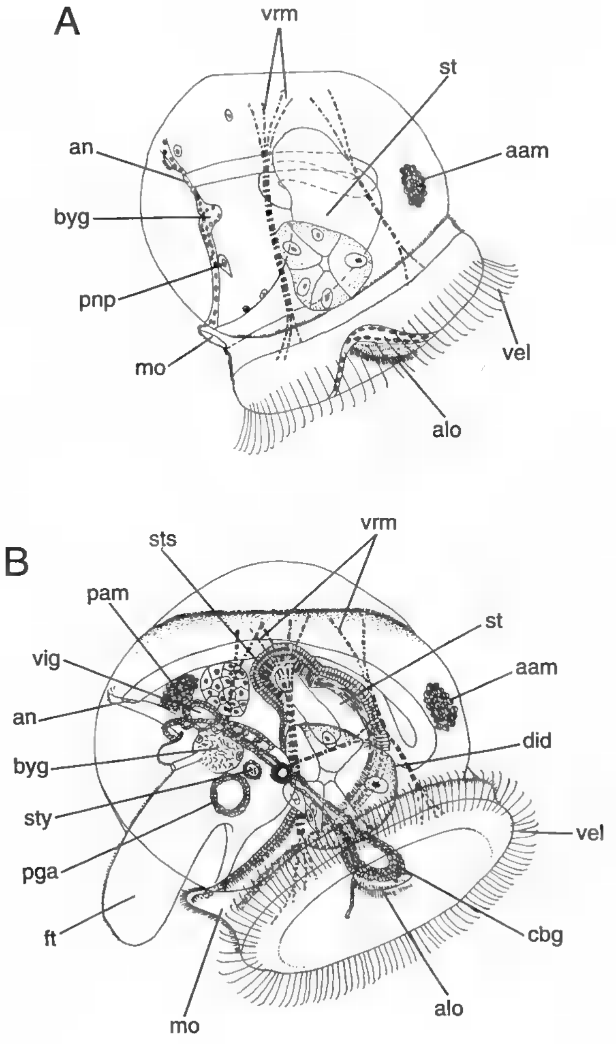

Figure 4.20 *Ostrea edulis* (Ostreidae), larval anatomy: **A**, a six day old veliger; **B**, a pediveliger larva. **aam**, anterior adductor muscle; **alo**, apical organ; **an**, anus; **byg**, byssus gland; **cbg**, cerebral ganglion; **did**, digestive diverticula; **ft**, foot; **mo**, mouth; **pam**, posterior adductor muscle; **pga**, pedal ganglion; **pnp**, protonephridium; **st**, stomach; **sts**, style sac; **sty**, statocyst; **vel**, velum; **vig**, visceral ganglion; **vrm**, velar retractor muscles. (After Erdmann 1935) [B. Morton]

Embryology

For the great majority of the Bivalvia, eggs and sperm (Fig. 4.19A, B) are released for external fertilisation. These eggs are small, contain little yolk (oligolecithal) and are very numerous (in *Ostrea edulis*, for example, numbering 1.5×10^6; *Mytilus edulis*, 1.0×10^7; and in *Tivela stultorum*, $7.5–9.8 \times 10^7$) (Pelseneer 1935). Following fertilisation, a planktotrophic veliger larva (Fig. 4.20A) is produced with residence time in the plankton of a few weeks.

This pattern of development is typical of the Pteriomorphia, Veneroida and Myoida. However, many hermaphroditic and brooding bivalves, which retain their eggs within the mantle cavity and may to a greater or lesser degree be self-fertilising, produce only a few large eggs containing much yolk (telolecithal), for example, species of the Galeommatoidea, Sphaeriidae and Anomalodesmata. Following release, residence time in the plankton for larvae of this group is short. Allen (1961) has shown that for species in the anomalodesmatan genus *Pandora*, less than 1 day is spent in the plankton and development is completed within 4 days. Similarly for *Entodesma* species, the larval life is no more than two days (Campos & Ramorino 1981). Thus, direct development, with ctenidial brooding, as in the freshwater Unionoidea and some species of the Corbiculoidea and wood-boring Teredinidae, or a short larval life as in the Anomalodesmata and the majority of deep-water bivalves (Knudsen 1979), equip such groups for occupation of specialised, often narrow, microhabitats, or the deep sea.

The Sphaeriidae can be regarded as ovoviviparous (Mackie 1978), the specialised brood pouch in effect being an egg capsule. External egg capsules, so typical of the Gastropoda, are rare in the Bivalvia and have only been reported for *Nucula delphinodonta* (Drew 1901), *Modiolaria* spp. and *Loripes lacteus* (Myazaki 1938) and *Turtonia minuta* (Fig. 4.19C; Oldfield 1955). In *Nucula*, the ctenidial hypobranchial gland secretes the egg sac. In *Turtonia*, the mantle margin secretes an egg capsule which is attached to the byssus.

Following fertilisation, cleavage is spiral, the first two dividing the eggs into four quadrants (A, B, C and D). In the next four cleavages four micromere quartettes are formed at the animal pole by alternating dexiotropic and laevotropic divisions. At early cleavage stages, a polar lobe is often formed at the vegetal pole, the substance of which ultimately passes into the D quadrant. The second and fourth micromeres of this quadrant, 2d and 4d, are important, the former giving rise to most of the shell gland and foot, the latter to the primary mesoderm. Gastrulation (Fig. 4.19D) may take place by invagination, or by epiboly, or by a combination of the two. The blastopore is originally situated in the centre of the vegetal hemisphere, but is later displaced towards the ventral side. The stomodeum is formed at a point corresponding with the final position of the blastopore.

For most bivalves the first larval stage is a trochophore (Fig. 4.19E–G) which later transforms into a veliger (Fig. 4.19H). This metamorphoses after a variable time in the plankton and acquires the adult form. As noted above for certain groups, however, the larval stage is more or less suppressed and a part or even the whole period of development passes within ctenidial brood pouches (or rarely, in an egg capsule). The trochophore is divided by a band of cilia, the prototroch, into pre- and post-trochal regions (Fig. 4.19G). The pretrochal apex bears a tuft of cilia. Two small cephalic plates, separated by a median apical plate, give rise to the cerebral ganglia and cephalic eyes. In the post-trochal region, the dorsal side bears the shell gland, and the stomodeum and foot are situated ventrally. The anus breaks through later at the posterior end. The paired mesoderm bands also lie in the post-trochal region.

In the veliger (Figs 4.19H, 4.20), the shell gland (Fig. 4.19E) develops from a disc of ectodermal cells which initially lies below the level of the surrounding ectoderm, later evaginating to become a raised disc (Fig. 4.19F) which is first capped with an uncalcified larval shell, the pellicle (Waller 1981). The lateral marginal cells of the disc proliferate and grow laterally outward over the body as a pair of mantle lobes which progressively enclose the body. The external epithelium of each lobe secretes calcium carbonate with a scleroprotein matrix. Two calcification centres thus develop to create the bivalved shell. The dorsal epithelium between these two centres secretes scleroprotein, typically without calcium carbonate – although a calcified ventral lithodesma is produced by many anomalodesmatans (Yonge & Morton 1980) – forming the primary ligament of the larval shell, the prodissoconch.

As the mantle envelops the body, the laterally compressed body organs are also differentiating. The mouth is anterior, the anus posterior. The foot develops as a mid-ventral outgrowth of the body, just posterior to the mouth. Symmetrical paired larval pedal retractor muscles develop, and from the posterior edge of the foot a uniquely bivalve structure, the byssus, develops, which may act as a drogue to assist in larval flotation in the late planktonic stage. Later it will secure the metamorphosed juvenile to the substratum and sustain attachment in some adults. The trochophore prototroch remains, and enlarges into an extensively ciliated bilobed velum that provides propulsion and also assists in food gathering, while the shell, foot and rudimentary ctenidia are forming.

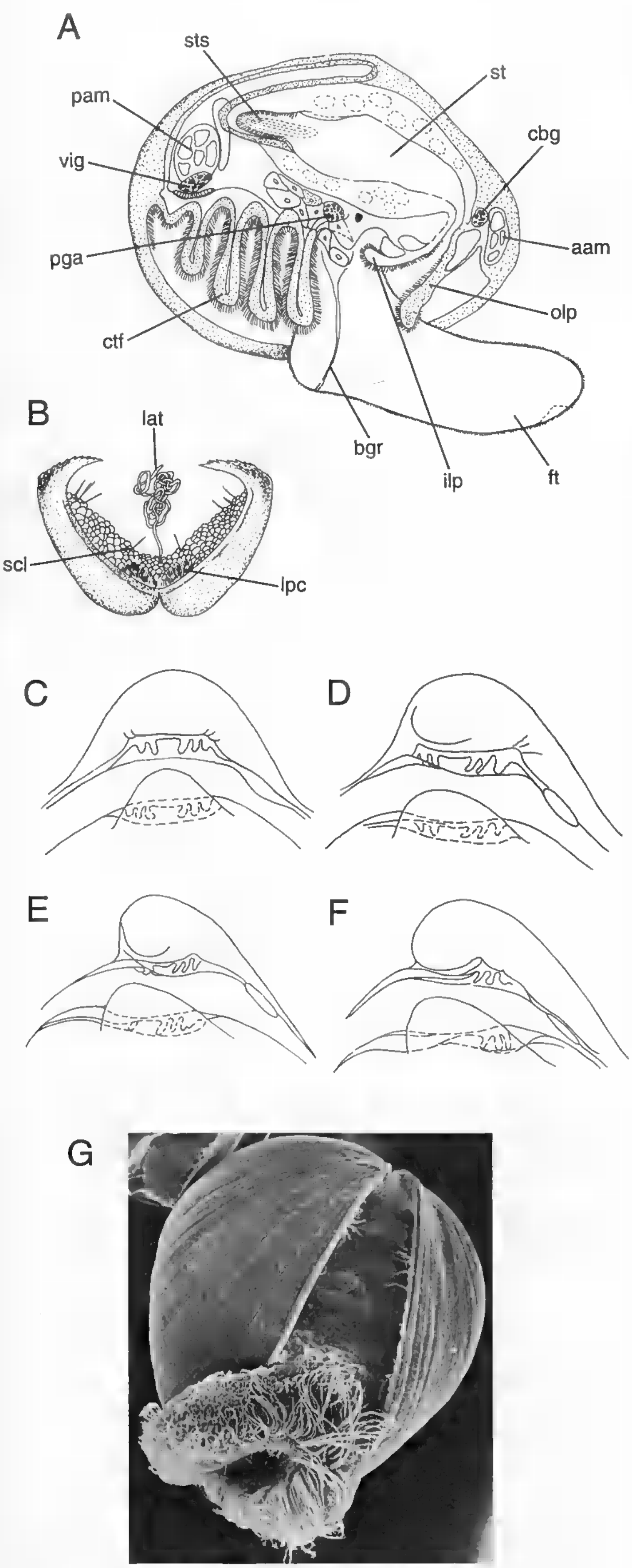

Figure 4.21 Bivalve larval anatomy. **A**, diagrammatic representation of an early plantigrade larva of *Mytilus* species (Mytilidae). **B**, the parasitic glochidium larva of *Anodonta* species (Unionidae). **C–F**, oyster prodissoconchs: **C**, *Saccostrea glomerata* (Ostreidae); **D**, *Crassostrea virginica* (Ostreidae); **E**, *Crassostrea angulata*; **F**, *Crassostrea gigas*. **G**, a mid-prodissoconch II, stage 3, larva of *Ostrea edulis* (Ostreidae). **aam**, anterior adductor muscle; **bgr**, byssal groove; **cbg**, cerebral ganglion; **ctf**, ctenidial filaments; **ft**, foot; **ilp**, inner labial palp; **lat**, larval thread; **lpc**, lateral pit cells; **olp**, outer labial palp; **pam**, posterior adductor muscle; **pga**, pedal ganglion; **scl**, sensory cells; **st**, stomach; **sts**, style sac; **vig**, visceral ganglion. (A–F, after various sources; G, reproduced with permission of the Trustees of the Smithsonian Institution) [A–F, B. Morton]

In the settled juvenile (Fig. 4.21A), the velum is lost, its remnant forming the lips of the mouth. Lateral extensions of these form the labial palps. The intestine develops as a simple tract along the antero-posterior axis and differentiates into fore, mid and hind sections. The midgut develops a swelling, the stomach, from which the rudimentary digestive diverticula arise laterally. The crystalline style, at first developing within the midgut may, in some, ultimately form in a discrete sac.

The developing shell gives the larva weight and although all bivalve prodissoconchs superficially seem very similar, in fact each has its own character, particularly with regard to larval teeth (Fig. 4.21C–G). Differentiation of the mantle margin proceeds with the secretion of shell and overlying periostracum by the outer fold. A second fold divides into two to form the inner and middle folds. Prior to settlement, ctenidia, heart, kidney, and nervous system rudiments form and the complex adult stomach differentiates (Fig. 4.21A).

Settlement occurs after a predetermined time, though it may be delayed in the absence of a suitable substratum (Bayne 1965). The loss of the velum is the most obvious event immediately following settlement, but of additional importance are changes to the foot. In the pediveliger (Fig. 4.20B), the tip is extensively ciliated and, in the absence of functional ctenidia, assists in shoving food into the mouth. Upon settlement the tip loses its distinctive cilia (Fig. 4.21A), flattens and assumes a locomotory role, searching out, in the selected substratum, the right microhabitat. Later it will either assume a digging role or function as a plantar of byssal threads.

Of most larval adaptations, the anterior inhalant stream is the most significant. The flow-through mechanism of respiration is a larval character retained by the most primitive of extant bivalves (that is, the Protobranchia and many of the Pteriomorphia, notably the Arcoidea) and probably reflects the original post-larval bivalve condition. It is also retained in many of the Galeommatoidea which, with their small size, are considered to be neotenous. Only later, with the assumption of a deeper burrowing mode of life, the evolution of the lamellibranch ctenidium and extensive pallial fusions, has the anterior inhalant stream come to be directed posteriorly, allowing in some the evolution of an epibyssate life style.

NATURAL HISTORY

Life Histories

The impressive diversity of form demonstrated by the Bivalvia, within the limitations of their stereotyped 'design', is probably matched by an equal diversity in life history traits. Reproductive strategies fall into three categories: planktotrophy, lecithotrophy and direct development (Sastry 1979). Similarly, there is a wide range of size, from the minute species of *Pisidium*, for example, *P. casertanum*, attaining a shell length of 2–4 mm. Some bivalves are smaller than this; *Condylocardia limaeformis* is only 1 mm long. In contrast, the giant clam *Tridacna gigas* has a shell length in excess of 1.50 m.

The majority of species, both freshwater and marine, are iteroparous, but in the marine Galeommatoidea and the freshwater Sphaeriidae, semelparity characterises some species, there being rapid growth to a small adult size, and a short pre- and post-reproductive period.

A few bivalves, notably members of the Pholadidae which secrete a callum over the pedal gape when they run out of available habitat for boring, commence breeding only after they have stopped growing, whereas iteroparous species have phases of growth interspersed with reproductive periods.

To understand bivalve life history traits it is necessary to understand the broader characteristics of the aquatic habitats they occupy. Generally, the marine environment can be regarded as ecologically stable both in terms of space and time. In marine conditions most bivalves exhibit iteroparity, with moderate life-spans, pelagic larvae and high vagility (that is, broadly, the

K-selection strategy of MacArthur & Wilson 1967). Exceptions to this are those bivalves living in temporary habitats, such as biogenic calcareous or wooden substrata that are bored (particularly by members of the Pholadoidea) or those microhabitats that are temporally limited by the life span of the host, the latter, in turn, influencing life history traits of commensal or parasitic species (notably members of the Galeommatoidea).

Estuarine environments are notoriously unstable with large daily or seasonal ranges in salinity. Most estuarine bivalves release eggs and sperm and there is a short pelagic larval stage at risk of loss to the sea with tidal flow. Brief larval development and keying the breeding cycle to the environmental conditions are common features of estuarine bivalve life histories. The breeding and life cycles of the temperate Australian estuarine mytilid *Xenostrobus securis* are regulated by salinity (Wilson 1969). In the upper parts of the Swan Estuary, growth and sexual maturity of *X. securis* are inhibited during the winter months when low salinities prevail, individuals live for two years or more, and spawning occurs during late summer of the second year when salinity rises to close to that of seawater. In downstream localities, however, where conditions are closer to marine, growth is inhibited only for a few weeks during winter floods, if at all. The mussels reach sexual maturity and spawn intensively in early summer at about one year of age, and there is massive post-reproductive mortality. Another abundant Western Australian estuarine bivalve, *Arthritica semen* in the Galeommatidae, like other members of that group, is hermaphroditic and broods the young in the mantle cavity (Wells & Threlfall 1980). There is no pelagic larval stage: the young are released directly onto the substratum as shelled pediveligers. Fecundity in this species is low but breeding continues throughout most of the year so that the population is able to take advantage of suitable conditions whenever they occur. This life strategy is broadly typical of the r-selection type of MacArthur & Wilson (1967).

In freshwater domains a spectrum of stability exists. Riverine and large lentic habitats, *i.e.*, lakes, are more stable and therefore more temporally predictable than either streams or small ponds. Larger, iteroparous, K-selected bivalves, such as hyriids in Australian situations, occupy the more stable freshwater habitats. In unstable freshwater habitats which are relatively transient (Russell-Hunter 1970, 1978) there is likely to be an emphasis upon semelparity and brood protection, that is, r-selection. In these relatively unstable freshwater habitats in Australia, common inhabitants include members of the Sphaeriidae which are semelparous brooders. In addition to life history strategies which allow sphaeriids to live in variable environmental regimes, some extralimital sphaeriids also show burrowing and aestivating behaviour which protects them from desiccation (Gale 1976; McKee & Mackie 1980). It is likely that Australian sphaeriid species are similarly equipped to survive seasonal drought.

Morton (1987d) has reviewed the reproductive strategies and life history traits of Hong Kong's fresh and brackish water bivalves and the principles described there may be applicable to Australian situations. Many freshwater bivalves display variable life history tactics or switching of strategies for survival in ephemeral habitats or under highly variable environmental regimes (Heard 1977; Mackie 1979; McKee & Mackie 1981; Mackie & Flippance 1983; Morton 1985b, 1986). This has been termed 'bet-hedging' by Hornbach, Way & Burky (1980) in their discussion of the life history characteristics of a population of *Sphaerium* (see also Way, Hornbach & Burky 1980). For example, Holopainen (1979) has shown that littoral populations of the lake-dwelling *Pisidium casertanum* produce one litter of larvae per year, but that profundal populations of the same species have two litters per year.

For marine bivalves there is considerably less detailed information on life history traits and it is restricted to relatively few species – notably the economically important oyster, mussel and clam species. *Mytilus edulis* is dioecious, living for up to 16 years and having one or two phases of recruitment per annum (Seed 1976). The extreme variability expressed by different populations of this mussel, however, demonstrates the probability of mixed tactics in species which characteristically dominate the dynamic rocky shore environment worldwide.

In the mytilid *Musculista senhousia*, an Indo-Pacific endobyssate inhabitant of intertidal muds, larval settlement occurs periodically and massively so that the species comes to dominate a shore, but quickly dies after a life span of but 18 months and successful reproduction, and vacates the habitat (Morton 1973b). Lee (1985, 1986) has shown that in unpolluted waters the epibyssate *Perna viridis* lives for three years, that reproduction is year round, and growth is to a maximum length of 160 mm. In polluted waters, however, reproduction is confined to a short period in summer, growth rates are reduced and the species dies after but two years. Such mixed tactics are probably more typical of shallow-water marine bivalves than is generally appreciated. It has been shown, for example in the protandric oyster *Crassostrea virginica*, that rapid growth at an early stage may eclipse the initial male phase. Environmental conditions thus influence not just the expression of sexuality (Coe 1938), but also the life history of existing and future generations. On a Washington shore, Suchanek (1981) has shown that *Mytilus californianus*, a large, sturdy, slow-growing mussel with an effective predator-defence mechanism, has a reproductive strategy based on continuous spawning at a very low level. *Mytilus edulis*, on the other hand is a classic fugitive species which rarely attains a large size but matures early and is characterised by a single massive reproductive output each year.

Estimates of bivalve life span generally range from less than one for freshwater sphaeriids to over 67 years for the freshwater unionid *Margaritifera margaritifera* (Stober, 1972). Life span estimates for giant clams (*Tridacna* species) range from eight years (Pelseneer 1894) to several hundred years (Comfort 1957). Bonham (1965) showed that a 520 mm *T. gigas* was in its ninth year at Eniwetok. McMichael (1974) investigated *T. maxima* on One Tree Island, Queensland, and showed that a period of 10–17 years was needed for the clam to attain modal size, but that it may not attain maximum size for 40 years. Similar results were obtained on Takapoto Atoll by Richard (1977) who showed that at a length of 118 mm, a specimen of *T. maxima* had attained 95% of its maximum theoretical length.

Turekian, Cochran, Kharkar, Cerrato, Vaisnys *et al.* (1975) used ^{228}Ra to determine the age of *Tindaria calistiformis* from 3800 m in the West Atlantic and demonstrated that a length of 8.4 mm is attained in about 100 years. Thus almost certainly, abyssal and hadal bivalves exhibit the greatest longevity among bivalves. Under such stable environmental conditions, the maintenance of a population with a reduced fecundity is associated with (a) better survival and/or (b) a longer reproductive life span. Deep-sea bivalves must thus either live longer and/or reproduce more often.

The teredinids are true r-strategists that bore in wood, progressively (sometimes rapidly) destroying their own habitat. Turner & Johnson (1977) have investigated the life history traits of various teredinid groups, demonstrating that reproductive strategies and environmental tolerances dictate their life histories. This is best illustrated in deep sea species such as the wood-boring Xylophagainae, the life histories of which contrast sharply with those of other deep-sea denizens that are K-strategists. Turner (1973) demonstrated that at *ca* 2000 m, wood placed on or near the sea floor was riddled by species of *Xylophaga* and *Xyloredo* within 104 days, with evidence of two settlements (Culliney & Turner 1976). Burrows were 30 mm long and occupants were mature, containing up to 35 000 extremely small eggs. These bivalves are reminiscent of freshwater opportunists.

Ecology

Concomitant on the Mesozoic Marine Revolution (Vermeij 1977) and the stamp of modernity upon the present day fauna, the Bivalvia has radiated into all major aquatic habitats. Bivalves are either epifaunal, typically living attached by proteinaceous byssal threads or cement to the surface of stones or other organisms, or are infaunal, living buried to various depths within the substratum. Some bivalves, such as the teredinid shipworms, bore into wood. Others, such as the lithophagine date mussels, bore into calcareous substrata. A few are endosymbionts, living within other organisms. Bivalves can be found from the intertidal to hadal reaches of the oceans as well as in streams, lakes, ponds and most other freshwater or estuarine systems.

The filter-feeding mode of life imposes obvious constraints upon the bivalve lifestyle, restricting the animals to aquatic habitats. During seasonal or tidal droughts, certain highly specialised species can survive without access to water for long periods, for example, the African lake unionid *Aspatharia* for many months, and the mangrove corbiculid *Polymesoda erosa* (Morton 1985d) for up to 90 days. At these times, as can occur in many intertidal bivalves, for example, *Mytilus* and *Perna* (Davenport 1983), aerial respiration can take place across the exposed posterior mantle margin.

High population densities are not uncommon for some bivalves. One estimate gives mactrid densities reaching 8000 per m^2 and covering about 2500 km^2 of the Dogger Bank in the North Sea (Russell-Hunter 1983). Similarly in fresh waters, the invasive pest *Corbicula fluminea* attained densities of 131 000 per m^2 in the Delta-Mendota canal, California (Eng 1979). Wells *et al.* (1980) found densities of the galeommatid *Arthritica semen* in the Peel-Harvey estuary of Western Australia to be extremely variable over time, with a maximum of 27 847 per m^2.

Specialisation in another lineage has led to representatives of the Galeommatoidea becoming symbiotic and developing what appears to be a semi-parasitic relationship with holothurians (Boss 1965). Little is know of these taxa, some of which are probably among the rarest of species.

The basic bivalve form is specialised for close contact with the substratum. No extant bivalves are truly pelagic, the closest being *Planktomya henseni* (Moore 1983) that is benthic as an adult, but has an unusually long planktonic larval stage. A few bivalves, however, can swim. 'Swimming' in solemyids (Reid 1980) and solens (Stanley 1970) cannot be considered true swimming for in reality the jets of water they produce from the pedal gape are currents to facilitate faster slippage through the sediment. Similarly, swimming in *Lima* is for retreating into caves (Gilmour 1967). True swimming is seen only in the Pectinoidea (Yonge 1953) and is used largely for defence, as an escape reaction. Only species of *Placopecten* (Caddy 1968) and *Amusium* (Morton 1980a) are capable of sustained horizontal flight which is not an escape reaction and may be concerned with reproductive migrations. Australian scallop trawlers are familiar with the propensity of *Amusium* species to swim in mid-water. Except for this one group, therefore, bivalves generally either burrow into soft deposits, or attach themselves to (sometimes boring into) hard substrata.

The Bivalvia probably arose as a burrowing deposit-feeder on the continental shelf. Radiation from this base has taken the group offshore into the deepest seas where the protobranchs are still dominant (Knudsen 1979), and the anomalodesmatan septibranchs are carnivorous (Morton 1987b). Benthic lamellibranch bivalves dominate generalist habitats in shallow waters worldwide. Of the various subclasses, two – the Heterodonta and the Pteriomorphia – are important ecologically. The majority of the Heterodonta are burrowers. They are relatively modern and are mostly suspension-feeding bivalves although a few are deposit-feeders. The Pteriomorphia, a relatively older lineage, is epibyssate and dominates hard substrata everywhere. Some of their older representatives are endobyssate, occurring sometimes in byssal cocoons; thus they illustrate the way the group has evolved (Stanley 1970). Shallow-water Protobranchia are infaunal or epifaunal solitary species.

The great majority of the Pteriomorphia and Heterodonta are ecological generalists, occupying a wide diversity of microhabitats. Most rely upon lecithotrophy and a planktonic larval life to effect dispersal. They thus apportion the shallow marine domain virtually everywhere. In direct contrast are the Anomalodesmata. Modern day representatives of this ancient group are highly specialised, occupying narrow niches inshore, but wider zones of the abyssal plains (Morton 1985c). They are self-fertilising hermaphrodites, with a very short or no planktonic stage. The option is for low vagility, and thus to maintain colonisation of a specialised microhabitat. The Anomalodesmata, inshore, therefore can be considered to have failed ecologically in competition for broad environmental dominance, and have survived as specialised remnants of a once populous stock.

In fresh waters, the Heterodonta play effectively the same role as in the sea, except that, because they originated in sea there has been profound physiological and reproductive change, facilitating sustained colonisation of flowing waters. The Palaeoheterodonta in fresh waters occupy similarly soft deposits in larger lotic and lentic water bodies. The Etheriidae (Unionoidea) have produced cemented species in South America (Yonge 1978b). Only a few epibyssate groups, for example, the Dreissenoidea and *Limnoperna fortunei* (Mytiloidea), have colonised hard substrata in fresh waters.

With the exception of the largely abyssal, predatory septibranchs, the Bivalvia are primary consumers, typically exploiting the rich soup of organic material of the ocean. The reproductive vigour of the two dominant subclasses provides great potential for trophic transfer. Bivalves are highly placed in the diets of many predatory groups. Of special importance in this respect are crabs, starfishes, fishes and caenogastropods, with representatives of many families, to a greater or lesser extent, feeding upon them. Among gastropods, such families include the Muricidae, Naticidae, Buccinidae and Fasciolariidae (Taylor 1981).

Behaviour

The behaviour of bivalves has elicited little interest because most are sessile, acephalic filter-feeders.

All bivalves show alternating phases of quiescence and activity, expressed in the phasic adduction of the shell valves. This has been most researched in the Unionoidea (Salanki 1964), though it is characteristic of all studied bivalves, and is concerned with feeding. Morton (1973c) proposed that the adductions pumped water into and out of the mantle cavity to make the filter-feeding process more efficient. The period of quiescence corresponds to a phase of digestion. Such a rhythm is related to and regulated by the environmental variables of the tides and night and day (Morton 1983a).

Protectively enclosed within their shell valves and either immured in or attached to the substratum, bivalves lack complex behavioural patterns. The settling larva has a range of responses to light-dark, up and down, current flow and substratum composition, that enable it to seek out the microhabitat suitable for adult occupation. Such responses are best known for oysters and mussels (Waller 1981).

In the adult, behavioural responses mainly relate to defence; sensory reception is largely the function of the posterior mantle margin. Light sensitive nerves, photophores or more complex eyes, respond to light, resulting in a shadow reflex of siphonal contraction (Sharp 1883). In *Laternula*, the shadow reflex results in tentacles flicking sand grains over the siphon tips for camouflage. Stronger stimuli will cause an epifaunal bivalve to seal the shell tightly by contraction of the slow adduction muscle blocks; infaunal species respond by digging. In giant clams, the exhalant siphon can be directed and a jet of water expelled with sufficient force to drive off grazing fishes (Stasek 1965a).

Stasek (1967) has reviewed autotomy in the Mollusca. The bivalve mantle margin contains many glands, some of which may produce noxious defensive chemicals. Gilmour (1967) has described autotomy of the pallial tentacles of *Lima* (Fig. 4.22C) with concomitant release of such a chemical. Species of *Solen* have jointed siphons (Fig. 4.22B) which can autotomise and regrow (Morton 1984b). Many species among the commensal

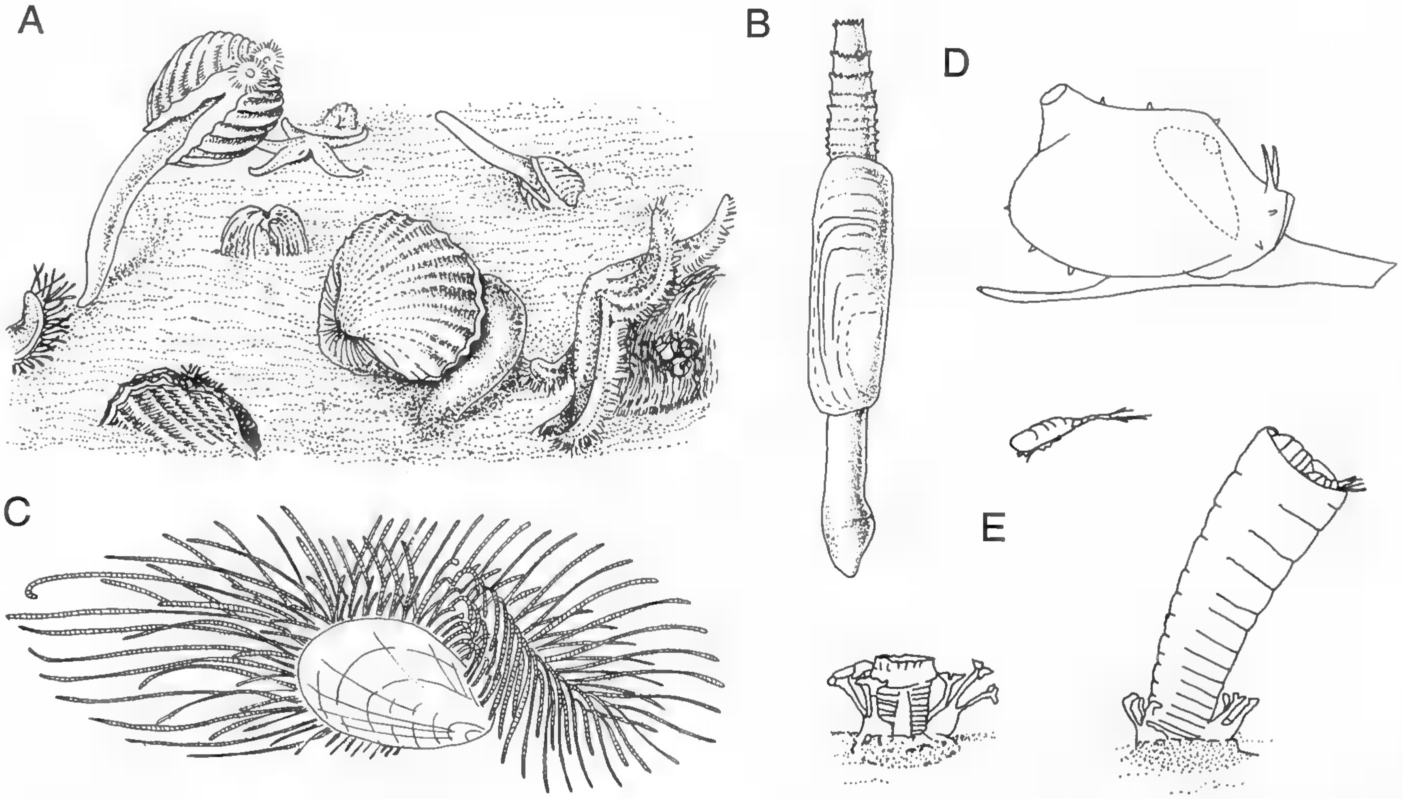

Figure 4.22 Bivalve behaviour. **A**, the escape response of *Cardium echinatum* (Cardiidae) when touched by the starfish, *Asterias rubens*. **B**, **C**, organs autotomised in defence: **B**, the siphon of *Solen* species (Solenidae); **C**, the tentacles of *Lima lima* (Limidae). **D**, the reflected mantle of *Phlyctaenachlamys lysiosquillina* (Galeommatidae) with defensive tentacles. **E**, the mechanism of prey capture in *Cuspidaria cuspidata* (Cuspidariidae). (A, after Gunnar Thorson's Christmas card for 1959; B, after other source; C, after Gilmour 1967; D, after Popham 1939; E, after Reid & Reid 1974) [B. Morton]

Galeommatoidea have large tentacles arising from the reflected mantle (Fig. 4.22D). Morton (1975) has described dymantic display in *Galeomma polita* whereby two large tentacles rapidly evert to thrash about, confusing a would be predator. In *Galeomma takii*, too, smaller pallial tentacles can erupt to release a noxious chemical (Morton 1973d).

In shallow-burrowing species such as members of the Cardioidea and other 'cockles', for example, *Neotrigonia*, defence lies in 'leaping': the foot is dramatically extended, followed by contractions that cause the animal to flip about energetically (Fig. 4.22A; Woodward 1851–1856). Scallops (Pectinoidea) can swim to avoid predation. 'Bites' of water are forced out from each side of the auricles to drive the animal through the water, as seen for example, in *Amusium* species (Morton 1980a).

The most complex behaviour is seen in the mostly abyssal septibranch predators where a raptorial siphon is everted to catch swimming prey (Fig. 4.22E). Complex siphonal receptors respond to the vibrations of living prey (Reid & Reid 1974) by orientating the siphon towards it. In all deep-water predatory bivalves, similarly complex behaviour patterns occur and have been reviewed by Morton (1987b). Their evolution attests to the remarkable plasticity of the bivalve form. Those features and simple behaviours that equip most Bivalvia to a passive filter-feeding life mode have been modified to evolve a lineage or lineages of passive predators.

Economic significance

The economic importance of the Bivalvia is centred around four aspects: (1), their food potential; (2), their pearls and other shell objects; (3), their role in marine biodeterioration and (4), their value as bioindicators of organic and industrial pollution.

Sea food

The FAO Yearbook of Fishery Statistics: Catches and Landings (1983) records that in 1983, the total world catch of molluscs included 302 000 tonnes from inland waters and 5.45 million tonnes from the sea. The majority of the marine molluscan catch is bivalve including: clams, 1.3 million tonnes; oysters, 1.0 million tonnes; mussels, 0.7 million tonnes; scallops, 0.5 million tonnes.

Australia has a small marine mollusc fishery. Bivalves are an economically important component of this, accounting for 70% of the catch by weight, and almost all production through aquaculture. Statistics for 1993–1994 break down the Australian bivalve production (for food) as follows: scallops (21 820 tonnes), oysters (11 002 tonnes) and mussels (540 tonnes), clams (705 tonnes) (ABARE 1994). Scallops and oysters have a high market value, compared with other mollusc fishery products, so that their relative financial value is much greater than their relative weight.

The most important marine bivalves that are fished for food in Australia include the scallops, *Pecten fumatus*, *Equichlamys bifrons*, *Amusium balloti* and *Amusium pleuronectes*; the oysters, *Saccostrea commercialis*, *Saccostrea amasa*, *Saccostrea echinata*, *Crassostrea gigas* and *Ostrea angasi;* and the mussel, *Mytilus edulis planulatus*. The scallops are harvested from the wild by dredging and trawling. Most of the mussel and oyster production is from 'farms' where juveniles collected from the wild are cultured in grow-out areas.

The Sydney rock-oyster (*Saccostrea commercialis*) has been harvested and cultivated in eastern Australia for more than 150 years. Production has varied enormously during that period. Currently the annual value of the industry is around $37 million from about 5000–6000 tonnes. Most of the production comes from oyster farms in bays and estuaries on the coast of New South Wales, but the species is also cultivated in southern Queensland. A review of the farming methods has been given by Holliday, Maguire & Nell (1988). In North Queensland two other species of *Saccostrea*, *S. amasa* and *S. echinata*, are harvested by hand-picking from the wild. The introduced Pacific oyster (*Crassostrea gigas*) is also cultivated in south-eastern Australia, most notably in Tasmania where the annual production is valued at around A$10 million. For many years the flat oyster (*Ostrea angasi*) has been harvested from the estuaries of southern Australia, particularly in Victoria, Tasmania and South Australia, but the scale of that fishery has always been minor. Attempts in Victoria to develop a culture industry using the flat oyster have not yet been successful.

There is a small fishery based on harvesting the blue mussel (*Mytilus edulis planulatus*) from the wild in southern Australia. Farming of this species was begun in the 1970s and now accounts for significant production in southern New South Wales, Victoria, Tasmania and southern Western Australia. Hickman, Sause & Johnstone (1983) reported an annual harvest of 750–1000 tonnes in Port Phillip Bay.

There is a small fishery based on the Pipi, *Donax (Plebidonax) deltoides*, which is harvested on open ocean beaches in south-eastern Australia, mostly in New South Wales where the fishery is valued at about A$0.5 million annually. Other bivalves fished from the wild in small numbers include cockles of the venerid genus *Katelysia* taken on intertidal sand flats in southern bays and estuaries, and an arcid species, *Anadara trapezia*, collected from intertidal mudflats in New South Wales, Victoria and Western Australia.

Pearl shell and pearls

The most valuable bivalve fishery in Australia is based on pterioid oysters of the genus *Pinctada* and, to a lesser extent, *Pteria*. The most important species is *Pinctada maxima* (the gold-lipped pearl oyster) which is fished and cultivated commercially in northern Australia, mainly in the vicinity of Broome, Western Australia and North Queensland between Cairns and the Torres Strait. Traditionally, the fishery was based on the harvest of shell from wild populations for the mother-of-pearl market, with the take of natural pearls being supplementary, but since World War II this species has been extensively cultivated for the production of cultured pearls. The annual production of cultured pearls in Western Australia is currently valued at about A$55 million and in North Queensland at about A$20 million. The technology of the industry is changing rapidly. At present the stock is collected by divers from wild populations, inoculated in the field, and later transferred to grow-out areas on 'pearl farms' in sheltered bays (Scoones 1988). Current research on the technology of hatchery culture may lead to changes in these procedures.

A smaller species, *Pinctada albina*, is cultured in Shark Bay. As early as the 1850s this oyster was harvested in Shark Bay mainly for its small, but colourful natural pearls, the shells being too small for the mother-of-pearl trade. The Shark Bay pearl industry collapsed in 1939 but it is now being revived as a pearl culture venture.

Biodeterioration

Shipworms (Teredinidae) are borers of wooden structures in the sea and have an economic importance which is difficult to quantify. Australian shipworms were reviewed by Marshall (1973). Species of the mytilid subfamily Lithophaginae bore in calcareous rocks, most commonly in relatively soft coralline limestone, but some bore in living coral colonies. Lithophagines undoubtedly have an important role in coastal erosion, especially in the intertidal zone, although it is not possible to determine their economic impact.

Bivalve fisheries, especially those based on cultivation in bays and estuaries, are vulnerable to pollution. For example, diatom blooms may have serious detrimental effects on the marketability of mussels and oysters. Although it is impossible to put a figure on the impact of pollution upon fishery resources, studies on bacterial contamination of oysters (Son & Fleet 1980), the thermal impact of power stations on mussels (Wallis 1977) and the impact of heavy metal on oysters and mussels (Talbot & Chegwidden 1982; Thompson 1982; Wootton & Lye 1982), reveal much for concern. Parasitic infections of commercial bivalves, especially pearl oysters are important and have been reviewed by Wolf (1979).

Smith (1992) noted that small freshwater bivalves of the genus *Corbicula* have become pests in inland towns of south-eastern Australia where they block water reticulation systems, irrigation pipes and monitoring equipment.

Bioindicators

Suspension-feeding bivalves, because they accumulate suspended particles on their gills, are useful indicators of water quality in coastal waters. The common mytilid *Mytilus edulis planulatus* is used extensively as a bioindicator in southern Australia. For example the Western Australian Environmental Protection Authority and Health Department regularly use this species to monitor bacterial and heavy metal pollutants in Perth metropolitan waters. The Sydney Water Board has initiated a monitoring programme of the same kind called 'Mussel Watch', seeking information on pollution of coastal waters by organochlorides and trace metals from sewage outflows. The New South Wales Environmental Protection Authority has initiated a similar programme but using the oyster *Saccostrea commercialis*. Background references may be found in Talbot (1985, 1987).

BIOGEOGRAPHY

General accounts of the distribution of Australian marine and inland aquatic plants and animals have been given by Ponder & Wells (Chapter 1), Williams (1980), Williams & Allen (1987), Williams & Campbell (1987) and Wilson & Allen (1987). These works all refer to Australian bivalves that exhibit similar distribution patterns to those of aquatic gastropods and other invertebrates. More detailed, but more restricted (geographically or taxonomically) accounts relating to bivalves are given by Wilson & Stevenson (1977, for marine Cardiidae), Walker (1981, freshwater mussels) and Smith & Kershaw (1979, freshwater molluscs of south-eastern Australia).

Keast (1981) suggested that the Australian fauna is composed of organisms having their 'roots' in New Guinea, Asia and Gondwana, as well as autochthonous members. This appears to be true of both the coastal marine and the inland aquatic bivalve faunas.

Long geographical isolation of the Australian continent, a generally flat topography, and an overall climatic aridity have led to the development of an inland aquatic fauna that is distinctly Australian (Williams & Campbell 1987). The freshwater bivalve fauna of Australia is depauperate. Only three families are represented: the freshwater mussels (Hyriidae), the pea-shell mussels (Sphaeriidae) and the orb-shell mussels (Corbiculidae). They were catalogued by Smith (1992).

The hyriids are moderately large mussels inhabiting mostly permanent waters of rivers, lakes and billabongs. There are six genera and 18 described species, some confined to particular catchments but others widespread. Like other unionoideans they have glochidia larvae that parasitise fish and this has an influence on their dispersal and distribution. The family is a Gondwanan relict, being known only from Australasia and South America. Only one of the genera is endemic to Australia. Walker (1981) has discussed the distribution of hyriids in Australia: as might be expected they are concentrated in the wetter areas of the north and east, with only one species in the wet areas of the south-west.

The Corbiculidae are a freshwater and estuarine family confined to Asia, Australia and Oceania. Three corbiculinid genera were listed by Smith, (1992) for the Australian fauna, none of which is recorded from the south-west. The Sphaeriidae is a cosmopolitan family and has two Australian genera. The species taxonomy of both families remains unresolved and little can be said of their distribution patterns at the species level. Some of these bivalves, however, live in ephemeral pools and streams, and both families are represented in the arid and semi-arid areas of Australia as well as in the wetter coastal areas.

There has been relatively little work specifically on the species distribution patterns of Australian freshwater bivalves. Some important works that outline the distribution of freshwater mussels include those of E.A. Smith (1882), May (1932), Gabriel (1939), Iredale (1943), McMichael (1967), Smith & Kershaw (1979) and Walker (1981). McMichael & Hiscock (1958) found high local endemism for some hyriids, but a wider distribution for sphaeriids

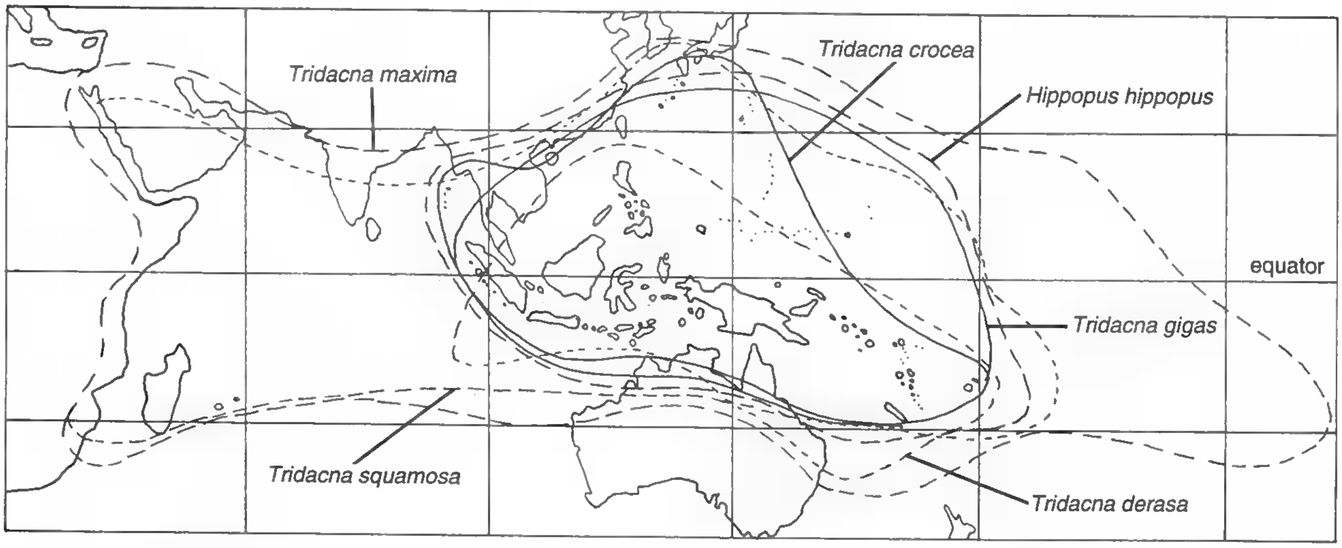

Figure 4.23 The distribution of the various species of *Tridacna* and of *Hippopus hippopus* in the Indo-Pacific. (After Yonge 1975) [B. Morton]

and corbiculids. Walker (1981) reviewed the concept of fluvifaunulae, as defined by Iredale & Whitley (1938) and revised by McMichael & Hiscock (1958), and found little correlation between the distribution of specific taxa and the provinces defined in the earlier works.

Of pivotal importance in the zoogeographic studies of inland water bivalves must be an analysis of dispersal mechanisms. Because adult bivalves are typically sedentary, they often take circuitous routes in their dispersal behaviours. Hyriids produce parasitic glochidial larvae (Fig. 4.21B) that attach for some time to host fish (phoresy) and it might be expected that geographic distribution of the mussel species would correspond to that of their more motile hosts. Although this type of dispersion is well known for unionids in North America, there is little documentation of it in Australian hyriids. Atkins (1979) examined the glochidial stages of *Hyridella drapeta* and its association with its host fish in Victoria. Adult freshwater mussels have been documented as being 'accidentally' carried by various waterfowl (Cotton 1934, 1961; McMichael & Hiscock 1958) and could be distributed along their migratory fly-ways.

Some extralimital corbiculoids, *i.e. Corbicula*, are able to disperse by a form of mucoid drogue line (Prezant & Chalermwat 1984), thus extending their downstream distribution. McMichael (1967) suggested that the small size and light shell of the Australian *Corbicula (Corbiculina)* species could allow ready dispersal in moving waters. Tan Tiu & Prezant (1989b) speculated that the numerous canals that penetrate the shell of *Corbicula* lighten the shell, thus making transport and dispersal easier. Sphaeriids, also small and light bivalves, could be dispersed by attachment to insects or birds, and have been reported to be transported by wind (McMichael 1967). Clearly the wide distribution of these viviparous bivalves reflects their high vagility.

Freshwater molluscs generally exhibit high intraspecific variability and wide geographic ranges (McMichael 1967). The distribution of extant freshwater bivalves in Australia may be primarily a reflection of historic drainage patterns that provided corridors for ancient dispersal. There is evidence that during the environmental fluctuations of the Pleistocene numerous streams and rivers merged and a land-bridge from Tasmania to mainland Australia existed (Walker 1969). This afforded opportunities for dispersal through aquatic confluences that no longer exist. Mulcahy & Bettenay (1972) have documented ancient water beds for Western Australia that could now explain distribution of present day hyriids. The existence of parallel hyriid faunas in Tasmania and mainland Australia also supports the concept of a transitory land-bridge as a migratory route (Walker 1969). Vicariance could also help to explain the present distribution of the Corbiculidae and Sphaeriidae. It is possible that they are very old groups that were widely dispersed prior to the breakup of Gondwana.

Some bivalves (anthropochores) are easily transported by humans and may be introduced to new habitats, often with detrimental effects. So far there are few records of foreign bivalves being introduced to Australian inland-water habitats but there is potential for this to occur as it has elsewhere. For example, the Asian clam *Corbicula fluminea* infiltrated North America in the 1930s and is now among the most common of freshwater bivalves on that continent. With few natural predators and dispersal by larval and juvenile stages, it rapidly became a pest species, clogging water intakes and power plants and perhaps disrupting the natural biota (Britton 1986). More recently, the zebra mussel, *Dreissena polymorpha*, has invaded North America through ballast waters dumped into Lake Erie. This prolific mussel is spreading at alarming rates and is also clogging water intakes, shutting down power plants and destroying the natural unionid fauna (Mackie 1991).

Estuaries and marine harbours are also vulnerable to the introduction of foreign bivalves. A striking Australian example has been the introduction of the prolific Asian estuarine mussel *Musculista senhousia* to eastern and western estuaries (Slack-Smith & Brearley 1987; Willan 1987). This aggressive species appears to have been introduced by means of ships' ballast water.

Wilson & Allen (1987) interpreted the fundamental difference between the tropical northern and temperate southern Australian marine faunas in vicariance terms. A distinct south-eastern Australian marine biogeographic province is recognisable throughout the middle and late Tertiary from rich fossil deposits in south-eastern Australia (Darragh 1986). This is believed to have had its origins in the southern high latitude fauna around Gondwana in the Mesozoic. The major portion of the large endemic element in the modern marine fauna of the Southern Australian Region has these affinities.

The marine fauna of northern Australia has a different composition. Most of its species and genera are widely distributed in the Indo-West Pacific Region (for example *Hippopus hippopus* and *Tridacna* species, Fig. 4.23) and local endemism is relatively low (Wilson & Allen 1987). The Tertiary ancestry of this fauna is found in the ancient pantropical Sea of Tethys.

These two great marine biological provinces interacted through the late Tertiary and the Pleistocene along the eastern and western margins of the continent. There is a significant degree of endemism in the eastern and western transition zones. Impingement of Tethyan elements into south-western temperate waters is particularly evident. Thus, the dispersalist model is relevant in the eastern and western zones of biogeographic overlap. Most bivalves, with their planktonic larvae, are highly vagile.

Wilson & Allen (1987) used two families, the pteriomorph Mytilidae and the heterodont Cardiidae, to illustrate the typical distribution patterns of Australian marine bivalves. Of the 26 mytilid genera in the Australian fauna, five are endemic to the eastern and southern coasts, five are confined to the tropical Indo-West Pacific, and sixteen are either cosmopolitan or pantropical. Of the ten cardiid genera six are either cosmopolitan or pantropical and three are confined to the Indo-West Pacific and Southern Australian regions. The tenth cardiid genus, *Nemocardium*, is cosmopolitan but has a subgenus (*Pratulum*) which at the present day is restricted to southern Australia and New Zealand. Tertiary fossil species of *Pratulum* are found in Europe and can be regarded as Tethyan taxa.

In both families the majority of species are in the tropical north, most of them being widespread in the Indo-West Pacific Region. In the east and west coast transition zones there is progressive loss of tropical species with increasing latitude and replacement by temperate species.

There are no endemic species among the 32 tropical mytilids in northern Australia, although one species, *Brachidontes ustulatus*, has an unusual distribution from Broome to the southern coast of Western Australia and possibly as far east as South Australia. Conversely, most of the 17 temperate mytilids are endemic to the Southern Australian Region or common to that region and New Zealand. There are four endemic mytilids on the west coast and 11 on the east coast. Of the 35 living Australian cardiids, seven are endemic to the north-west and west coasts, and three are endemic to the southern temperate region. The three southern endemics all have fossil antecedents in the Tertiary of south-eastern Australia.

Several marine bivalve genera warrant particular notice. The endemic genus *Neotrigonia* has a circum-Australian distribution with six species, one in the tropical north, one in the south-west and four in the south-east. The Trigoniidae had a cosmopolitan distribution in the Mesozoic but, bar this single Australian genus, is now extinct. According to Darragh (1986), *Neotrigonia* evolved in the Middle Miocene from its south-eastern Australian Palaeogene ancestor *Eotrigonia*.

The genus *Mytilus* is thought to have its origins not earlier than the Pliocene. *Mytilus edulis* has a temperate, bipolar distribution with populations in the temperate regions of both the Northern and Southern Hemispheres, including one in southern Australia. The southern Australian population is assigned subspecific status as *M. edulis planulatus*. However, biochemical studies of this species worldwide have indicated that it may be more complex than previously recognised and that more than one species may be present in Australian waters (McDonald, Seed & Koehn 1991).

Several other temperate Australian marine bivalves show similar bipolarity. The mytilid genus *Trichomya* has a Miocene fossil record in south-eastern Australia and Japan. The only surviving species is *T. hirsutus* in south-eastern Australia. *Pecten sensu stricto* is a temperate genus that appears to have originated in the Northern Hemisphere and arrived in temperate and subtropical waters of Australia in the Pleistocene. The means by which these temperate bivalves 'jumped' the tropical zone is not understood. Whether the explanations are to be found in either vicariance or dispersalist interpretations, or both, remains conjectural.

FOSSIL HISTORY AND PHYLOGENY

Bivalves have been recorded from the early Cambrian (Runnegar & Bentley 1983) and are well known from Cambrian strata of Australia (Pojeta & Runnegar 1985). Species of *Pojetaia*, among the earliest of the bivalve genera, are found in the Early Cambrian of South Australia (Pojeta & Runnegar 1985; Bengston, Conway Morris, Cooper, Jell & Runnegar 1990). *Fordilla* is another well known genus, distributed worldwide, from the Middle and Upper Cambrian, although it is unlikely that *Pojetaia* predates *Fordilla* significantly (Runnegar & Pojeta 1992).

It has been suggested that scaphopods and bivalves arose from an extinct, Palaeozoic group of bivalved molluscs known as rostroconchs. Pojeta & Runnegar (1976) distinguished the Palaeozoic class, Rostroconcha, placing it with the Bivalvia in the subphylum Diasoma (Runnegar & Pojeta 1974, 1985), the rostroconchs being perceived as the older of the two groups. Pojeta & Runnegar (1985) suggested that Early Cambrian Monoplacophora, in turn, were the stem group for the rostroconchs.

Rostroconch larvae had a single valve that became pseudobivalved during metamorphosis to adulthood (Pojeta & Runnegar 1985). This type of shell, which was laterally compressed, had a pair of valves that were inseparable, being united by continuous shell layers that traversed the dorsal margin. Although their internal anatomy may have been similar to that of primitive bivalves, rostroconchs may have had a radula (Pojeta & Runnegar 1985). Rostroconchs diversified and radiated in the Early Ordovician, prior to the large radiation of the bivalves in the Middle Ordovician (Pojeta 1978). As bivalves diversified, rostroconchs slowly decreased in numbers and range.

The lateral compression of the shell in rostroconchs, and later in bivalves, allowed these animals to occupy an infaunal position, yet still be able to move through the sediment. The development of a muscular, laterally compressed, burrowing foot in the bivalves was another important step towards their evolutionary success. Most importantly, the bivalves developed a flexible ligament joining the two shell valves. Runnegar & Pojeta (1985) suggested that an adductor muscle or, more likely, a pair of muscles of unequal size, preceded the development of the ligament. With development of the flexible hinge line and adductor muscles, the bivalves were able to diversify and radiate into new habitats.

Structure of teeth, ligament and muscle scars have been documented for both *Pojetaia* and *Fordilla*. There are many similarities between these two Cambrian genera including small size, an external opisthodetic ligament, heteromyarianism, a discontinuous pallial line and umbonal muscle scars (Pojeta, Runnegar & Kriz 1973; Pojeta & Runnegar 1974, 1985; Pojeta 1975, 1978; Jell 1980; Runnegar & Bentley 1983). Runnegar & Pojeta (1992) discerned a likely homologous shell microstructure in *Pojetaia* and *Fordilla*, helping to confirm a close relationship between the two genera. Additionally, the prodissoconch structure and shell ultrastructure of *Pojetaia* were described by Runnegar & Bentley (1983).

Both *Pojetaia* and the similarly small Middle Cambrian New Zealand bivalve *Tuarangia* (MacKinnon 1982) had characteristics similar to Ordovician members of the Nuculoida (= Paleotaxodonta). Clarkson (1986) discussed the possibility that these were in fact the 'rootstock' for most groups of bivalves. Based on similarities in shell structure and shell scars which give clues to internal morphology, Runnegar & Bentley (1983) suggested that *Pojetaia* actually represents the most primitive known member of the Nuculoida. During the Ordovician there was a significant radiation of protobranch bivalves into several hundreds of species spread over 30 genera.

Pojeta & Runnegar (1985) grouped *Fordilla* with the modiomorphid mytiloids (= Isofilibranchia) which may thus represent the earliest known representative of the Pteriomorpha.

The roots of all bivalve subclasses were in place by the Middle Ordovician (Pojeta 1978) – details of the Ordovician system of Australia can be found in Webby, VandernBerg, Cooper, Banks, Burrett *et al.* (1981). It appears that the so-called 'Cryptodonta' or solemyoid bivalves and nuculoids had a common origin and that the Solemyidae arose from the Ordovician nuculoid protobranchs. Some of the oldest known Ordovician bivalves are modiomorphid Mytiloida (pteriomorphs) found in the upper Lower Ordovician of Australia (Pojeta & Gilbert-Tomlinson 1977; Babin 1982). Mytiloids are also the likely stem group for anomalodesmatans, which are first recorded from the Middle

Ordovician (Pojeta & Runnegar 1985). All Ordovician pterioids have been placed in the Pterineidae. *Denticelox*, the oldest pterineid discovered to date, is from Australia in lower Middle Ordovician rocks (Pojeta & Gilbert-Tomlinson 1977). Also present by the Ordovician were deep-burrowing lucinoids, capable of constructing mucoid-lined feeding tubes from an infaunal position (Clarkson 1986).

Thus, by the Ordovician, all major bivalve feeding niches were being exploited: deposit-feeding (by protobranchs), shallow-burrowing asiphonate filter-feeding, epifaunal byssal-attached filter-feeding, and deep-burrowing filter-feeding (Clarkson 1986). Particularly due to the development of their burrowing ability through the use of a muscular foot, and the development of a fused mantle to produce elongate siphons, the bivalves have been more successful than the brachiopods and other 'less plastic' groups of sedentary organisms. The predatory life style of some Anomalodesmata arose later, in the Mesozoic, with septibranch ctenidia evolving through muscularisation of the otherwise filter-feeding gill filaments (Allen & Morgan 1981).

The post-Ordovician evolution of the Bivalvia shows few dramatic but many subtle departures from the early Palaeozoic basic stocks. The early development of the byssus, through neotenous retention of a larval structure, ensured many bivalves, particularly among the pteriomorphs, of success in epifaunal habits. Similarly, modifications of the siphons and ctenidia opened infaunal niches and new feeding habits to many bivalves.

Allen (1985) suggested that the stem nuculoids were similar, in many ways, to the juveniles of Recent, extant protobranchiate bivalves. It is thus suggested that aside from being small, the earliest nuculoids were fairly active, with a comparatively large muscular foot that allowed significant mobility. Although asiphonate, the early nuculoids, like Recent members, presumably retained sensory contact with the outside world through a series of small tentacles lining the pallial edge. The well-developed adductor muscles were of unequal size, the anterior being the larger. These bivalves probably lived in the upper few millimetres of organic rich sediments. No palp proboscides were present and palps proper remained small. Allen (1985) suggested that little sorting occurred. Ctenidia were typically protobranchiate, with a primary respiratory function (Stasek 1965b). More recent members of the Protobranchia, including the Nuculoida which are so successful in the deep oceans, have developed larger palps and palp proboscides for probing the sediment surface. The focus of evolution within the Protobranchia has been the ability to move through soft sediments and extract organic components through a deposit-feeding life style. Adaptations include not just enlarged palps and development of palp proboscides and a muscular foot, but also a gut modified to process sediments and remove organic material. Protobranchs have extracellular digestion and a long, coiled gut. Some members of the Nuculanoidea have evolved posterior siphons through separation of the posterior inhalant and exhalant channels (Yonge 1939). Siphonal development assisted in the voiding of faeces and pseudofaeces, as well as increasing respiratory flow to the small ctenidia.

The small order Solemyoida still retains small palps, but lacks palp proboscides. This group retains other primitive features including a more simplified hinge than the Nuculoida. Additionally, some solemyoids harbour chemoautotrophic bacteria in the ctenidia (Cavanagh 1983) that could provide compensatory nutrients in some species with reduced or atrophied guts (Reid & Bernard 1980).

Stanley (1970) categorised bivalves, including living protobranchs, into groups that highlighted their life styles as displayed by extant members, as well as those inferred on the basis of shell form and structure. These groups which help us to understand the radiation of the bivalves include infaunal shallow- and deep-burrowing forms, epifaunal attached forms (byssate or cemented), and free-lying, boring or crevice-dwelling and swimming forms. Examination of the Pteriomorphia, Heterodonta and Anomalodesmata reveals parallel trends leading to similar life styles. The Protobranchia and Palaeoheterodonta are more conservative in their overall life style trends.

Burrowing bivalves are represented in all Recent subclasses. Differences in pedal musculature and siphonal length are often reflected in internal shell scars and can give information on depth of burial. Shallow burrowers do not usually have long tapered shells, unlike, for instance, the deep-burrowing Solenidae. Some deep-burrowing bivalves, however, may not conform to this rule. Some lucinoid bivalves have a near-circular shell but also have a long exhalant siphon and an inhalant siphon associated with a mucoid tube that reaches the sediment surface.

Attached epifaunal forms include many of the Pteriomorphia. These attach by proteinaceous byssal threads (as in *Mytilus*) or through shell cement that attaches them permanently to the substratum. Examples of the latter are the oysters which are among the most successful bivalves. Thick and extensive beds of fossil oysters are known from the Mesozoic and Cainozoic. Among the extinct Heterodonta are hippuritoids or rudistids. These bivalves, from the Upper Cretaceous, were inequivalve with the left valve flattened and sitting on the attached cup-like right valve.

Differentiation of the importance of historical versus recent geographic distributions is of pivotal importance in understanding dispersal patterns in bivalves, but little work on this topic has been published for Australian bivalves. Gene flow among populations of *Tridacna gigas* was examined by Benzie & Williams (1995) who determined that the genetic structure of this species in the West Pacific was based on selection or historical distribution and migration patterns and not recent dispersals correlated with major surface currents.

Among the best known bivalves are some of the swimming pteriomorphs, including the scallops (see section on behaviour). At the other end of the motility spectrum are the bivalves that secure themselves in tight crevices, or bore into wood or limestone. Details of the adaptations and specific phylogenies of various bivalve groups are outlined in the chapters that follow.

CLASSIFICATION

Higher category classification of the Bivalvia is still in a state of flux although a degree of consensus has been reached in recent years. The greatest differences of view in the past have been between the palaeontologists who based their classifications on shell morphology, particularly hinge dentition and muscle scars, and the anatomists who based theirs on features of the anatomy, notably gill structure. Both schools of thought tended to consider single organ systems. In the last few decades, however, there has been a merging of ideas to some extent with more consideration given to multiple organ states together with the fossil record. A review of the history of the matter was given by Newell (1969).

There is now a high degree of consensus on groupings at superfamily level. The principal remaining difficulties are at subclass and ordinal levels. The major divergences within the class took place early in the Palaeozoic and the fossil evidence from that period is not well preserved so that interpretation of early relationships is difficult. Also, subsequent radiation of the main lines include many convergent and parallel trends. For example, the taxodont hinge has evolved twice, first in the protobranch nuculoids and independently in the pteriomorph arcoids. Monomyarian musculature has arisen several times in different lines of the Pteriomorphia. Descriptive words like taxodont and monomyarian that refer to single-organ states have often been converted to formal names of proposed higher category taxa, for example, Taxodonta and Monomyaria. (For a list of available higher category names in the Bivalvia see Cox 1969).

Studies of the comparative anatomy of living bivalves reveal many examples of grades of organisation within organ systems which may be useful for utilitarian classification but do not reflect phylogeny. Some of these studies led to the proposal of higher category classifications which are no longer used. For example, Ridewood (1903) recognised and named three orders on the basis of gill structure, the Protobranchia, Eleutherorhabda and

Synaptorhabda. Pelseneer (1906, 1911) recognised five grades of gill structure, protobranch, filibranch, pseudolamellibranch, eulamellibranch and septibranch and arranged the bivalves in orders accordingly, with those descriptive gill-grade words converted to formal names of five taxa. Iredale (1939) added Isofilibranchia to distinguish the mytiloids which he believed had sufficiently different gill structure to warrant ordinal separation. Atkins (1938c) described two types of latero-frontal ciliation on bivalve gill filaments and proposed division of the class into two groups, the Macrociliobranchia and Microciliobranchia. Purchon (1960, 1963) proposed a different classification and an entirely different set of subclass and ordinal names based on five grades of organisation in stomach structure. Stasek (1963) studied bivalve labial palp structure and recognised three basic types.

Students have great difficulty interpreting the literature because some of these descriptive names are in use as adjectives or vernacular names but not as the names of taxa. For example, one reads of monomyarian bivalves, taxodonts, and lamellibranchs. Some palaeontologists still use the term isofilibranchs when they mean mytiloids.

Newell (1969, table 1) summarised and tabulated available evidence on shell structure and anatomy and presented a classification of the Bivalvia which is now commonly accepted. In his scheme, six subclasses are recognised: the Palaeotaxodonta (= Nuculoida), Cryptodonta (= Solemyoida), Pteriomorphia (= Filibranchia), Palaeoheterodonta, Heterodonta and Anomalodesmata.

Purchon (1978) and Purchon (1987b) also synthesised the diverse available data and subjected it to computer analysis, concluding that his results produced clusters of superfamily groups that corresponded generally with the groupings of Newell. However, he disagreed that the bivalves with lamellibranch gills are worthy of separation at subclass rank and proposed only two subclasses, the Protobranchia and the Lamellibranchia.

The Russian school of malacologists has also attempted a synthesis of palaeontological and anatomical data but has reached rather different conclusions (Nevesskaja, Scarlato, Starobogatov, & Ebersin 1971; Scarlato & Starobogatov 1975, 1978). They recognised three subclasses, the Protobranchia, Septibranchia (= Anomalodesmata) and Autobranchia, the latter combining the pteriomorphs, palaeoheterodonts and heterodonts.

Most contemporary malacologists agree that the bivalves, including the Solemyoida, with protobranch gills plus a range of other distinctive features, are worthy of separation at subclass level. Whether or not the filter-feeding lamellibranch bivalves constitute a single subclass or should be divided as Newell has proposed, remains controversial.

The classification given by Newell (1969) is adopted in this volume, but with one important amendment. The nuculoids and the solemyoids are combined in the subclass Protobranchia and the names Palaeotaxodonta and Cryptodonta are not used. Thus, five subclasses are recognised.

The Protobranchia is considered by many malacologists to be the most primitive subclass. This group of infaunal marine bivalves is characterised by simple 'protobranch' gills, used primarily for respiration. Feeding is typically accomplished with palp proboscides, used to probe the sediment for organic material. Not all protobranchs, however, are deposit-feeders. Some solemyids have chemoautotrophic bacteria that supplement their diet and these bivalves have a reduced gut.

The Protobranchia is composed of two orders. The Nuculoida (by some considered equivalent to the subclass Palaeotaxodonta) has taxodont hinge dentition. The Solemyoida, or awning shells, lacks taxodont dentition and is considered by some to be different enough to be restricted to a separate subclass, the Cryptodonta. Reid (this volume), however, outlines the striking similarities between the two groups and supports the contention that they belong in separate orders but within the same subclass.

The order Nuculoida comprises three superfamilies, each of which has Australian representatives, either extant or extinct. The superfamily Ctenodontoidea, with the monotypic family Ctenodontidae, is Ordovician to Carboniferous bivalves. The Nuculoidea, made up of four families (two extinct), is a group of typically small asiphonate, protobranchiate bivalves. The Nuculanoidea, comprises five families, and its members frequently have posterior siphons as well as palp proboscides. Members of the order Solemyoida have larger ctenidia than nuculoids, as well as smaller palps. Solemyoids have symbiotic (chemoautotrophic) bacteria housed in their enlarged ctenidia. Correlated with this is a typically reduced gut. Only two families are included in the Solemyoida. These are the better known Solemyidae with two living genera, and the relatively poorly known Nucinellidae. The latter family also has a reduced gut and nucinellids are likely to harbour symbiotic bacteria in their ctenidia.

The subclass Pteriomorphia (= Filibranchia of some authors) contains some of the most familiar bivalves including several that are of great economic importance. These include oysters, marine mussels, and scallops. The three (Vokes 1980) to five (see, Chapter 6) orders within the Pteriomorphia contain bivalves that are typically either monomyarian or strongly heteromyarian. Although members of the subclass vary greatly in general shell form and also live in a wide diversity of habitats, they are united by their typically epifaunist habits (byssate or cemented), filibranch or pseudolamellibranch ctenidia (with exceptions), free mantle edge, and reduced foot. Individual pteriomorph species often occur in large numbers, forming, for example, mussel, oyster and scallop beds.

The byssate Mytiloida comprises the single family Mytilidae. These common marine and estuarine mussels have an origin in the Devonian and are common along Australian shores. Their gill structure is a variant on the filibranch scheme and is referred to as isofilibranch, a name which is sometimes used as a synonym of mytiloid.

The order Arcoida, also common in Australian waters and representing the oldest Pteriomorphia, is composed of two superfamilies, the Arcoidea and the Limopsoidea. The arcoids differ from other pteriomorphs in having taxodont hinge dentition and for this reason they were once classified with nuculoids in the order Taxodonta. It is now believed, however, that the taxodont dentition of arcoids is a secondarily derived feature and that there is no relationship with nuculoids.

The largest order within this subclass is the Pterioida which comprises two superfamilies (Pterioidea and Pinnoidea). Members of the order are typically sessile as adults, attached to the substratum by a byssus that emerges through a byssal notch on the right valve. The Pterioidea, consist of four families, the pearl oysters (Pteriidae), hammer oysters (Malleidae), toothed pearl oysters (Isognomonidae), and the monotypic pulvinitid oysters (Pulvinitidae). These groups are characterised by their inequivalve and inequilateral shells although general shapes range from the near circular Pteriidae to the elongate and strongly winged Malleidae.

The superfamily Pinnoidea is composed of the single family Pinnidae, the pen or fan shells. These large and strongly triangular shells, often found in large beds, are partially buried and attached by a strong byssus.

Limoids, all in a single superfamily, the Limoidea, and a single family, the Limidae, are known as file shells. Well known swimming bivalves, these shells often have elaborate and often highly colourful pallial tentacles emerging from the abducted valves.

The Ostreoida comprises two suborders, the Ostreina and Pectinina. The Ostreina which includes the oysters that cement to the substratum comprises three superfamilies, Ostreoidea, Plicatuloidea and Dimyoidea. The free-living or byssal-attached Pectinina comprises two superfamilies, the Pectinoidea (scallops) and Anomioidea.

Members of the subclass Palaeoheterodonta are represented among living bivalves by the primitive marine order Trigonioida and the freshwater mussels, the order Unionoida. The Trigonioida has a single extant genus, the Australian *Neotrigonia*, in the family Trigoniidae. The Unionoida comprises three superfamilies of which only the Unionoidea is extant. Among this superfamily, only members of the Hyriidae are found in Australia. The Unionidae, a much larger family of freshwater mussels, and the Margaritiferidae are most diverse in Asia (China) and North America. Unionoideans typically have a parasitic glochidium stage.

The largest bivalve subclass is the Heterodonta. Diversity is very high within the two extant orders, the Veneroida and Myoida; they contain the majority of living bivalves. The Veneroida comprises about 18 superfamilies, most of which are represented in Australia. Almost certainly polyphyletic in origin, the veneroids typically have a well-developed hinge line and often an active foot that is involved with burrowing. The superfamily Chamoidea has been considered a member of the order Hippuritoida, but is here included in the Veneroida. The Myoida is also probably polyphyletic and is represented by bivalves that are usually siphonate and have fused mantle margins. The Myoida contains four superfamilies: the Myoidea, Gastrochaenoidea, Hiatelloidea, and Pholadoidea, all with Australian representatives.

Perhaps the subclass with the most unusual bivalves is the Anomalodesmata. This large group, with many fossil representatives, contains some of the least known living bivalves as well as some of the most intriguing molluscs. Comprising only a single order, the Pholadomyoida, all members of this subclass are either marine or estuarine. The seven superfamilies contain in turn 13 families. The subclass is united by the presence of similar prismatonacreous shells, modified ctenidia, opisthodetic ligament, lithodesma, typically edentulous hinge, fused mantle margins, arenophilic mantle glands, and Type III or IV stomach, and are typically simultaneous hermaphrodites. The Pholadomyoidea comprises the primitive Pholadomyidae and the more highly derived Parilimyidae. The remaining superfamilies are the Thracioidea, Clavagelloidea, Pandoroidea, Verticordioidea, Poromyoidea and Cuspidarioidea. The latter superfamily contains many of the predatory bivalves.

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SUBCLASS PROTOBRANCHIA

CHAPTER 5

GENERAL INTRODUCTION

The Protobranchia is a group of primitive, marine, infaunal bivalves with origins in the Cambrian. As the name suggests, protobranchs are characterised by the form of their ctenidia, or gills. These resemble the aspidobranchiate or bipectinate gills of some of the Gastropoda, consisting of broad lamellae arising from a central septum (Fig. 5.1). This arrangement contrasts with the narrow, V-shaped gill filaments of most lamellibranchiate bivalves. Traditionally, the ancestral habit of the Protobranchia has been considered to be deposit-feeding, but this hypothesis is inadequate. There is no doubt that some Protobranchia supplement their detrital food by suspension-feeding, and the solemyoid protobranchs depend partially or wholly on a sulphide-oxidising symbiosis with intracellular ctenidial bacteria.

Some authors treat the Protobranchia as a natural subclass of Bivalvia, comprising two morphologically distinct subgroups, the Nuculoida, which have taxodont dentition, that is, a series of peg-like or spiky teeth on each side of the hinge, and the Solemyoida that lack such teeth (Fig. 5.2). Other authors question the legitimacy of Protobranchia as a subclass and recognise two subclasses: Palaeotaxodonta (equivalent to Nuculoida), and Cryptodonta (equivalent to Solemyoida) (see McAlester 1964; Newell 1969). The differences between the two groups of protobranchiate bivalves warrant their separation high in the taxonomic hierarchy. Both groups have the protobranch gill in common, and share striking embryological features, for example, similar pericalymma larvae, which move by action of the cilia of the outer test. There are also shared features of endoderm reorganisation and organogenesis during and after metamorphosis (Gustafson & Reid 1986, 1988a). These similarities suggest a common origin for the two groups and support the argument that Protobranchia is the appropriate subclass, containing two orders, the Nuculoida and Solemyoida. Implicit in this scheme, which is followed by Sanders & Allen (1973), is the argument that dentition alone is an unreliable criterion for distinguishing the orders, since some Solemyoida are not cryptodont and some Nuculoida may not be entirely taxodont. Many of the differences in soft morphology between the orders can be correlated with the establishment of a sulphide-oxidising symbiosis in the Solemyoida, putatively in the Ordovician (Pojeta 1988). This triggered a major divergence of the group, affecting gill morphology and ultrastructure, reducing the other pallial organs, enlarging the foot, reducing or losing the gut, altering shell form, and locomotory and ventilatory behaviour, and effecting correlated biochemical adaptations.

The Silurian bivalve, *Janeia silurica*, has been postulated to be the earliest primitive solemyid (Liljedahl 1984), and living Nucinellidae provide some clues to the functional morphology of types that may have been intermediate between nuculoids and solemyoids (Allen & Sanders 1969; Kuznetzov & Shileiko 1984). Traditionally, Ordovician nuculoids have been considered to be ancestral not only to solemyoids, but also to the lamellibranchiate bivalves. This makes the assumption that the bivalves are monophyletic, which is based on the common bivalved shell structure, affinities in shell and resilium make up, similarities in pallial morphology, and the presence of a common pedal feeding habit in the early juveniles (Reid 1994). However, a sceptical cladist, rejecting tradition for its own sake, might offer the alternative suggestion that the Bivalvia is diphyletic, protobranchs and lamellibranchs having converged from separate origins. The bivalved form is not unique to the Bivalvia, being found in a few gastropods, certain crustaceans and all brachiopods. Moreover, the differences between the two groups are extensive. Among these are the contrast between the pericalymma larva of the protobranchs and the veliger of the lamellibranchs (Gustafson & Reid 1986, 1988a; Gustafson & Lutz 1992); the protobranch gastric structure, which has more in common with some gastropods than with lamellibranchs (Graham 1949; Morton, J.E. 1953; Purchon 1956); the possibly independent origins of the ligament in the protobranchs and lamellibranchs (Waller 1990); and the marked contrast between post-metamorphic pallial morphogenesis in the two groups (Mortimer 1962). In addition, some protobranchs have the blood pigment haemocyanin, which is absent from lamellibranchs, but common in other molluscs (Morse, Meyhofer, Otto & Kuzirian 1986), and recent unpublished research into the mitochondrial DNA of molluscs shows a closer affinity between protobranchs and gastropods than between protobranchs and lamellibranchs (R.G. Gustafson personal communication). All of these points certainly strengthen the case for at least separate subclass status for the Protobranchia.

The question of the ancestral feeding habit has always been central to discussions of the origins of the bivalves, the nuculoid protobranchs being regarded as archetypal (Yonge 1939). The view that the ancestral bivalves were infaunal deposit-feeders, in which the bivalved form was adapted to movement in soft sediments (Yonge 1939), was challenged by Stasek (1972) on the grounds that deposit-feeding organs were secondary developments, and that suspension-feeding using the gills is more important than generally realised. Reid & Brand (1986) supported Stasek's contention and noted that the large palp lamellae of some Nuculidae are also suspension-feeding organs. Early juvenile nuculid protobranchs are pedal feeders, like most other juvenile bivalves, but beyond this early stage the similarity ends and both habit and functional morphology develop in distinctly different ways (Mortimer 1962; Reid, McMahon, O'Foighil & Finnegan 1992). Thus even if protobranchs share a common origin with lamellibranchs, their mature structure and habit constitute a poor model for the ancestor of lamellibranchs. The possibility remains that a minute, epifaunal, pedally feeding, bivalved mollusc with simple labial palps and gill filaments, gave rise to the two groups, Protobranchia and Lamellibranchia (Reid 1994).

The subsequent radiation of protobranchs was discussed by Allen (1978), with particular reference to deep-water representatives. These have undergone a greater diversification than their littoral and continental shelf relatives, possibly due to the lack of competition from lamellibranchiate bivalves. A major factor in their evolution was the elongation of the gut, supposedly correlated with a diet of refractory detritus that required a more extended

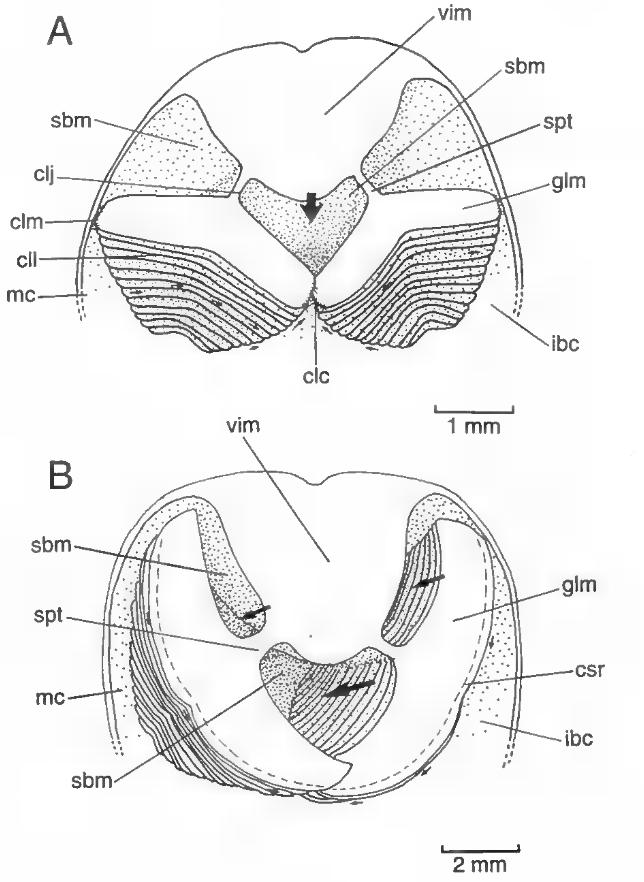

Figure 5.1 Protobranch ctenidia. **A**, solid section of posterior portions of ctenidia of a generalised nuculoid or palaeotaxodont; the lamellae are held together by groups of cilia on the filament faces. **B**, solid section of posterior portions of the ctenidia of a generalised solemyoid (cryptodont); the lamellae are supported by marginal chitinous skeletal elements. Cilia between the filaments are sparse; most of the gill tissue is composed of bacteriocytes that house symbionts. Large arrows depict the direction of water currents; small arrows depict directions of ciliary cleansing and food collecting tracts. Note the differences in proportions in the two figures; the gills of solemyoids are relatively larger than those of nuculoids. **clc**, interlocking cilia between the left and right lamellae; **clj**, ciliary junctions with next leaflet; **cll**, columellar lamella; **clm**, terminal cilia which attach to the mantle; **csr**, marginal chitinous skeletal elements; **glm**, gill lamella; **ibc**, infrabranchial chamber; **mc**, mantle cavity; **sbm**, suprabranchial chamber; **spt**, septum attaching ctenidium to the visceral mass; **vim**, visceral mass. [R.G.B. Reid]

period of extracellular digestion. The general question of digestion in protobranchs, and its evolutionary consequences, has not been investigated adequately. Owen (1959) concluded that nuculid digestion is entirely extracellular, but did not take into account the possibility of pinocytosis in the digestive gland. Reid (1977) compared nuculid digestion with that of carnivorous septibranchs and suspension-feeding and deposit-feeding lamellibranchs, and found that extracellular digestion of protein in nuculids was not much more active than in lamellibranchiate detritus feeders. If deep-sea protobranchs were dependent on refractory scleroproteins, as Allen (1978) argued, one might expect them to have paralleled the septibranchs by increasing the secretion of trypsin and cathepsin B, thus obviating the need for gut elongation. An enlarged gut suggests an active, alimentary symbiosis with bacteria. Allen (1978) noted, however, that there is no evidence of bacterial activity in the guts of deep-sea protobranchs. He also pointed to another, more generally accepted, evolutionary consequence of feeding behaviour in protobranchs, namely, a marked diversification in the Nuculanoidea arising from the shift posteriorly of the inhalant current, and the development of siphons.

All protobranch families are cosmopolitan. The majority of species are subtidal, some are intertidal, and some families extend into the deepest marine abysses. Knudsen (1970) listed 21 hadal species in his survey of deep-water bivalves.

Australian Protobranchia were first collected at the beginning of the nineteenth century. The first solemyids, including the holotype of *Solemya australis*, were taken from King George Sound in Western Australia by *Le Géographe* in 1804 and deposited in the French National Museum by the naturalist Péron (Slack-Smith 1977). Angas collected protobranchs in the 1850s (Angas 1865). In the 1870s the *Challenger* expedition discovered protobranchs at stations 164 and 164B off New South Wales, and at station 185 off the East coast of Cape York. Among these specimens, Smith (1885) identified five new nuculanid species and one new nuculid. Hedley's dredge-samples from the *Thetis*, and his subsequent studies, helped to lay the foundations of Australian protobranch taxonomy (Hedley 1902, 1914). Iredale made important contributions to the discipline between 1915 and 1939. An inveterate 'splitter', he made two of Smith's new '*Leda*' species from the *Challenger* into types of new genera, and revised two of Hedley's nuculanid genera. Concerning Thiele's (1930) 'lumping' of all the Nuculidae under the single genus *Nucula* he remarked, 'such treatment is scarcely worth consideration and incites confusion in every sense' (Iredale 1939). Iredale's publications, especially in the Great Barrier Reef Scientific Reports in 1939, make frequent, illuminating reference to the history of Australian malacology. Further Australian protobranchs were collected by the *Galathea* Expedition from several Australian and New Zealand stations (Knudsen 1970). Cotton (1961) outlined the protobranchs of southern Australia. The early palaeontological literature includes works by Tenison Woods (1879, 1880), Hutton (1885), Tate (1886, 1887), Harris (1897), Pritchard (1901), and Chapman & Singleton (1927). Pojeta & Runnegar (1985) commented on the early evolution of bivalves. Maxwell (1988a) provided taxonomic information on numerous New Zealand fossil protobranch species, and commented on the status of some Australian species.

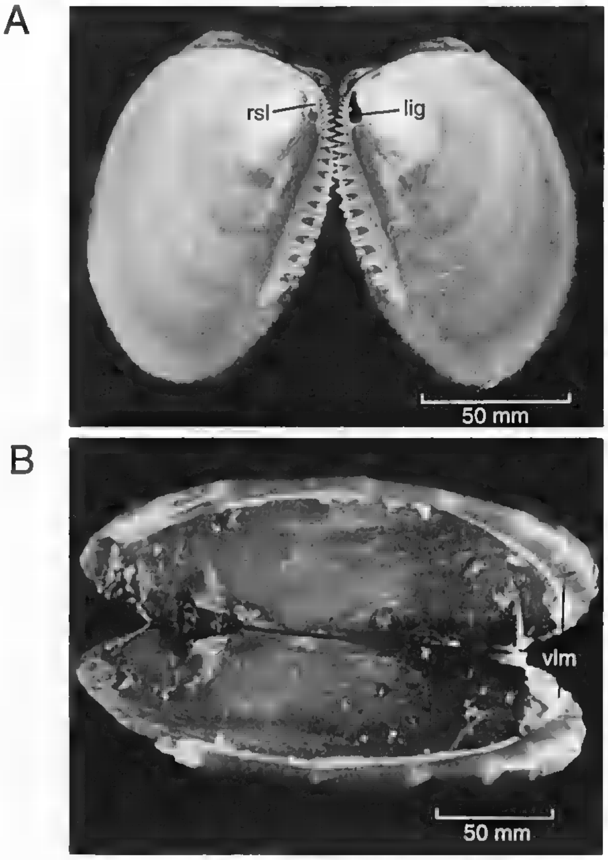

Figure 5.2 Protobranch internal shell features. A, interior of valves of the nuculoid *Acila castrensis* (Nuculidae), showing the peg-like taxodont teeth, the resilifers, the remains of the ligament in the resilifer of the right valve, and the iridescent nacreous layer of the valve interior. B, interior of the valves of the solemyoid *Solemya reidi* (Solemyidae), showing the distinctive ligament of *Solemya sensu stricto* (on the left of the photograph), and the cryptodont hinge which lacks distinctive teeth; also shown are the infolded, non-calcified valve margins. **lig**, ligament; **rsl**, resilifer, **vlm**, infolded, non-calcified valve margin. [R.G.B. Reid]

The most significant early taxonomic work on Protobranchia in general was carried out by Lamarck (1801, 1815–1822), Goldfuss (1820), Gray (1821), Adams & Adams (1853-1858), Neumayr (1883) and Pelseneer (1906). Subsequent general reports and reviews of functional morphology, systematics and evolution of Protobranchia are by Schenk (1934), Atkins (1936), Heath (1937), Yonge (1939, 1959), Korobkov (1954), Ockelmann (1954), Vokes (1955), Purchon (1956), Cox (1959, 1960), Owen (1959, 1974), Stasek (1963, 1972), McAlester (1964), Allen & Sanders (1969, 1973, 1982), Newell (1969), Sanders & Allen (1973, 1977), Allen (1978), B. Morton (1983a), Allen & Hannah (1986), Pojeta (1978, 1988), Maxwell (1988b) and Scarlato & Starobogatov (1978).

CLASSIFICATION

The classification of the Protobranchia is unstable, contributing to considerable confusion in the preparation of this chapter. The higher level classification is outlined in Table 5.1. Maxwell (1988a, 1988b) has addressed some of the problems with the taxonomy of the subclass, but further revisionary work is required and for that reason, the family Malletiidae which is not yet recorded for Australia, although known from the Australasian region, is included among the following family treatments.

Table 5.1 Classification of extant families in the subclass Protobranchia. Families indicated with an asterisk are not recorded for the Australian fauna.

Subclass **PROTOBRANCHIA**
Order NUCULOIDA
    Superfamily NUCULOIDEA
        Family Nuculidae
        Family Pristiglomidae*
    Superfamily NUCULANOIDEA
        Family Malletiidae*
        Family Neilonellidae
        Family Nuculanidae
        Family Sareptidae
        Family Siliculidae*
        Family Lametilidae*
Order **SOLEMYOIDA**
        Family Solemyidae
        Family Nucinellidae

Order NUCULOIDA

Nuculoids have relatively small gills and large labial palps. They usually have taxodont dentition, and, when present, the external ligament (the elastic proteinaceous element that attaches the two valves), is never globular (Sanders & Allen 1973). This group is the taxonomic equivalent of the Palaeotaxodonta of Korobkov (1954).

Superfamily NUCULOIDEA

The Nuculoidea have small, protobranchiate gills. Their valves are taxodont and possess resilifers and internal ligaments. There are two extinct families, Praenuculidae and Thoraliidae, as well as two extant families Nuculidae and Pristiglomidae. Only the family Nuculidae is listed for the Australian fauna. The Pristiglomidae are distinguished from nuculids in having rounded, rather than wedge-shaped shells, and smaller ctenidia; the inhalant current is anterior, siphons are absent and the palps are rounded.

Family Nuculidae

The Nuculidae, commonly called 'nut shells', have valves with iridescent, nacreous (mother-of-pearl) interiors and opisthogyrate beaks (pointing in a posterior direction). The outer, periostracal layer is of variable thickness and ranges in colour from pale straw to dark brown. The shell surfaces are often smooth, but occasionally are sculptured. Eight extant genera are known. However, the taxonomy of this group is unsettled and needs careful reassessment. *Nucula* and *Rumptunucula* both occur in the Australian and New Zealand faunas (Fig. 5.3A–C; Keen 1969; Bergmans 1978); at least 18 species are recorded for the Australian fauna (K. Lamprell personal communication; S. Slack-Smith personal communication). The name *Ennucula* was suppressed in synonymy by Keen (1969), and Bergmans (1978), in his revision of some Australian Nuculidae, assigned *Pronucula* and *Deminucula* to *Nucula*, while proposing the new genus *Rumptunucula* for *Pronucula vincentiana*. Bergmans also provided a key to Australian Nuculidae (other than *Ennucula*). Van de Poel (1955) reviewed the conchology of the Nuculidae. Ludbrook (1961) revised the nuculids described by Tate (1886, 1887) from the Australian Tertiary. Maxwell (1988b) argued for the retention of *Ennucula*, *Pronucula* and *Deminucula* as distinct genera, adding *Lamellinucula*, *Brevinucula* and *Linucula*, as being worthy of generic rank. Maxwell noted that synonymy of *Deminucula* with *Tindaria* was unwarranted, being based on badly preserved specimens. *Nuculopsis* is not a valid extant genus since unfortunately the name has been used twice; the valid name applies to a Palaeozoic genus and cannot be used for Recent species, which should be assigned to *Ennucula* (P. Maxwell personal communication).

The Nuculidae burrow in the superficial sediment layers, remaining close to the surface of the substratum. The foot forms two lateral flaps that anchor the animal, allowing the body to be advanced by contraction of the pedal retractor muscles. These bivalves are detritus-feeders, using the palp proboscides to move deposit material into the mantle cavity. These ciliate organs are tentaculate extensions of the posterior ridge of the palp lamellae (Fig. 5.3D, E). Detrital particles collected by the palp proboscides are consolidated into mucous food strings that are carried in the food grooves between the palp lamellae to the mouth. The vertically ridged and grooved inner surfaces of the palp lamellae (Fig. 5.3D, E) are sorting areas, but since the food collected by the palp proboscides is already consolidated into food strings, the sorting only involves rejection of excessive masses of material. However, the inner surfaces of the palp lamellae can collect and sort individual suspended particles that are drawn between them by the anterior inhalant current. The complex of ciliated, dorso-ventral rejectory and acceptance grooves of the inner lamellar surfaces is shown in Figure 5.3F. Only the smallest, potential food particles can fit into the acceptance grooves. The lamellae are held apart by their haemodynamic turgor, thus providing collecting surfaces exposed to circulating mantle water as shown in Figure 5.3F. *Nucula sulcata*, from the north-eastern Atlantic, and *Acila castrensis*, from the north-eastern Pacific, frequently lie close to the surface of the substratum (R.G.B. Reid personal observation), with the anterior end of the valves gaping open to the water column, so that ingestion of suspended particles is possible. The palp lamellae can therefore be regarded as suspension-feeding organs. The ctenidia, although small, also collect suspended particulate material and pass it anteriorly to the palp pouch, from whence it is passed to the food groove (Stasek 1961). Whether this is a significant adult feeding mode, or little more than a cleansing function, has not been determined quantitatively, but the gills are important temporary feeding organs in the early juvenile, complementing pedal food collection (Mortimer 1962). In adult Nuculidae, the foot's ciliary and muscular behaviour appears to be entirely cleansing.

Nuculids have large stomachs with relatively simple ciliated sorting areas (Graham 1949; Purchon 1956). The large, cuticular gastric shield protects the gastric epithelia and reduces the size of food masses by abrasion. A rod-shaped gastric inclusion, the protostyle (Yonge 1939; Morton, J.E. 1953) is formed from a mixture of dense mucus and ingested food, and is believed to be a homologue of the crystalline style of the lamellibranchiate bivalves, although it lacks the starch-digesting enzyme, amylase, found in the lamellibranchs. A similar structure is found in some gastropods. Arising from the stomach are a small number of ciliated ducts, leading to acini, composed of groups of

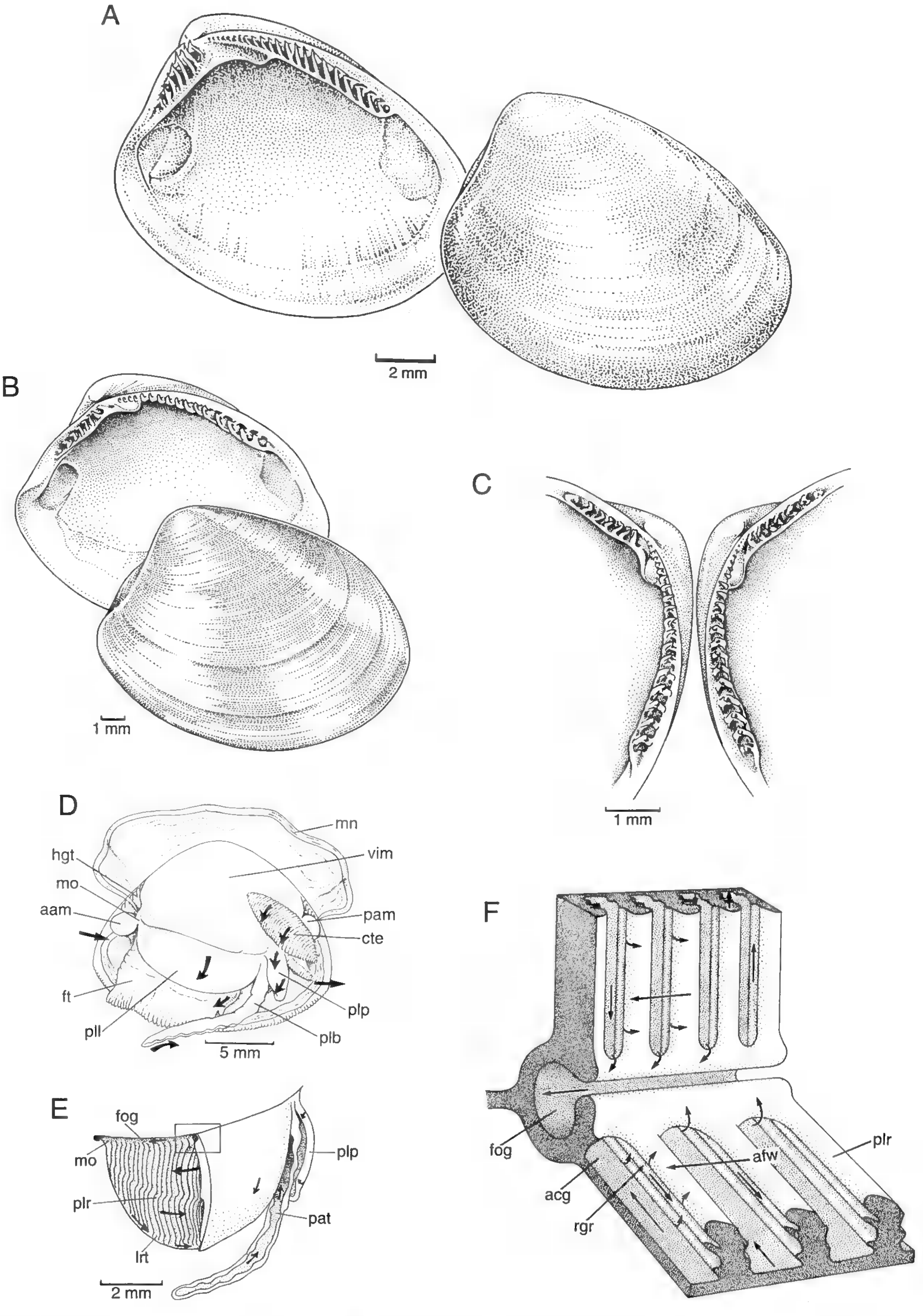

Figure 5.3 Family Nuculidae. **A**, *Nucula (Leionucula) superba*, shell valves, left valve in internal view, right valve in external view. **B**, **C**, *Nucula (Leionucula) obliqua*: **B**, shell valves, left valve in internal view, right valve in external; **C**, hinge, left and right valves showing taxodont dentition. **D**, mantle cavity and pallial morphology of *Nucula sulcata*, left mantle flap reflected to expose the interior organs. **E**, solid section of the left labial palp apparatus; the palp proboscis is rotated outwards, exposing the inner, concave food-collecting surface of this conveyer-belt-like appendage. **F**, modelled section (as indicated in E) of the left labial palp showing the ridged and grooved inner faces of the labial palp lamellae which house acceptance tracts deep in the grooves and rejection tracts along the side of the ridges. **aam**, anterior adductor muscle; **acg**, acceptance groove; **afw**, adoral flow of water; **cte**, ctenidium; **fog**, food groove; **ft**, foot; **hgt**, hinge tooth; **lrt**, lamellar rejectory tract; **mn**, mantle; **mo**, mouth; **pam**, posterior adductor muscle; **pat**, palp proboscis acceptance tract; **plb**, palp proboscis; **pll**, palp lamella; **plp**, palp pouch; **plr**, ridge of palp lamellar interior; **rgr**, rejectory groove; **vim**, visceral mass. [A–D, R. Plant; E, R.G.B. Reid; F, C. Eadie]

blind-ending digestive tubules responsible for the endocytosis of food in the form of very small particles and fluid (Owen 1959). Undigested material from the digestive cells is exocytosed and returned to the stomach for rejection via the intestine.

In most respects the physiology of the Nuculidae is unexceptional. The glandular portions of the kidneys are prominent, and sometimes contain metal-sequestering granules, but they are not elaborated into anatomically complex organs. They are, however, ultrastructurally distinctive (Morse & Meyhofer 1990). Morse *et al.* (1986) discovered the blood-pigment haemocyanin in Nuculidae. Nuculids are dioecious, their larvae lecithotrophic. The eggs contain large quantities of yolk that supports the early development of the larvae and juveniles. In some deep-water species, development is direct (Allen & Sanders 1973; Sanders & Allen 1973; Knudsen 1979). Like other Protobranchia, the Nuculidae have a pericalymma larva. This larval type is described in detail in the section on Solemyidae.

The Nuculidae have been recorded as far back as the Ordovician (Keen 1969), but their earliest occurrence in Australia may be the Early Permian. Fossils of the widespread genus *Nuculopsis* are present in the Perth Basin and also in other Basins in the north of Western Australia (Dickins 1963). Fossils from the Early Cretaceous have also been recorded from the Aptian/Albian deposits of the Gibson Desert, Western Australia. Other Early Cretaceous fossils include species of *Nucula* from Queensland and possibly South Australia (Ludbrook 1966). *Lamellinucula pyrenoides* has been recorded from the Palaeocene in Victoria (Darragh 1994); this genus also occurs in the Palaeocene of Europe, Asia and North America. *Lamellinucula pyrenoides* has not been found above the Palaeocene in Australia, but there are forms which are similar to and perhaps congeneric with it found in the Oligocene and Miocene of Australia.

Superfamily NUCULANOIDEA

Nuculanoideans have posterior feeding and inhalant currents, and usually have inhalant and exhalant siphons and pallial sinuses. The ctenidia are usually larger than those of the Nuculoidea. The taxodont shells are elongate posteriorly, and with or without a resilifer. Historically, the taxonomy of the superfamily has been confusing. Several synonyms for nuculanoidean genera were cited by Dell (1955) in his synopsis of Tertiary and Recent Australian Nuculanidae. However, Puri (1969) did not recognise the generic status of the majority of these. The taxonomy of the group has been revised radically by Scarlato & Starobogatov (1979), Allen & Hannah (1986), and Maxwell (1988b); Maxwell provided a table of comparisons of the different taxonomic systems. There is, however, no complete consensus regarding the number of groups that merit family status, or for some taxa, nomenclature. The system of Allen & Hannah (1986), with some modifications suggested by Maxwell (1988b), is adopted here. Representatives of three families have been recorded from Australian waters, Nuculanidae, Neilonellidae and Sareptidae (= Yoldiidae). A fourth family, Malletiidae, has not been recorded formally, but is treated here as there is some uncertainty about the current placement of some of the species in the Australian fauna. Two other families unknown in the Australian fauna are the Siliculidae and the Lametilidae. Both are abyssal groups. The Siliculidae are characterised by small, fragile shells with elongate teeth; a distinct exhalant siphon is present, but the posterior inhalant opening does not form a siphon (Allen & Sanders 1973). The Lametilidae have rounded, tumid shells with a pair of elongate teeth anterior and posterior to the umbones; a small inhalant siphon is present, but not fused ventrally.

Family Malletiidae

The shell in the Malletiidae lacks a resilifer, and has a prominent external ligament. The valves are smooth, oblong and moderately inflated. The siphons are elongate. The living genera include *Malletia*, *Malletiella*, *Minormalletia* and *Pseudoglomus*, and these are mostly cosmopolitan in the deep benthos.

Living *Malletia* were first described by Sars (1878), and Yonge (1939) described *Malletia obtusata* from the north-eastern Atlantic (Fig. 5.4). It is laterally flattened and has almost transparent valves. The siphons are fused and elongate. This malletiid burrows rapidly in a horizontal attitude, always close to the surface of the sediment. Palp proboscides, arising from the posterior of the large palp lamellae, and a single posterior tentacle extend out of the mantle cavity through a posterior opening which is bounded by a pair of enlarged mantle folds. The ctenidial lamellae are enlarged in comparison with those of the Nuculanidae, and may have a pumping function.

At present, no malletiids have been recorded from Australia, however, future revisions of several nuculoid taxa of rather uncertain placement may change this situation.

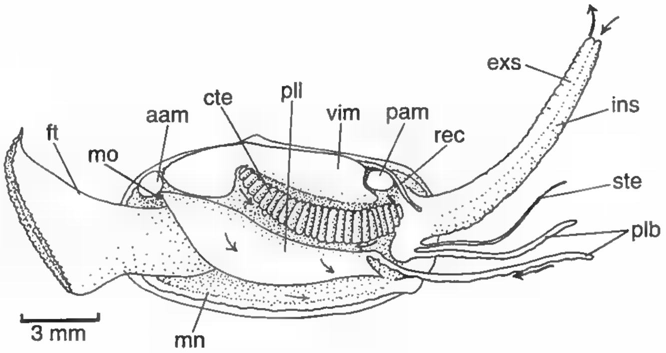

Figure 5.4 Family Malletiidae. Pallial morphology of *Malletia obtusata*; arrows indicate water movement and ciliary currents. **aam**, anterior adductor muscle; **cte**, ctenidium; **exs**, exhalant siphon; **ft**, foot; **ins**, inhalant siphon; **mn**, mantle; **mo**, mouth; **pam**, posterior adductor muscle; **plb**, palp proboscis; **pll**, palp lamella; **rec**, rectum; **ste**, sensory tentacle; **vim**, visceral mass. (After Yonge 1939) [R.G.B. Reid]

Family Neilonellidae

Neilonellids have robust valves which are inflated, ovate, and may be slightly rostrate (Fig. 5.5). The ligament is external or internal, and siphons are present. Using the name Saturniidae, Allen & Hannah (1986) included the genera *Saturnia*, *Pseudotindaria*, *Neilo* and *Protonucula*. Maxwell (1988b), however, has since argued convincingly that Neilonellidae has the better and prior claim as the family name. *Protonucula verconis* (Fig. 5.5) is a deep-water species from southern Australia (Cotton 1930). *Neilo australis* (Marshall 1978) is a Recent New Zealand species and another Recent New Zealand species, *Austrotindaria wrighti*, may also belong in this family (Maxwell 1988a).

Family Nuculanidae

The family Nuculanidae is equivalent to the Ledidae of older literature, and is the group that has undergone the most radical recent revision. The shells are often compressed and rostrate with chevron-shaped hinge teeth, and often have commarginal sculpture (Fig. 5.6A, B). Inhalant and exhalant siphons and pallial sinuses (siphonal muscle attachment scars in the valve interiors) are present. In the hinge the ligament is partly internal and a resilifer is present. Maxwell (1988b) discussed the status of the extant nuculanid genera. There is no clear consensus on the lower level taxonomy of this family. According to K. Lamprell (personal communication) the family is represented in the Australian fauna by six subgenera of the genus *Nuculana*: *Nuculana sensu stricto* (four species); *Jupiteria* (two species); *Ledella* (five species); *Poroleda* (one species); *Propeleda* (two species); *Scaeoleda* (eight species); and *Thestyleda* (one species). Several of these subgenera are accorded generic status by other workers.

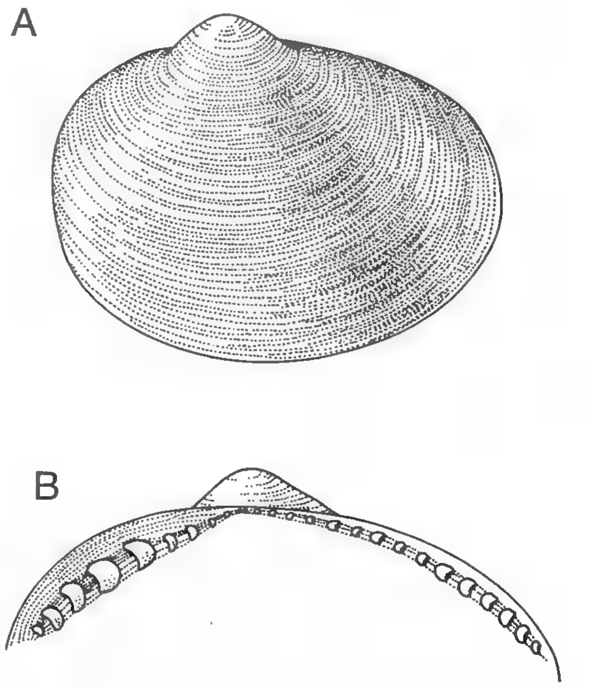

Figure 5.5 Family Neilonellidae. *Protonucula verconis*, a deep-water species from southern Australia: **A**, shell valve, external view; **B**, hinge. (After Cotton 1961) [C. Eadie]

In common with the foot of most other protobranchs, the nuculanid foot forms two large lateral flaps which allow rapid burrowing. Detritus-feeding by the palp proboscides is supplemented by the pumping action and suspension-filtration of the gills (Stasek 1965). Figure 5.6C shows the general anatomy and ciliation of the mantle cavity of *Nuculana minuta* from the north-eastern Atlantic (Yonge 1939). The gills are small relative to those of nuculids, and the palp pouch is small or absent. Yonge observed that in order for the gills to function in food collection there would have to be direct contact between them and the proboscides. R.G. Gustafson & R.A. Lutz (personal communication) have discovered a new abyssal nuculanid from thermal vents which has endosymbiotic bacteria involved in sulphide oxidation (see below under Solemyidae for a discussion of this).

The family Nuculanidae is one of the oldest bivalve families, apparently having its origin in the Devonian. Among the earliest records of this family in Australia are Early Permian fossils of *Nuculana* from the Carnarvon and Fitzroy Basins, Western Australia (Dickins 1956, 1957, 1963) and from the Maitland Group in New South Wales (Dickins & Thomas 1959), and of *Veteranella (Glyptoleda)* also from the Carnarvon Basin (Dickins 1956). *Nuculana hoelscheri* is known from the Early Cretaceous (Carnarvon Basin) and *Yoldia freytagi* has been recorded from later in the Early Cretaceous in the faunas of the Great Artesian Basin, South Australia (Ludbrook 1966) and of the Gibson Desert, Western Australia (Skwarko 1967). Darragh (1994) recorded three species from the Palaeocene of the Otway Basin, Victoria.

Family Sareptidae

In the Sareptidae, the usually smooth, fragile nuculanoidean valves are often compressed and posteriorly elongated (Fig. 5.7A, B). The anterior and posterior hinge teeth are interrupted and the ligament may be carried on a chondrophore. In splitting off the Yoldiidae as a new family, Allen & Hannah (1986) also proliferated the number of genera to include *Yoldia*, *Megayoldia*, *Cnesterium*, *Orthoyoldia*, *Yoldiella*, *Portlandia*, *Adrenella*, *Microyoldia*, *Ovaleda* and *Sarepta*. Maxwell (1988b) argued that while the new family is legitimate, the name 'Sareptidae' has priority, and that decision is accepted here; *Ovaleda* is a junior synonym of *Sarepta*. Rabarts & Whybrow (1979) reviewed the Antarctic and Subantarctic *Yoldia*. K. Lamprell (personal communication) lists three sareptids for the Australian fauna: two species of *Yoldia* and one *Sarepta* species.

The biology of *Yoldia* has been investigated more thoroughly than that of most other protobranchs since it is common, large, easy to manipulate, and has a major role in the food chain of commercial fish species and in the bioturbation of sediments. It has a burrowing mechanism similar to that described for *Nuculana*. Some species excavate a subsurface feeding chamber and there browse upon bacteria (Fig. 5.7D; Bender & Davis 1984). This excavation causes significant bioturbation: old sediments and their toxic loads are returned to the water column (Bender & Davis 1984; Brand & Reid 1995). The palp proboscides may collect food both from the surface and from the feeding chamber. Since exhalant and inhalant siphons are present, suspension-feeding is also important, and the gills can

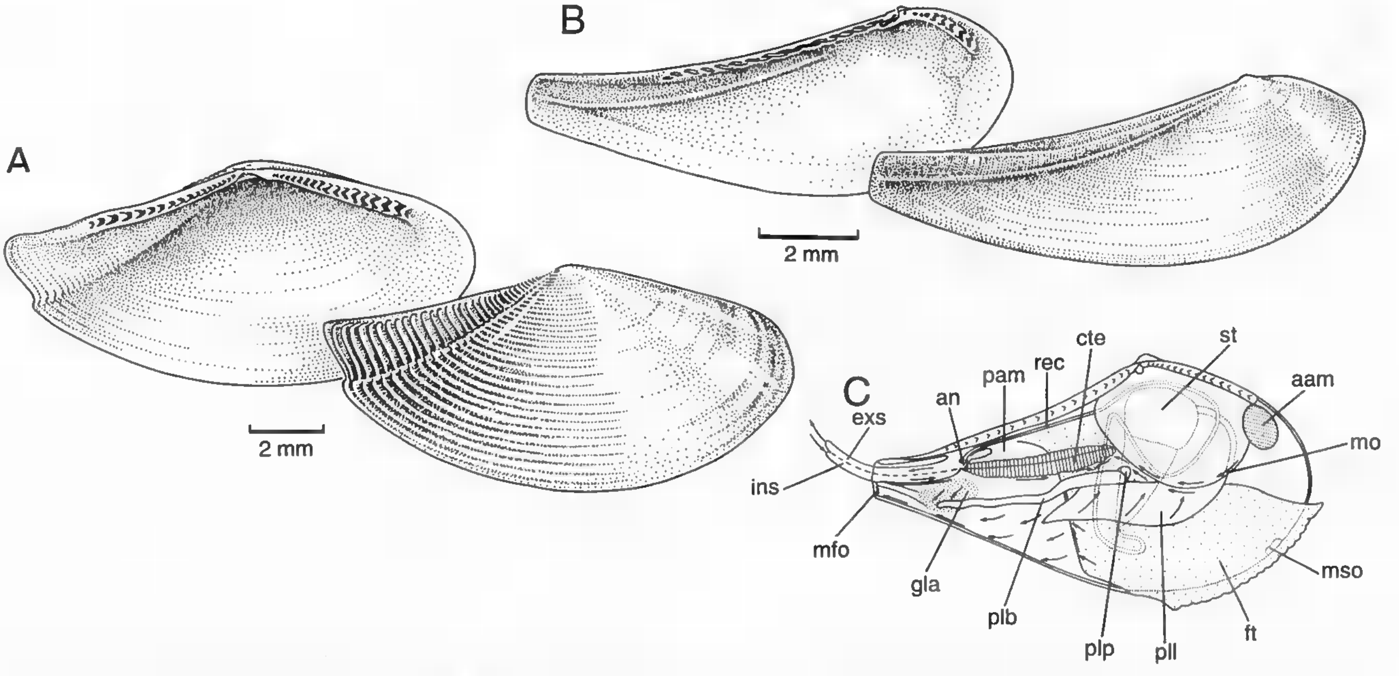

Figure 5.6 Family Nuculanidae. **A**, **B**, shell valves, left valves in internal view, right valves in external view: **A**, *Nuculana dohrni*; **B**, *Nuculana* sp. **C**, pallial morphology of *Nuclulana minuta*, right view. **aam**, anterior adductor muscle; **an**, anus; **cte**, ctenidium; **exs**, exhalant siphon; **ft**, foot; **gla**, glandular area in mantle cavity; **int**, intestine; **ins**, inhalant siphon; **mfo**, mantle folds; **mo**, mouth; **mso**, marginal sense organ; **oes**, oesophagus; **pam**, posterior adductor muscle; **plb**, palp proboscis; **pll**, palp lamella; **plp**, palp pouch; **rec**, rectum; **st**, stomach. (C, after Yonge 1939) [A, B, R. Plant; C, C. Eadie]

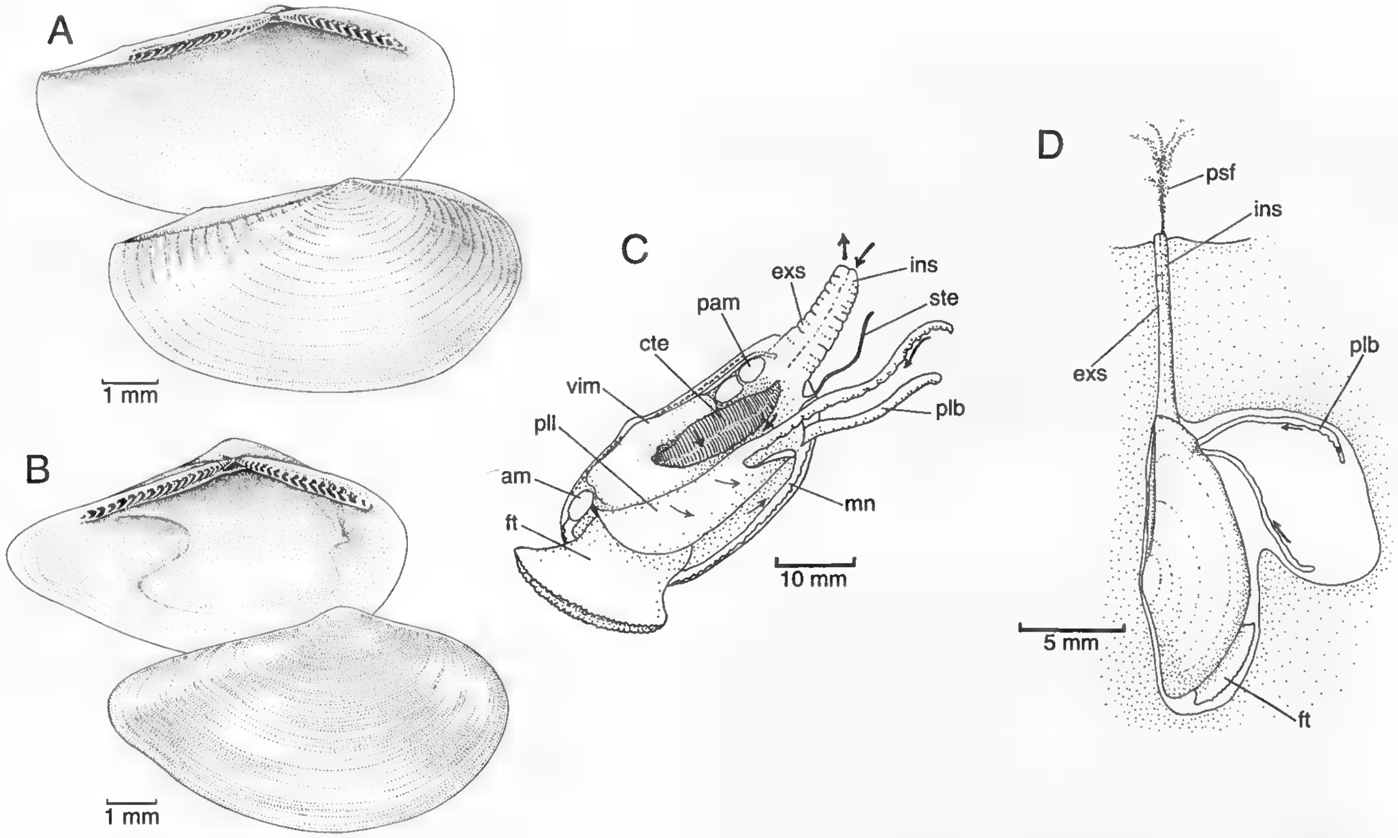

Figure 5.7 Family Sareptidae. **A**, **B**, shell valves, left valves in internal view, right valves in external view: **A**, *Yoldia lata*; **B**, *Yoldia narthecia*. **C**, pallial morphology of *Yoldia thracaeiformis*, left view; arrows indicate water movements and ciliary currents. **D**, *Yoldia limatula*, feeding in a subsurface chamber that might contain bacterial food. Indigestible silt is ejected as pseudofaeces from the inhalant siphon, thus contributing significantly to bioturbation. This species also feeds at the surface on recently deposited detritus. Subsurface feeding is indicated by Yonge (1939) for other protobranchs. **aam**, anterior adductor muscle; **cte**, ctenidium; **exs**, exhalant siphon; **ft**, foot; **ins**, inhalant siphon; **mn**, mantle; **pam**, posterior adductor muscle; **plb**, palp proboscis; **pll**, palp lamella; **psf**, pseudofaeces; **ste**, sensory tentacle; **vim**, visceral mass. (C, after Stasek 1965; D, after Bender & Davis 1984) [A, B, R. Plant; C, D, R.G.B. Reid]

draw in water by ciliary action as well as by a pumping action (Stasek 1965). Figure 5.7C shows the general anatomy and ciliation of the mantle cavity.

Order SOLEMYOIDA

Solemyoids have large ctenidia, reduced labial palps, and an enlarged foot. Iredale (1939) was convinced that the Solemyoida should be separated from the Protobranchia, in contrast to Thiele (1930), who included them with taxodonts. However, Iredale shrewdly observed that the gills represent ‘extreme specialisation’ and are not remnants of a generalised primitive condition. That specialisation is related to the possession of symbiotic gill bacteria, a condition that may characterise the whole order. However, only the Solemyidae have been surveyed in this regard. The guts of all known living representatives are reduced or absent. Most members of the order lack taxodont dentition (Fig. 5.2B), and a globular, opisthodetic, external ligament is often present. Representatives of the order are found in the fossil record from the Ordovician to Recent. The Solemyoida is equivalent to the subclass Cryptodonta of other classifications. The superfamily Solemyoidea, considered redundant by Sanders & Allen (1973), would comprise only the Solemyidae, and another superfamily would be required for the Nucinellidae. The same argument applies to the status of the Ctenodontidae which Pojeta (1978) and Waller (1990) have assigned to the Solemyoida on the grounds of hinge and ligament structure.

One of the solemyoid families, the Ctenodontidae, is recorded from the Ordovician to the Carboniferous. In this group, the valves are taxodont, and the hinge has a cylindrical external ligament and no resilifer (the vertical plate in the hinge to which the ligament is attached). Of six known genera only one is represented in the Australian fossil record, by the Silurian *Praectenodonta raricostae*.

Family Solemyidae

Solemyidae are elongate, ovoid, thin-shelled protobranchs, in which the periostracum extends beyond the calcified valve margins (Fig. 5.8A; Pl. 10.1). Secretions of anterior and posterior oil glands give the valves a hydrofuge surface that sheds the sticky mud found in the usual environment of these organisms (Beedham & Owen 1964). Radial lines on the weak shell sculpturing extend into the marginal periostracum as narrow, untanned, thin areas that allow folding of the margins when the adductor muscles are contracted. The thin folded lines in the marginal periostracum tear in preserved specimens (Fig. 5.8D), giving a frilled appearance, and this feature has occasionally been misused as a taxonomic character.

The Solemyidae include two living genera, *Solemya* and *Acharax*. *Petrasma* is regarded as a sub-genus of *Solemya*, and *Adulomya* and *Janeia* are fossil genera (Bernard 1980). Australian species include *Solemya australis* (Fig. 5.8D, E; type locality King George Sound, Western Australia); *S. velesiana* (type locality Sydney, New South Wales) and *S. terraereginae* (type locality Green Island, Queensland). *Solemya parkinsonii* is a New Zealand species which features prominently in accounts of the functional morphology of the genus. According to P. Maxwell (personal communication), *Solemya velesiana* is the type species of *Solemyarina*, which differs from *Solemya* in having internal ribs, and is worthy of at least subgeneric separation (see Cox 1969: N241).

Solemyids are active burrowers in anoxic silts, making U-shaped, V-shaped, or Y-shaped burrows. The foot lines the burrow with mucus from the large pedal gland. Prominent pedal ganglia are associated with burrowing. *Solemya* species swim actively by extending the foot, and relaxing the valves to take water into the mantle cavity through the anterior gape. The mantle margin then forms a seal around the foot, and when the valves are rapidly adducted, water is jetted out through the exhalant aperture, propelling the animal forward. This swimming cycle may be

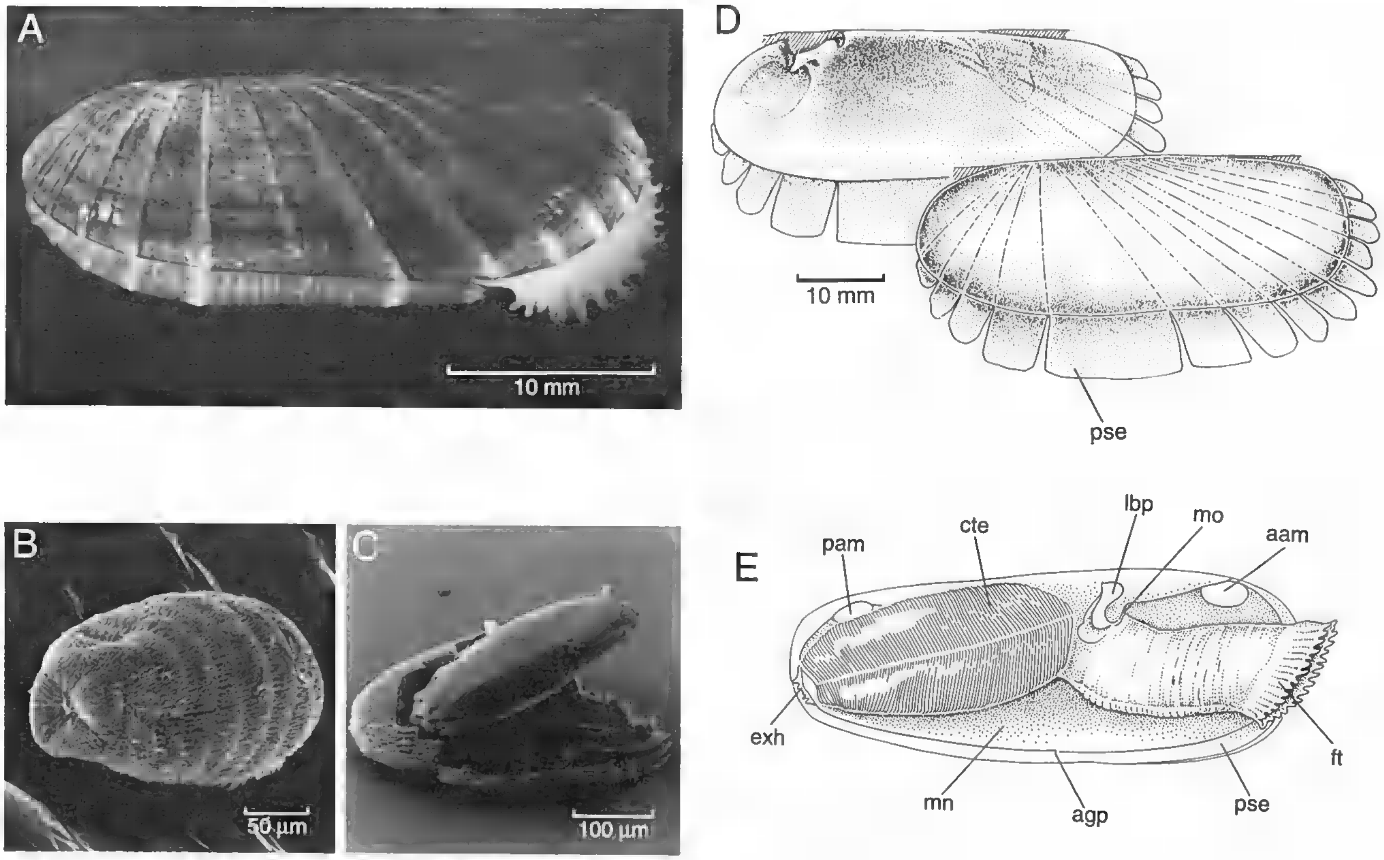

Figure 5.8 Family Solemyidae. A–C, *Solemya reidi*: **A**, adult showing infolded, uncalcified mantle margins with untanned radii; the tip of the foot appears anteriorly at the right; **B**, planktonic pericalymma larva; **C**, late pericalymma larva broken out of the pericalymma test to show the definitive prejuvenile with two valves. **D**, *Solemya australis*, shell valves, left valve in internal view, right valve in external view, showing the mantle margin which is intact in live animals, but here in this preserved specimen the thin radial folds have torn apart. **E**, pallial morphology of *Solemya* cf. *australis* from the right side. The large ctenidium contains intracellular sulphide-oxidising bacterial symbionts. The labial palps in this species collect particles of food from the ctenidium and mantle water. **aam**, anterior adductor muscle; **agp**, posterior limit of anterior gape; **cte**, ctenidium; **exh**, exhalant aperture; **ft**, foot; **lbp**, labial palp; **mn**, mantle; **mo**, position of mouth; **pam**, posterior adductor muscle; **pse**, periostracum extended beyond calcified valve margin. (E, after Reid & Brand 1987) [A–C, R. Gustafson; D, E, R. Plant]

repeated frequently for up to a minute or more (Drew 1900; Reid 1980). Swimming, which has also been observed in *S. australis* (Cotton 1961) and *S. velesiana* (Reid & Brand 1987), allows escape from unfavourable environments as well as the selection of favourable environments.

Availability in the environment of both oxygen and sulphide is important for the symbiosis between the bacteria in the ctenidia and the bivalve; it is likely that the bivalves have chemoreceptors sensitive to both of these metabolic constituents. Bacteria in the ctenidia of *Solemya reidi*, from the north-eastern Pacific, and *S. velum*, from the south-western Atlantic, have enzymes that are characteristic of the Calvin-Benson cycle, and fix carbon dioxide. The bacteria provide the bivalves with carbohydrates (Cavanaugh 1983; Felbeck 1983; Fisher & Childress 1986). The ATP (adenosine triphosphate) which provides energy to drive the cycle is derived from the oxidation of environmental sulphide by the mitochondria of the bivalves (Powell & Somero 1985, 1986). The bacteria also appear to convert nitrates to amino acids that become available to the bivalves (Felbeck 1983). The sulphide may come from various sources: the anaerobic decomposition of organic molecules by bacteria in the sediment; from sulphide bound to sediment; or, in the case of animals inhabiting hydrothermal vents, from volcanic activity. All bivalves with sulphide-oxidising symbionts require oxygen for normal respiration, as well as sulphide as an energy source. By their behaviour, the bivalves themselves play an important role in partitioning oxygen and sulphide before they reach the target cells, since otherwise the two constituents would interact, becoming unavailable. Ventilatory behaviour is important: *S. reidi* may acquire oxygen by active ventilation of the burrow, and then cease ventilating, whilst remaining passively open to the burrow

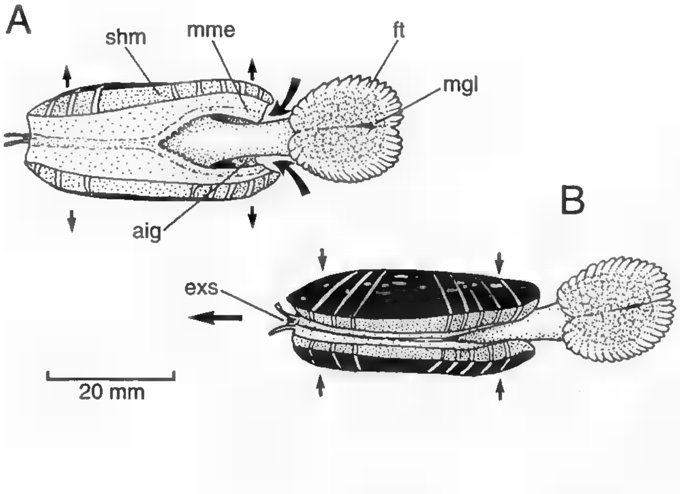

Figure 5.9 Family Solemyidae. Two stages in the swimming cycle of *Solemya reidi*; large arrows depict water movements; small arrows indicate valve movements: **A**, relaxed condition during which water is drawn anteriorly into the mantle cavity as the adductors relax; **B**, contracted condition during which the muscular mantle margins at the anterior gape form a seal round the foot and water is expelled suddenly from the exhalant siphon provides jet propulsion. **aig**, anterior inhalant gape; **exs**, exhalant siphon; **ft**, foot; **mgl**, mucous gland; **mme**, muscular mantle edge; **shm**, uncalcified shell margin. (After Reid 1980) [R.G.B. Reid]

water in which sulphide begins to accumulate in the absence of oxygen (McMahon & Reid 1984). Figure 5.10A, B summarises these events. Alternatively, as in *S. velum*, the organism may swim up and down in its burrow between oxygenated and anoxic regions (Doeller 1984). Both oxygen and sulphide are reversibly combined with the ctenidial haemoglobin of *Solemya*, and are thus partitioned at the molecular level (Doeller, Kraus, Colacino & Wittenberg 1988). Sulphide oxidases are found in the mitochondria in all tissues of *S. reidi*, but the occurrence of mitochondria in the gills is especially important to the symbiosis. Figure 5.11 shows the relevant anatomical and cytological details in *S. velesiana*. The mitochondria of the frontal, ciliated portion of the filaments (Fig. 5.11B) may convert sulphide energy for ventilatory ciliation, but it is the mitochondria of the intercalary cells that are particularly interesting. These cells are derived from mucoid flask cells, as B. Morton (1983b) has pointed out. They have a microvillar distal surface that overlaps with the alternating, adjacent bacteriocytes that house the symbiotic bacteria (Fig. 5.11B, C). The intimate physical relationship between the bacteriocytes and intercalary cells suggests that they exchange ATP and the products of bacterial metabolism (Reid 1990).

Like *Solemya velum*, *S. togata* (Mediterranean), *S. valvulus* (eastern Central Pacific) and *S. parkinsonii* (New Zealand), the Australian species, *S. australis* and *S. velesiana*, have reduced guts, and depend to some extent on deposit-feeding (Reid & Brand 1987). Only *S. reidi*, *S. borealis* (north-western Atlantic), *S. solen* (north-eastern Atlantic), *Acharax eremita* (Arctic Ocean) and *Solemya (= Petrasma) atacama* (Arctic Ocean), all species of the Northern Hemisphere, are known to lack guts completely (Kuznetzov & Shileiko 1984; Reid 1990).

Reproduction is continuous in *Solemya reidi*, presumably due to the constant availability of nutriment from the symbiosis, and there are no marked year classes in terms of valve size (Gustafson, Gustafson & Reid 1987). As also occurs in some nuculoideans, a pericalymma larva (Fig. 5.8B, C) develops with a ciliated, locomotory outer pericalymma, or test (Drew 1899; Gustafson & Reid 1986, 1988a). The systematic importance of these pericalymma larvae is reviewed by Gustafson & Lutz (1992). Prior to metamorphosis, bacteria begin to appear in the test cells of *S. reidi*, apparently from undifferentiated granular, ground material, which possibly represents a wall-less phase in the life cycle of the bacteria (Gustafson & Reid 1988b). Figure 5.8C shows a larva at this stage that has been broken out of the pericalymma test. During metamorphosis the oesophageal rudiment and the unconnected gastric and rectal rudiments disintegrate, releasing their contents, including the putative bacterial symbionts, into the perivisceral cavity, which gives rise to the blood system and hence has direct access to the gills (Gustafson & Reid 1988b).

An ecological study of *Solemya reidi* in British Columbia, Canada, by Shepard (1986) demonstrated that the densest populations of *S. reidi* occur where refractory (large particle) wood debris is most abundant, provided that oxygen is available at the interface between the water column and the substratum. At one station with abundant, finely divided wood fibre, where the overlying water was anoxic, the bivalves were absent. In an analogous situation in California this species has been found in deposits of human hair from the Los Angeles sewage outfall. In these environments, anaerobic bacteria generate not only sulphides, but also significant levels of dissolved organic material that may contribute to the nutrition of the bivalves.

In Australia the genus *Solemya* is found in a variety of habitats. *Solemya velesiana* occurs intertidally in sandy silt with relatively low levels of free sulphide (Reid & Brand 1987). This species may utilise iron-bound sulphide in the sediment, since the burrows are found to be lined with deposits of ferrous iron. The relatively large labial palps and gut indicate significant dependence on normal alimentation. The species is not found in the high-sulphide mangrove environment of the upper intertidal, or in clean, coarse sand in the mid-intertidal. *Solemya australis* is found in fine benthic silt along the southern coast of Australia. In Western Australia,

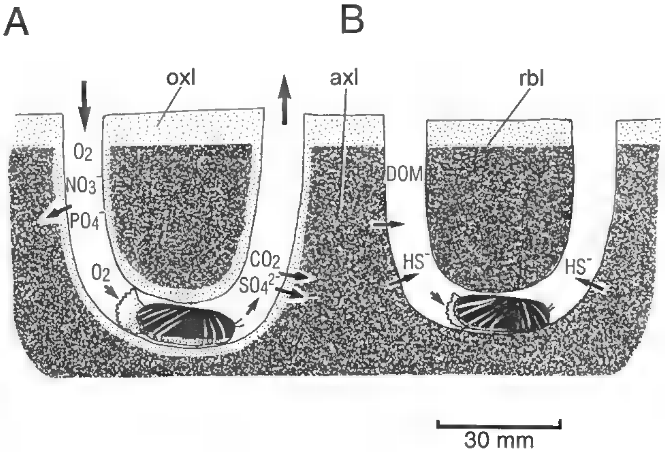

Figure 5.10 Family Solemyidae. Diagrammatic representations of *Solemya reidi* in burrows; large arrows show water movements; small arrows indicate diffusion of metabolic and nutrient compounds. **A**, ventilating mode in which the animal inhales oxygenated water through the burrow and releases some sulphate (SO_4^{2-}) and carbon dioxide (CO_2) into the exhalant stream. These compounds may also be used by anaerobic bacteria. Nitrate (NO_3^-) and phosphate (PO_4^-) enter from the water column and are used as bacterial nutrients. **B**, non-ventilating mode in which there is no respiratory water flow, but the animal may remain open to the environment to allow inward diffusion of some sulphide (HS^-). Dissolved organic matter (DOM), from exogenous anaerobic bacteria may be used by the bivalve. Burrow water becomes anoxic. **axl**, anoxic layer; **oxl**, oxygenated layer; **rbl**, redox boundary layer between the oxygenated silt and anoxic layers, which is typically about 10 mm below the surface. [R.G.B. Reid]

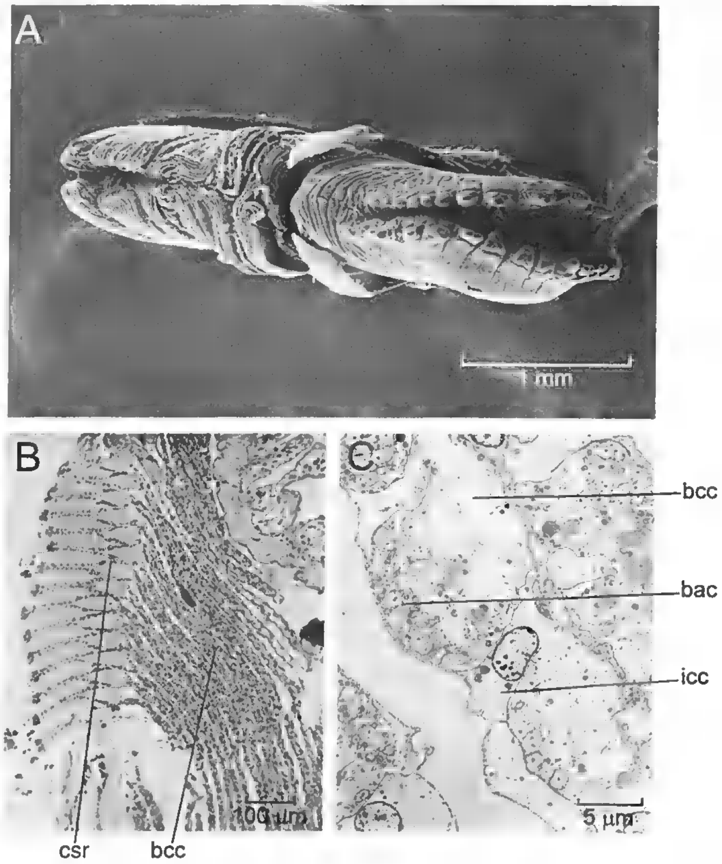

Figure 5.11 Family Solemyidae. *Solemya velesiana*. **A**, adult with shell removed. **B**, fine structure of gill lamellae showing the frontal ciliated portions and the proximal region containing bacteriocytes. **C**, ultrastructure of the proximal region of the gill lamella. Each lamella consists of a bilayer of cells with blood sinuses between them. Bacteriocytes are interspersed with intercalary cells which have mitochondria but no bacterial symbionts. **bac**, bacteria; **bcc**, bacteriocyte; **csr**, chitinous supporting rod; **cte**, ctenidium; **ft**, foot; **icc**, intercalary cell; **lbp**, labial palp. (A, from Reid & Brand 1987) [B, C, R.G.B. Reid]

species presently assigned to *S. australis* and *S. terraereginae* occur in fine benthic silt and also intertidally in association with eelgrass (Roberts & Wells 1980; Reid & Brand 1987; S. Slack-Smith personal communication). Interestingly, the roots of seagrass appear to provide photosynthetic oxygen to associated Lucinidae, bivalves that also depend on sulphide- oxidation (Fisher & Hand 1984). As a matter of commercial interest, the solemyid *Acharax agassizi* is a significant food organism for the sablefish in the north-eastern Pacific (F.R. Bernard personal communication) and small specimens of *Solemya terraereginae* are important in the diet of young Western Australian spiny lobster *Panulirus cygnus* (S. Slack-Smith personal communication).

Solemya species are readily collected from shallow waters and, with their sulphide-oxidising symbioses, have become important models for the study of these metabolic systems. They are of special importance in relation to the marine hydrothermal vent communities from deep water, members of which are fragile and difficult and expensive to collect. Already studies on these *Solemya* species have provided important insights into bacterial-bivalve associations at the biochemical, ultrastructural, physiological and functional-morphological levels, as well as providing clues to the evolution of the solemyoid bivalves and their mitochondria.

Dickins (1963) recorded *'Solemya' holmwoodensis* from the Early Permian of Western Australia. A series of Quaternary fossils have been obtained from the Ascot Formation of the Swan Coastal Plain, Western Australia (Ludbrook 1978). These appear to belong to *Solemya (Solemyarina)*.

Family Nucinellidae

Smith (1885) recognised the affinities of *Nucinella* with the Protobranchia; Allen & Sanders (1969) discovered its close relation- ship with the Solemyidae, and suggested that nucellids are modern relatives of the actinodont bivalves of the Lower Ordovician.

The Nucinellidae have external ligaments, four to eight cardinal teeth and at least one long lateral tooth in each valve, features that confused some taxonomists. The monomyarian condition (posterior adductor muscle absent) of *Nucinella serrei*, from the western Central Atlantic and the best-known species, was recognised by Allen & Sanders (1969). These authors suggested that the large ctenidia, small palps and reduced gut represent the primitive condition of the Protobranchia, but it has become evident more recently that this condition is again correlated with a sulphide-oxidising symbiosis. Kuznetzov & Shileiko (1984) have demonstrated that *Nucinella viridula* (Arctic Ocean) has only a vestigial gut, and that *N. maxima* (Arctic Ocean) lacks both gut and labial palps. While there is no positive evidence as yet for the presence of symbiotic bacteria in these relatively rare, deep-water species, the absence of a gut is strongly indicative of a sulphide-oxidising symbiosis. They are thus of particular interest in the study of the evolution of protobranchs. Two species are known to occur in the Australian fauna: *Cyrilla dalli* and *Nucinella concentrica* (P. Maxwell personal communication).

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SUBCLASS PTERIOMORPHIA

CHAPTER 6

INTRODUCTION

Pteriomorphs are mostly byssate epifaunal bivalves. Among them are well known and economically important bivalves such as mussels, arks, oysters and scallops.

Pteriomorphs are heteromyarian or monomyarian bivalves with inequilateral or equilateral shells. The foot is reduced or lacking; when present it functions as a locomotory organ only in the juvenile, post-settlement stage. In adults, the foot is used for byssal attachment and not for burrowing. The free edges of the mantle lobes have two or three folds. Ventral mantle fusion is usually lacking or restricted to a posterior septum separating incurrent and excurrent apertures. There is no true incurrent siphon although apposition of the inner lobes in the postero-ventral area may form a functional excurrent siphon (some Mytiloida).

It is evident that the Pteriomorphia is a polyphyletic group. The included orders have significantly distinctive features, separate fossil lineages dating from the Ordovician, and display convergent and parallel evolutionary trends in some character states. Consequently, it is not possible to provide a simple morphological diagnosis for the subclass. Details of morphology, physiology, ecology and distribution may be found in the sections on the relevant orders.

Most pteriomorphs are heteromyarian, that is, the anterior adductor muscle is reduced in size relative to the posterior adductor, with a corresponding reduction in the size of the anterior end of the shell. This condition probably relates to the fixed, byssally attached life style. The incurrent and excurrent apertures have moved to a more postero-ventral position, held a little away from the substratum, with the animal lying on edge with the hinge uppermost. An alternative posture adopted by many other pteriomorphs is horizontal with one valve on the substratum. In this arrangement the incurrent aperture may remain central and the shell tends to be monomyarian and equilateral. The monomyarian condition has evolved independently in six lineages: in the Mytiloidea, Pterioidea, Limoidea, Ostreoidea, Plicatuloidea, and in the ancestral stock of the Anomioidea and Pectinoidea (Waller 1978).

Ligament type is variable within the subclass. The ligament is elongate, parivincular and opisthodetic in heteromyarian forms such as mytiloids and pinnoids, duplivincular in arcoids and some pterioids, multivincular in isognomonids, and alivincular and amphidetic in equilateral monomyarians such as ostreoids and pectinids. The duplivincular ligament appears to have evolved independently at least three times within the Pteriomorphia (Pojeta 1978). The ancestral pteriomorphs (with the exception of the Mytiloida) had a duplivincular ligament. This was retained by arcoids but replaced by other ligamental types in most pterioids (Trueman 1969). Because of the frequency of convergent and parallel evolution of this organ, it has limited use as a taxonomic character. Waller (1978) discusses and illustrates the structure and evolution of the ligament in the Pteriomorphia.

Ligamental types relate functionally to habitat. The duplivincular type of the sedentary, byssally attached arcoids is a relatively ineffective structure, acting more as a flexible hinge than an opening mechanism (Trueman 1969). Conversely, the elongate, parivincular, opisthodetic ligament of mytiloids and some pterioids is a powerful mechanism for opening the valves. It is particularly well developed in burrowing species which tend to have long, cylindrical shells. The alivincular, amphidetic ligament of the monomyarian pectinoids, in which the fibrous layer is partly uncalcified, is an efficient mechanism for opening the valves and this is probably a factor in the swimming abilities of some members of that group.

Epifaunal habits and byssal attachment to firm substrata are ancient features of pteriomorphs and have been retained by most forms in each of the orders of the subclass. Some mytiloids, arcoids, pectinoids and ostreoids have adopted byssal attachment for life in burrows excavated in hard substrata or in the living tests of other animals such as corals and ascidians. In these situations, the byssus functions in opposition to the byssal retractor muscles to maintain the position of the animal in the burrow. The evolution of mucus-embedded byssal cocoons in some mytilids is another special adaptation within the subclass for burrowing in soft substrata. The unattached habits and swimming capacities of some pectinids and limids are unusual in the group, allowing them to inhabit soft substrata.

Byssal attachment limits adult pteriomorphs to sedentary life styles. They are unable to move about to seek food and nearly all are suspension-feeders relying on water movements to bring particulate food to them. Choice of attachment site is therefore critical and most species have narrow site preferences and some means for site selection at the larval settlement stage.

Also related to their fixed positions, many pteriomorphs are gregarious. Females rely on water currents to bring sperm from spawning males to them, and proximity of adults during spawning maximises the probability of fertilisation. Pheromonal spawning cues are a feature of these bivalves. The majority of species are gonochoristic but hermaphroditism and protandry are common.

In the classification adopted here, five orders are recognised within the subclass Pteriomorphia: Mytiloida, Arcoida, Pterioida, Limoida and Ostreoida. There are, however, several alternative contemporary arrangements. Pojeta (1978) adopted the subclass Pteriomorphia but separated the mytiloids as a distinct subclass (Isofilibranchia). Waller (1978) used the subclass name Autobranchia for the taxon considered here, restricting the name Pteriomorphia to superorder status. In that arrangement, there are three superorders in the subclass, the Isofilibranchia (= Mytiloida), Prionodonta (= Arcoida) and Pteriomorphia (Pteroida, Limoida and Ostreoida). Scarlato & Starobogatov (1978) used the subclass name Autobranchia to encompass all these taxa and heterodonts as well.

The first mytiloids, the family Modiomorphidae, appeared in the Early Ordovician and became extinct in the Permian. The other mytiloid family, the Mytilidae is believed to have evolved from modiomorphids in the Carboniferous. Unlike other pteriomorphs, the modern mytilids have a degree of ventral mantle fusion, forming at least a horizontal septum between the ventral incurrent

Table 6.1 Classification of the extant Pteriomorphia. The family not represented in Australia is indicated with an asterisk.

Subclass PTERIOMORPHIA
- Order MYTILOIDA
  - Family Mytilidae
- Order ARCOIDA
  - Superfamily ARCOIDEA
    - Family Arcidae
    - Family Cucullaeidae
    - Family Noetiidae
  - Superfamily LIMOPSOIDEA
    - Family Limopsidae
    - Family Glycymerididae
    - Family Philobryidae
- Order PTERIOIDA
  - Superfamily PTERIOIDEA
    - Family Pteriidae
    - Family Malleidae
    - Family Isognomonidae
    - Family Pulvinitidae
  - Superfamily PINNOIDEA
    - Family Pinnidae
- Order LIMOIDA
  - Superfamily LIMOIDEA
    - Family Limidae
- Order OSTREOIDA
- Suborder OSTREINA
  - Superfamily OSTREOIDEA
    - Family Gryphaeidae
    - Family Ostreidae
  - Superfamily PLICATULOIDEA
    - Family Plicatulidae
  - Superfamily DIMYOIDEA
    - Family Dimyidae
- Suborder PECTININA
  - Superfamily PECTINOIDEA
    - Family Pectinidae
    - Family Propeamussiidae
    - Family Spondylidae
    - Family Entoliidae*
  - Superfamily ANOMIOIDEA
    - Family Anomiidae
    - Family Placunidae

gape and the posterior excurrent aperture. Mytiloid shells have an outer calcitic layer of fibrillar ultrastructure and inner nacreous or crossed-lamellar aragonitic layers. This shell structure is evident in fossil mytilid shells from the Early Carboniferous onwards and probably has been characteristic of the order since its origin (Waller 1978). The mytiloid ligament is parivincular and opisthodetic, with fibrous material extending continuously from one valve to the other (Waller 1978). In the presumed early ancestors of the other Ordovician heteromyarian pteriomorphs, the ligaments are duplivincular, suggesting that the Mytiloidea diverged at a very early stage. Partly for this reason, Pojeta (1971) advocated raising the Mytiloida to subclass rank. Whether or not this is justified, the mytiloids are clearly well separated from other pteriomorphs (see cladogram in Waller 1978).

Arcoids lack any ventral mantle fusion. They have only two folds at the edges of the mantle lobes, the outer folds bearing eyespots. Their ligaments are duplivincular and their shells are composed entirely of complex, prismatic aragonite. In this latter respect they differ from mytiloids and other pteriomorphs. The extinct Cyrtodontidae (Early Ordovician to Devonian) appear to be ancestral to the order (Newell 1954; Cox 1960; Pojeta 1978) although there is some doubt about the interpretation of cyrtodontid ligaments. These are traversed by a series of grooves and ridges which do not seem equivalent to the banded insertion areas of a typical duplivincular ligament but may be regarded as pre-duplivincular (Pojeta 1978).

The Pterioida, Limoida and Ostreoida all lack ventral mantle fusion and have three folds along the edges of the mantle lobes. Waller (1978) has shown that these folds are probably not homologous with those of mytiloids. In all three orders, the shell has a simple prismatic or foliated outer layer of calcite and nacreous or cross-lamellar inner layers of aragonite. In Palaeozoic pterioids, the ligament has a duplivincular structure but in later forms the ligament is usually alivincular or elongate opisthodetic.

These three orders appear to have been much more active in evolutionary terms than the Mytiloida and Arcoida, diverging into several superfamilies with a wide range of habitats and life styles. The Pterioida is the most ancient of the three (Waller 1978). It is represented in the Middle Ordovician by the extinct Ambonychiidae and the extant Pterioidea. The former have ligaments resembling the pre-duplivincular condition of the cyrtodontids but the Ordovician pterioideans were the first bivalves to have a true duplivincular ligament (Waller 1978). The Limoida and Ostreoida originated later in the Ordovician, both apparently from a sister group of the Middle Ordovician pterioids.

Order MYTILOIDA

Mytiloids are byssate, epifaunal bivalves (some forms secondarily burrowing or boring) with equivalve and inequilateral shells made of calcite with fibrillar ultrastructure. The umbones are anterior and prosogyrous. Hinge dentition, when present, is dysodont, the ligament is opisthodetic and parivincular, and the musculature is heteromyarian. The mantle lobes have three marginal folds. The inner folds are fused postero-dorsally behind the ligament and by a horizontal septum postero-ventrally enclosing a posterior excurrent aperture which may have extended sides, so forming a short excurrent siphon. Ventrally the mantle lobes are usually free with a long ventral incurrent gape although in some forms the sides of the lobes are extended posteriorly forming an extensible, non-tubular siphon. Ctenidia are filibranch or eulamellibranch.

The Mytiloida is an ancient group. The sole living family, the Mytilidae, is said to have originated in the Devonian (Newell 1969a) or the Carboniferous (Pojeta 1978). A second family, the Mysidiellidae, is sometimes separated (Cox 1969a). It is known only from Triassic fossils and comprises only three genera. An extinct Palaeozoic family known as the Modiomorphidae (Early Ordovician to Early Permian) has similar shells and may have been ancestral to the mytilids (Pojeta 1978). Modiomorphids differ mainly in lacking a resilial ridge. They may be regarded as the first mytiloids, although Newell (1969a) introduced a separate order for them.

Family Mytilidae

Mytilids are marine and estuarine mussels. Some of the species are gregarious and are among the most conspicuous animals of the shore (see Pls 10.2, 10.3).

The family Mytilidae is currently divided into six subfamilies, distinguished mainly by shell characters: Mytilinae, Modiolinae, Crenellinae, Lithophaginae, Dacrydiinae and Bathymodiolinae. All but the last subfamily are represented in the Australian marine fauna which includes approximately 70 species in about 27 genera. No revision of the Australian fauna is available. Older revisions of extra-limital mytilid taxa that are relevant to the Australian fauna are by Lamarck (1801, 1818–1822), Reeve (1856–1858), Jukes-Browne (1905), Lamy (1936–1937) and Soot-Ryen (1969). Regional check-lists are available in Laseron (1956) and Iredale & McMichael (1962, for New South Wales), Macpherson & Gabriel (1962, for Victoria), May (1923, for Tasmania) and Cotton (1961, for South Australia). Iredale (1939) included descriptions of mytilids in a paper on bivalves from Queensland. A useful regional reference from New Zealand is the work by Fleming (1959).

The earliest description of an Australian mytilid is that of the widespread Indo-West Pacific species, *Septifer bilocularis*, based on material collected by Rumphius in eastern Indonesia.

Subsequently, from the late 18th century onwards, many species were described by European workers, often from Australian type material. The first described by an Australian taxonomist, Tate (1897), was *Modiolaria recens*.

Mytilid shells may be externally smooth, radially sculptured or bear commarginal sculpture. In the Mytilinae, Crenellinae and Dacrydiinae a few weak dysodont teeth are usually present anteriorly and often there is a series of taxodont-like teeth along the posterior hinge line, especially in the zone behind the ligament. The hinges in Modiolinae, Bathymodiolinae and Lithophaginae are typically edentulous.

The ligament in the genus *Mytilus* has been described by Trueman (1950) and Yonge & Campbell (1968). The prodissoconch has a small internal ligament. This is replaced by the adult structure which extends along the dorsal margin of the valves for a distance of roughly half the shell length (Fig. 6.1B–F). It is situated between the valves and does not extend above them; in section it is rectangular and consists of an inner layer of vertical fibres and an outer layer of two parts. There is a resilial ridge beneath the ligament.

The mantle lobes have three folds, the outer and middle folds adhering closely to the shell margins. There may be complex ciliary rejection tracts on the inner and middle lobes bordering the incurrent gape, along which particulate matter rejected from the gills is carried to a position at the entrance of the incurrent aperture from whence it may be forcibly ejected from the mantle cavity. Such tracts are particularly well developed in the Crenellinae.

The degree of mantle fusion is variable within the family. The primitive state seems to be one in which there is fusion of the inner lobes in a short antero-ventral area just behind the anterior adductor, a postero-dorsal area behind the hinge, and a posterior horizontal branchial septum separating the incurrent and excurrent apertures (as in *Modiolus* species; Fig. 6.1E). The inner lobes around the excurrent aperture and the posterior portion of the incurrent ventral gape are thickened, muscular, slightly extensible, and with either simple or digitate margins. In some forms, prominent tentacles along the margins of the ventral gape serve to exclude larger particles from the mantle cavity (as in *Xenostrobus* and *Mytilus* species).

In the boring and burrowing Lithophaginae there is extensive muscular development of the inner mantle lobes posteriorly, forming relatively long, extensible siphons (Yonge 1955; Wilson 1979; Wilson & Tate 1984). The incurrent siphon becomes functionally tubular by apposition but there is no fusion of the ventral edges.

Antero-ventral fusion of the mantle lobes is a feature of the Crenellinae, reaching its maximum development in *Lanistina*, in which the ventral gape is reduced to a short zone accommodating incurrent water flow and extrusion of the foot.

Musculature is relatively consistent throughout the family and typical of the subclass (Fig. 6.1E, F). Posterior pedal and byssal retractors usually insert contiguously along an arched zone above and anterior to the posterior adductor, but they may be divided into two or more muscle blocks inserting separately. Although the pallial muscles are small and form only a thin pallial scar in most mytilids, in the siphonate Lithophaginae there are also siphonal retractor muscles and scars posteriorly.

The mytilid foot is a long, finger-like structure with a basal byssal gland. There is a ventral byssal groove originating at the gland and terminating at a distal depression. Post-settlement juveniles tend to be active and crawl rapidly by means of the foot. Juveniles of epifaunal species are capable of detaching the byssal threads and moving to another location but once a substantial byssal anchor is in place adults become sedentary and movement is limited to on-site re-orientation by means of differential contraction of the byssal retractor muscles. Burrowing and boring species are able to move up and down within the burrows by means of byssal muscle contraction.

Most mytilids are suspension-feeders although bathymodiolines appear to supplement their nutrition by means of a symbiosis with sulphur-oxidising bacteria in the gills (Kenk & Wilson 1985). The gills are of typical filibranch structure (Atkins 1937; Fankboner 1971; Morton 1974). There is minor variation in the nature of the inter-filamentary junctions. For example, in *Mytilus* the ascending and descending arms are connected by occasional cross bars, but in *Modiolus* some filaments are joined by a vertical septum termed a 'principal filament' by Atkins (1937) or a 'baffel' by Haggard & Wood (1980). Most mytilids have the free edges of the ascending lamellae free in the mantle cavity but in some, for example, *Amygdalum*, *Septifer*, *Musculista*, they are attached to the mantle lobes (outer demibranchs) and visceral mass (inner demibranchs) by means of ciliary junctions.

The circulatory and nervous systems are typical of the class and have been described for *Mytilus* by White (1937).

Thin-walled folds of tissue known as plicate membranes are often present, crossing between the mantle lobes and gill axes on the outer side, and the visceral mass and gill axes on the inner side. They may extend for most of the length of the gill axes. Their function is uncertain. They carry blood vessels connecting the mantle veins with the longitudinal veins above the gill axes and are thought by some authors to have an important respiratory function.

In most species the rectum passes longitudinally through the ventricle, but in the American genus *Ischadium*, it leaves the heart through the dorsal side of the ventricle (Pierce 1973). In *Amygdalum* it passes below the pericardium and in *Modiolusia* it passes above the pericardium (Wilson unpublished data).

The labial palps are large and subequal. The gill/palp junction is of Type 1 (Stasek 1963).

The gut is long with a loop in the intestine, on either the right or left side. The stomach is a thin-walled, two-chambered sac with a narrow anterior chamber and a more spacious posterior chamber; the internal structure is usually complex (Nelson 1918; Graham 1949; Owen 1955; Reid 1965; Morton 1977) but relatively simple in the Bathymodiolinae (Kenk & Wilson 1985). In most species, the crystalline style has no separate sac but lies in a fold of the midgut. In *Lanistina* the style lies in a separate sac below the rectum, opening into the posterior end of the stomach (Wilson unpublished data).

The mytilid kidneys are paired, sacular organs extending along the sides of the body. They are usually dark coloured and thick-walled, the inner surface being much convoluted. An anterior arm extends forward above the gill axis, and a posterior arm extends backwards but recurves to terminate at a slit-like renal aperture in the roof of the mantle cavity. The genus *Amygdalum* is unusual in that the kidneys are thin, tubular structures without a convoluted interior (Wilson unpublished data). There is a reno-pericardial aperture in the antero-lateral corners of the pericardial floor.

Mytilids are synchronous spawners. Exogenous factors stimulating the gametogenic cycle and spawning of *Mytilus* have been described by Bayne (1976). Reproductive cycles of five species, including *Mytilus*, near Fremantle have been described (Wilson & Hodgkin 1967). The reproductive cycle of *Mytilus edulis planulatus* in Port Phillip Bay, Victoria, has been described by Sause & Hickman (1983). Brood protection has been described in the eastern Pacific species *Musculus pygmaeus* (Glynn 1964) and the Atlantic *Dacrydium viviparum* (Ockelmann 1983). Salinity tolerance and reproduction of the estuarine species *Xenostrobus securis* have been studied and the anatomy and taxonomy of *Xenostrobus* reviewed (Wilson 1967, 1968, 1969).

The majority of mytilids are epifaunal, living attached by byssal threads to firm substrata, either solitarily or gregariously. The southern Australian mytiline species, *Xenostrobus pulex* and *Austromytilus rostratus*, and the western species, *Brachidontes ustulatus*, often live in densely packed mats on rocks in the upper intertidal zone.

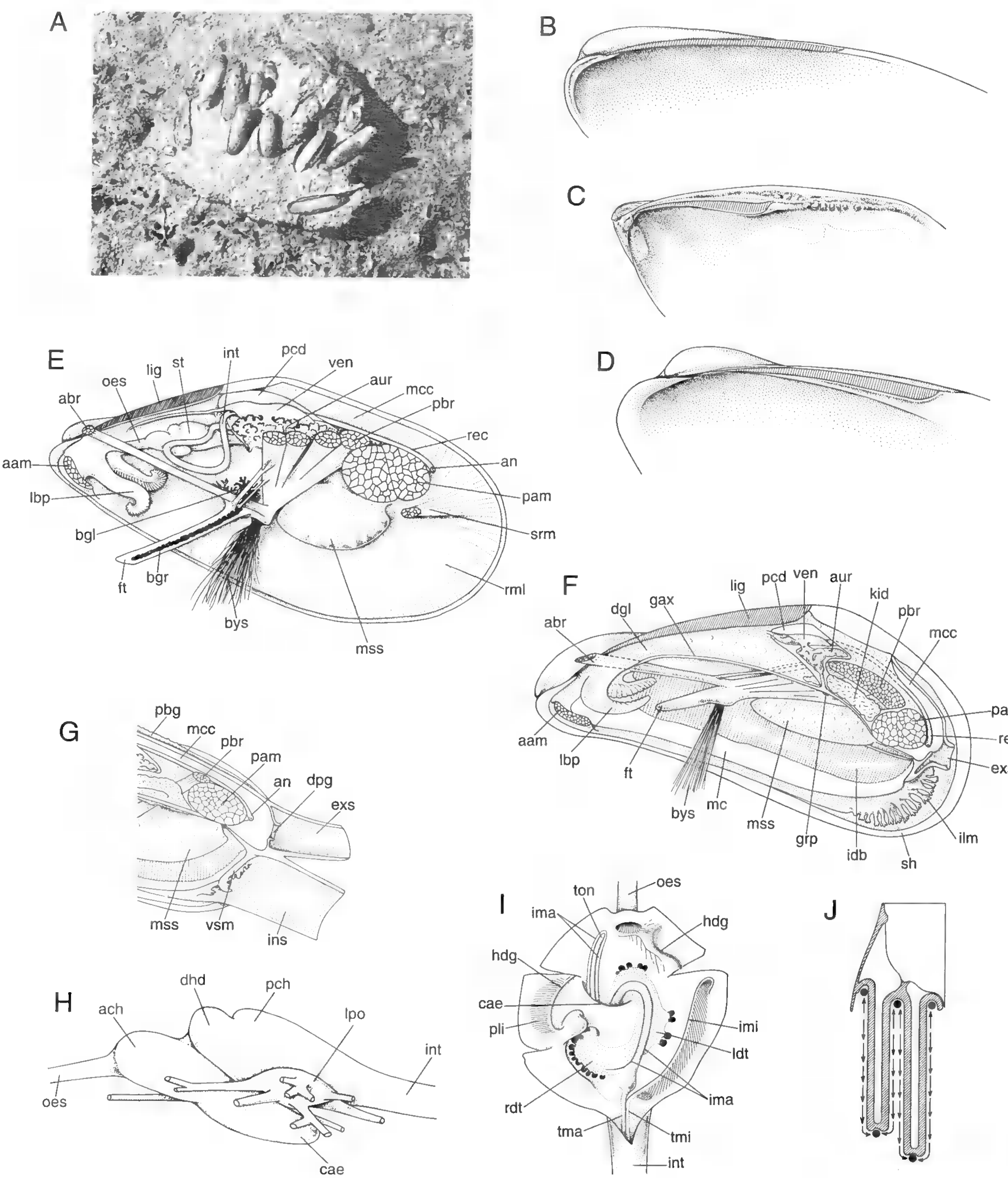

Figure 6.1 Family Mytilidae. A, *Lithophaga* sp., in their burrows exposed in a broken piece of coral rock; note hour-glass shaped burrow entrances *in situ* in the rock surface. B–D, hinges: B, *Lithophaga teres*; C, *Brachidontes erosus*; D, *Modiolus areolatus*. E–J, anatomy: E, *Modiolus areolatus*, internal anatomy, left shell valve and mantle lobe removed; F, *Xenostrobus* sp., internal anatomy, left shell valve and mantle lobe removed; G, *Botula* sp., posterior region, left shell valve and mantle lobe removed showing siphons; H, *Modiolus areolatus*, left side of stomach; I, *Modiolus areolatus*, stomach slit open dorsally, sides folded back to expose the interior; J, *Modiolus metcalfei*, the right ctenidium, vertical section, showing the ciliary currents; acceptance tracts are indicated by a closed circle. **aam**, anterior adductor muscle; **abr**, anterior byssal retractor muscle; **ach**, anterior chamber; **an**, anus; **aur**, auricle; **bgl**, byssal gland; **bgr**, byssal groove; **bys**, byssus; **cae**, sorting caecum; **dhd**, dorsal head; **dgl**, digestive gland; **dpg**, diaphragm within exhalant siphon; **exs**, exhalant siphon; **ft**, foot; **gax**, gill axis; **grp**, genital and renal papillae; **hdg**, hood groove; **idb**, inner right ascending demibranch; **ilm**, inner lobe of mantle; **ima**, major intestinal groove; **imi**, minor intestinal groove; **int**, intestine; **ins**, inhalant siphon; **kid**, kidney; **lbp**, labial palp; **ldt**, left duct tract; **lig**, ligament; **lpo**, left pouch; **mc**, mantle cavity; **mcc**, mantle cavity cul de sac; **mss**, mesosoma; **oes**, oesophagus; **pam**, posterior adductor muscle; **pbg**, postero-dorsal boring gland; **pbr**, posterior byssal retractor muscle; **pcd**, pericardium; **pch**, posterior chamber; **pli**, plicae; **rdt**, right duct tract; **rec**, rectum; **rml**, right mantle lobe; **sh**, shell; **srm**, siphonal retractor muscle; **st**, tomach; **tma**, major typhlosole; **tmi**, minor typhlosole; **ton**, tongue; **ven**, ventricle; **vsm**, valvular siphonal membrane. (F, after Wilson 1967; G, after Wilson & Tate 1984; J, after Morton 1977)

[A, K. Atkinson; B–D, F–J, R. Plant; E, B. Wilson]

Byssal attachment to firm substrata in the sublittoral zone is also the typical life style of the Modiolinae. The deep-water modioline genus *Adipicola* is unusual in living attached to hard objects such as sunken wood or whale skulls in the bathyal zone. The modioliform *Amygdalum* are 'byssal bag-forming' mussels. The bag is made of byssal threads and mucus and envelops the animal in its soft substratum habitat. *Lioberus* and *Modiolusia* are also byssal bag-forming burrowers in soft substrata. Although they have modioliform shells and are currently assigned to the Modiolinae, they are siphonate and may be better placed in the Lithophaginae.

Within the Crenellinae there are several life styles. *Gregariella* and *Musculus* species live attached by byssal threads to the underside of stones and other firm objects. *Musculista* are soft substratum burrowers and form byssal bags like those of *Amygdalum*. *Lanistina* species live embedded in the tests of ascidians. Species of *Tibialectus* are borers in hard rocks.

Several tropical genera of the Lithophaginae live in burrows which they bore in hard calcareous rocks. In *Lithophaga* and *Leiosolenus* boring is achieved by means of a chelating agent secreted by pallial glands (Jaccarini, Bannister & Micallef 1968; Morton & Scott 1980). Pallial glands have been described in *Botula* and this means of boring is assumed in that genus also (Wilson & Tate 1984).

Of special interest is the boring habit of *Leiosolenus* species which live among the polyps of living corals (Wilson 1979, 1985; Kleemann 1980; Morton & Scott 1980). This association appears to be host specific although some species bore in either dead or living coral. The mussel pediveligers enter the polyps via the coelenteron, without being digested, and there is evidence that longevity, growth and reproduction are enhanced when the mussel is surrounded by living coral tissue (Scott 1988).

The ecology of the southern Australian species, *Mytilus edulis planulatus*, has been well studied, especially with respect to its reproductive cycle and methods of commercial cultivation (Wisely 1964; Wilson & Hodgkin 1967; Johnstone 1985). There have been brief studies of the vertical zonation of the intertidal rocky shore species, *Xenostrobus pulex*, *Brachidontes erosus* and *Austromytilus australis*, in southern Australia (Bennett & Pope 1953). Much less attention has been given to other Australian mytilids. However, there are very extensive bibliographies on the taxonomy, anatomy, physiology and ecology of the Northern Hemisphere species *Mytilus edulis* and *Modiolus modiolus* (for references see Pelseneer 1911; Field 1922; Soot-Ryen 1955, 1969; Morton 1974, 1977; Bayne 1976). The taxonomy, anatomy and habitats of Australian tropical rock and coral-boring species of the lithophagine genera *Lithophaga*, *Leiosolenus* and *Botula* have been described (Otter 1937; Kleemann 1977, 1980; Wilson 1979, 1985; Wilson & Tate 1984).

There are no endemic mytilid genera in the northern Australian fauna and only two or three endemic species. The majority of northern species are widely distributed in the Indo-West Pacific region. However, the temperate species of southern Australia exhibit a high degree of regional endemism with at least two endemic genera (*Austromytilus*, *Exosiperna*). The genus *Trichomya* is of special interest in that it occurs as a Miocene fossil in New Zealand, but survives today only in eastern Australia. Several southern species also occur in New Zealand. The cosmopolitan genus *Mytilus* is represented in southern Australia by a mussel commonly treated as a subspecies of the Northern Hemisphere *M. edulis*, namely *M. e. planulatus*. Multivariate and allozyme analyses have suggested that the Australian population may be aligned with the Northern Hemisphere species *M. galloprovincialis* rather than with *M. edulis* (McDonald, Seed & Koehn 1991; Seed 1992). Whatever its genetic affinity may be, this remarkable species complex has a circumpolar distribution in both the Northern and Southern Hemispheres.

The introduction of the eastern Asian bag mussel, *Musculista senhousia*, to the Swan Estuary in 1982 was reported by Slack-Smith & Brearley in 1987. This species has also been introduced into the Mediterranean and the waters of California.

The southern Australian *Mytilus* species is harvested from the wild and cultivated commercially at several southern Australian localities (Hickman, Sause, Johnstone & Burgess 1983; Johnstone 1985). The same species is widely used as an indicator of heavy metal pollution of coastal waters, including those of southern Australia (Talbot, Magee & Hussain 1976a, 1976b; Harris, Fabris, Statham & Tawfik 1979).

Order ARCOIDA

Members of the Arcoida are characterised by having a filibranch gill and a shell with an aragonite, crossed-lamellar structure. With the exception of philobryid species, arcoids are also distinguished by having taxodont hinge dentition and being isomyarian. They also have a duplivincular ligament extending across all or part of the cardinal area, except in the Philobryidae and the Limopsidae.

Two superfamilies are included in the order, the Arcoidea and the Limopsoidea. Most arcoideans have elongate to quadrate, inflated shells with external radial sculpture and a long straight hinge line. Most limopsoideans are characterised by orbicular shells with external radial sculpture and a curved hinge line.

All arcoids are marine (with the exception of the genus *Scaphula* recorded from India and Burma) and are shallow burrowers or byssate nestlers. Living arcoids show very little specialisation of their internal anatomy (Heath 1941), but have an extensive array of shell forms which reflect adaptations to a wide variety of habitats. Thomas (1978a) provided a detailed analysis of the arcoid form, examining aspects of phylogeny, growth and adaptation, and the potential of the group to exploit available habitats and life style possibilities.

The first record of the Arcoida is in the Early Ordovician (Newell 1969b). Thomas (1978b) considered that this early appearance of the group indicates that it originated directly from an ancestral bivalve lineage, close to the initial divergence of pterioids and the progenitors of heterodonts. The phylogeny of the order is not well understood, and Newell (1969b) suggested a gradation from the ancestral Cyrtodontidae, to Parallelodontidae and then to the Cucullaeidae. Tevesz (1977) suggested that the Limopsidae and the Arcidae were also derived from the Parallelodontidae, with the Limopsidae giving rise to the Glycymerididae and the Philobryidae, and the Noetiidae derived from the Arcidae. The fossil record indicates that a major diversification of the order took place in the Mesozoic, with the appearance of most of the modern families in the Jurassic (Arcidae, Cucullaeidae, Limopsidae) and the Cretaceous (Noetiidae, Glycymerididae).

Superfamily ARCOIDEA

Australian species of this group are all marine and generally have heavy, inflated, equivalve shells. Shells are often large, obliquely ovate to quadrate, radially ribbed and have a distinct posterior umbonal keel. The taxodont hinge is straight and is below the usually broad cardinal area separating the umbones. The ligament is of the duplivincular type and in section has fibrous portions interrupted along the hinge line by a medial wall of lamellar material. In the Arcidae and Cucullaeidae, the ligament occupies all of the cardinal area, but is restricted to only part in the Noetiidae. A conspicuous periostracum is present.

The adductor muscles are isomyarian or almost so, and generally the pedal-byssal retractor muscles are well developed. The pallial line is without a pallial sinus. The mantle is not fused ventrally, but anterior and posterior inhalant currents may be produced. The generally stout foot is present throughout ontogeny, and has a byssus, which may be lost in the adult (Boss 1982).

Four families, the Arcidae, Cucullaeidae, Noetiidae and Parallelodontidae, are included in the superfamily Arcoidea. The Australian fauna includes representatives of each of these families except for the Parallelodontidae, which is restricted to the northern Pacific region (Newell 1969b). The Arcidae are a large and diverse family with many species recorded from the Australian region, whereas the Cucullaeidae and the Noetiidae are represented by one and a few species, respectively.

The classification in this work follows that used by Newell (1969b), which is based largely on gross shell morphology, and places the Australian fauna in a worldwide context. Lamy (1907) reviewed all recent species of the superfamily as here defined. Primarily on the basis of shell morphology, Lamy placed all species in the single family Arcidae, and included a significant amount of Australian material. Reinhart (1935) also proposed a classification of the family Arcidae based mainly on shell morphology, that included the Noetiidae, but excluded the Cucullaeidae, of the present arrangement.

In general, Recent Australian arcid species are characterised by a long straight hinge line, composed of numerous similar teeth, and an elongate ligament, occupying the entire cardinal area. Cucullaeids can be recognised by a myophoric flange associated with the posterior adductor muscle and the differentiation of hinge teeth into median, transverse denticles and distal, elongate 'pseudolaterals'. Australian noetiid species are characterised by the ligament being restricted to only part of the cardinal area.

Arcoideans were included in the earliest systematic accounts of the Australian molluscan fauna. Lamarck (1818–1822), Reeve (1844) and Smith (1885) all recorded and described species based on Australian specimens. The southern Australian fauna was subsequently documented extensively at a local level by a number of authors: southern Western Australia by Hedley (1915), South Australia by Cotton (1961) and Ludbrook & Gowlett-Holmes (1989), Victoria by Macpherson & Gabriel (1962), Tasmania by May (1923) and New South Wales by Iredale & McMichael (1962). The northern Australian fauna, which includes many broadly distributed Indo-West Pacific species, has not been documented comprehensively. Iredale (1939) reported on the Queensland species, listing 27 genera, 18 of which he defined and described. Many of these genera have been placed in synonymy, but a critical assessment of the taxa is needed and must await comprehensive regional revisions of the higher taxa. Iredale in his treatment was unaware of the wide Indo-West Pacific distributions of many of the northern Australian arcoideans.

Family Arcidae

Commonly known as ark shells, Australian members of this large and diverse family of marine bivalves range from minute (length 4–5 mm) to large (100 mm), living in nearly all marine environments, but are most common in the intertidal and shallow sublittoral zones. Most species have heavy, elongate, inequilateral shells, with a well-defined radial sculpture and dense periostracum. The taxodont hinge and the broad ligament are elongate, with the umbones well separated.

Newell (1969b) recognised two subfamilies within the family, Arcinae and Anadarinae, with a total of twelve extant genera, seven of which occur in Australia: *Arca*, *Barbatia*, *Trisidos*, *Anadara*, *Bathyarca*, *Samacar* and *Scapharca*. There is no comprehensive account of Australian species, but regional reports are available for a number of areas, as listed above for the superfamily.

Shells are generally white, equivalve to slightly inequivalve, inequilateral, with the umbones placed anterior to the midline. The shape of the shell is variable (Fig. 6.2): elongate and mostly rather flat in *Barbatia*, elongate and inflated in *Arca* and *Anadara* or quadrate and inflated in *Scapharca*. Species of the genus *Trisidos* have a twisted shape, due to torsion around the hinge axis. Shells of most genera are large and heavy, excepting *Bathyarca* and *Samacar* in which the small thin shells are obliquely ovate. Some *Arca* and *Barbatia* species have a byssal gape in the ventral shell margin.

Externally the shells are variously sculptured. *Arca*, *Barbatia* and *Trisidos* have numerous, narrow, radial ribs or striae, whereas *Anadara* has many broad flat radial ribs, and *Bathyarca* and *Samacar* have a number of commarginal lamellae. The external shell surface is generally covered by a dense brown, fibrous or hairy, periostracum. The taxodont hinge comprises numerous small, straight or chevron-shaped teeth, arranged transversely along the hinge line. The hinge line varies from narrow and straight in species of *Arca* and *Anadara*, to broader and slightly curved as in species of *Barbatia* and *Trisidos*. In some species the teeth decrease in size below the umbones. The ligament is elongate and of the duplivincular type, and in *Arca* and *Scapharca* species, occupies an extensive broad flat area between the umbones.

The anatomy and functional morphology of only a few Australian species have been examined. Sullivan (1961) reported in detail on *Anadara trapezia* (Fig. 6.2E) and Tevesz & Carter (1979) reported on *Trisidos yongei*. Pelseneer (1911) and Heath (1941) included information on the soft-parts of a few species recorded from Australia, but used non-Australian material. Other studies on non-Australian species are by Rost (1955) on eastern Pacific species and Oliver & Allen (1980a) on the functional morphology of deep-water Atlantic species.

The work of Sullivan (1961) on the anatomy of *Anadara trapezia* is presented as the basis of this account of the family (Fig. 6.2E), but future comprehensive comparative studies may indicate that some characters are restricted to that particular species or genus. The large, flat mantle is without fusion or siphons, the lobes are normally apposed along the mantle edge, except in certain regions posteriorly where the primary inhalant and exhalant apertures are formed, and anteriorly where the aperture for the secondary, weaker inhalant current is produced. Mantle lobes are attached to shell valves along the pallial line, peripheral to which is the mantle edge. The mantle is composed mainly of connective tissue, with large blood spaces. Muscle fibres are restricted to the mantle edge where they are abundant and can be used to retract the mantle edge in response to irritation. Both surfaces of the mantle have abundant gland cells, and the epithelium of the inner mantle surface is ciliated. The epithelial cells along the pallial line are modified to form a union with the shell, and to provide an origin for the radial muscle fibres of the mantle edge. Small hemispherical compound eyes are present in the mantle margin of some species, such as *Arca noae* from the Atlantic (Hesse 1900 *fide* Sullivan 1961), but are not present in *Anadara trapezia*.

The mantle cavity contains the foot, gills (ctenidia) and labial palps. The foot is elongate, with a ventral byssal groove, found even in species without a byssus in the adult. It has a complex musculature including two pairs of pedal retractors and is used by burrowing forms such as *Anadara*, *Scapharca* and *Trisidos* to establish shallow burrows in either sand or mud, and by byssally attached nestling forms such as *Arca* and *Barbatia* to re-establish after being dislodged. The epithelium is glandular in the area of the byssal groove. Two pairs of labial palps extend from the anterior end of the gills to the mouth, and the oral groove extends from the dorsal extremity of the palps to the mouth. The palps have a ridged dorsal area which is used to sort food before it is conveyed, via the oral groove, to the mouth. The palps consist mainly of connective tissue with many blood spaces. The epithelium of the outer palp surfaces is glandular and lacks cilia, whereas that of the inner palp surfaces is strongly ciliated for sorting and transporting of food. The ctenidial-palp junction is the of Stasek (1963) category 3 Type. The alimentary system consists of a short oesophagus, a stomach with a crystalline style, an intestine and a mass of digestive tubules. The stomach is of the Purchon (1957) Type III. Heath (1941) reported the intestine length as variable, short in the Arcinae, but long and convoluted in the Anadarinae. The gut passes ventral to the heart in most genera, but in *Trisidos* the heart surrounds the intestine (Heath 1941).

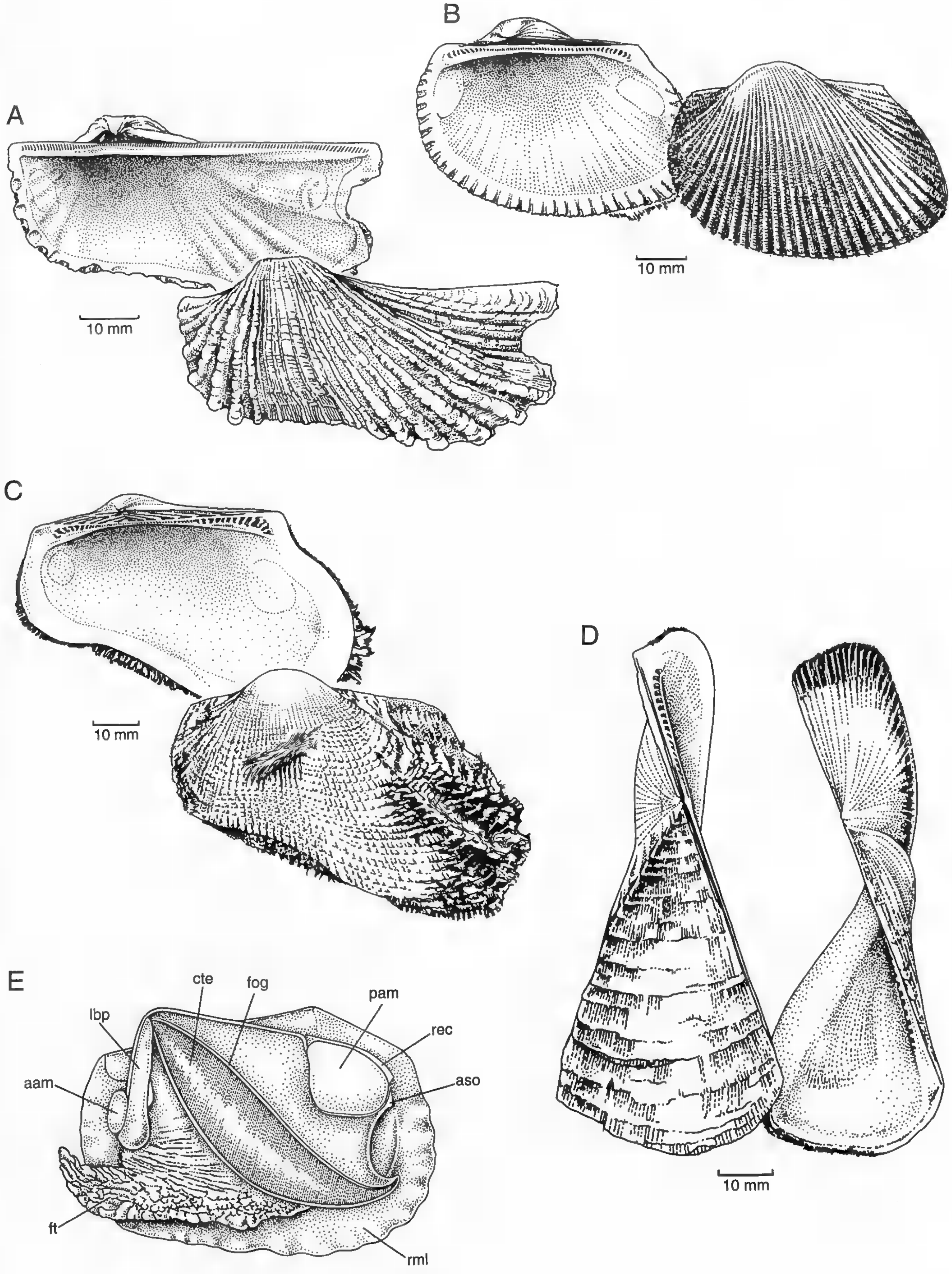

Figure 6.2 Family Arcidae. Shell valves: **A**, *Arca navicularis*; **B**, *Anadara crebricostata*; **C**, *Barbatia* cf. *helblingii*; **D**, *Trisidos tortuosa*. **E**, *Anadara trapezia*, organs of the mantle cavity, left shell valve and mantle lobe removed. A, B, C, right valve in internal view, left valve in external view; D, left valve on left, right valve on right. **aam**, anterior adductor muscle; **aso**, abdominal sense organ; **cte**, ctenidium; **fog**, food groove; **ft**, foot; **lbp**, labial palp; **pam**, posterior adductor muscle; **rec**, rectum; **rml**, right mantle lobe. (E, after Sullivan 1961)

[R. Plant]

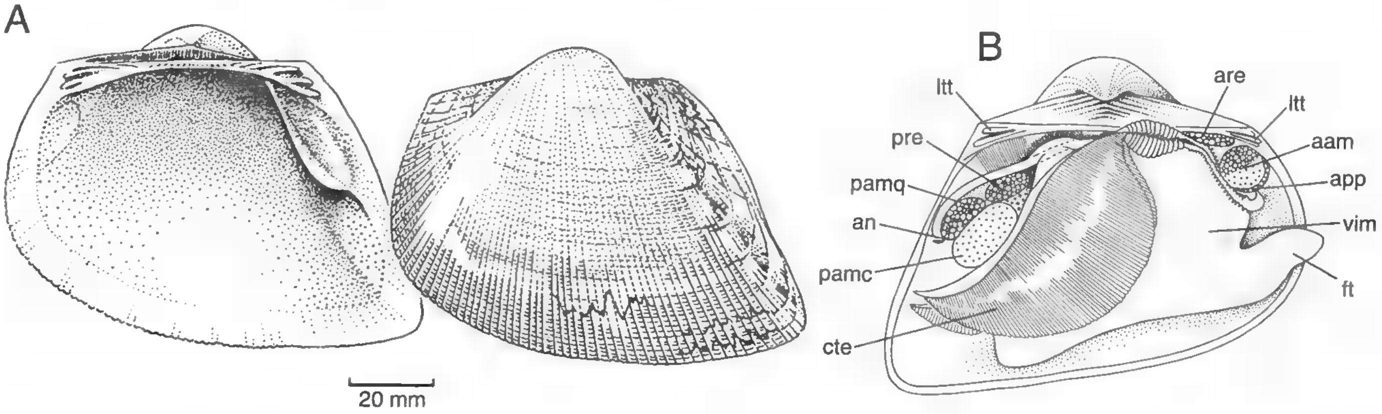

Figure 6.3 Family Cucullaeidae. *Cucullaea labiata*: **A**, shell valves, right valve in internal view, left valve in external view; **B**, organs of the mantle cavity, right shell valve and mantle lobe removed. **aam**, anterior adductor muscle; **an**, anus; **app**, anterior pedal protractor muscle; **are**, anterior retractor muscle; **cte**, ctenidium; **ft**, foot; **ltt**, lateral teeth; **pamc**, posterior adductor muscle 'catch component'; **pamq**, posterior adductor muscle 'quick component'; **pre**, posterior retractor muscle; **vim**, visceral mass. (B, modified after Morton 1981) [R. Plant]

The heart structure is variable within the family. Heath (1941) reported that species of *Arca* have 'paired hearts', with the pericardium and the ventricle duplicated, whereas species of *Anadara*, *Trisidos* and *Barbatia* have only a single ventricle. Haemoglobin is present in the erythrocytes of a number of arcid species, including Australian species of *Anadara*, giving them their common name of blood cockle. The paired kidneys consist of branched tubules and are connected with the pericardial cavity in front, via a renopericardial canal. The sexes are separate, and in *Anadara trapezia* spawning occurs in summer (Hadfield & Anderson 1988), when the ovaries are a bright orange colour. The oviduct and kidney open by a common pore. Three pairs of ganglia are present: cerebropleural, pedal and visceral. Near the anus are two small swellings, the abdominal sense organs, which Morton (1983a) suggested may be used in photoreception.

Narasimham (1968), in one of the very few studies on development, reported that Indian specimens of *Anadara granosa* (a species common in northern Australia) reach sexual maturity at seven months old, and that shell length after the first year of life was 31.5 mm and after the second year 49.5 mm.

Most arcids live intertidally or in shallow water, as byssate nestlers in corals, rocks and stones (*Arca*, *Barbatia*) or as shallow burrowers in sand or mud (*Anadara*, *Scapharca* and *Trisidos*). Mud-dwelling species such as *Anadara trapezia* occur in abundance in suitable habitats. Nestling forms, such as some *Barbatia* species, can show considerable variation in shell shape and sculpture. *Bathyarca* and *Samacar* are deeper water groups that are poorly known.

Some species of the genus *Anadara* have been extensively exploited for food throughout Asia, and have been cultured since the 17th Century in China and since the mid 19th Century in Japan (Pathansali & Soong 1960). *Anadara trapezia* is harvested from wild populations in Victoria and New South Wales, where specimens are occasionally available for sale in markets. Shells of *Anadara* species are found in middens, indicating that they were used for food by Aboriginal people: reports include *Anadara trapezia* from south-eastern Australia (Simmons 1984) and *Anadara granosa* from north-western Australia (M. Smith personal communication).

The southern Australian fauna includes four endemic species, *Barbatia pistachia*, *Barbatia squamosa*, *Anadara trapezia* and *Bathyarca perversidens*. The *Barbatia* species are distributed across southern Australia, *Anadara trapezia* has a disjunct distribution in suitable habitats, from Queensland to Victoria, with a single isolated population in southern Western Australia. *Bathyarca perversidens* is recorded from only a few localities in eastern Western Australia, South Australia and New South Wales.

The northern Australian fauna, which includes more than 20 species, is considerably more diverse with most species distributed beyond Australia in the Indo-West Pacific region. The genera *Anadara* and *Barbatia* are represented by many species, including *Anadara antiquata*, *Anadara granosa*, *Barbatia helblingii* and *Barbatia fusca*. The other genera are represented by one to a few species. *Anadara crebricostata* is one of the few endemic northern Australian species, with a distribution from Hervey Bay, Queensland, to Shark Bay, Western Australia.

The earliest fossil records of the family Arcidae in Australia are the Late Eocene records of *Barbatia* and *Arca*. *Barbatia (Acar)* and the extinct genus *Notogrammatodon* occur in the middle Miocene and *Anadara* is known only form the Holocene and Recent faunas (T. Darragh personal communication).

Family Cucullaeidae

Cucullaeids are marine bivalves with large (up to 100 mm), heavy, strongly inflated, quadrate shells, with a truncate posterior and an elongate hinge line.

The family can be separated from other Australian families in the Arcoidea (Arcidae and Noetiidae), by the structure of the hinge, which in the Cucullaeidae has the teeth differentiated into centrally placed transverse denticles and distally placed, elongate pseudolaterals (Fig. 6.3A). It can be further separated from arcids by the presence of the myophoric flange along the margin of the posterior adductor muscle.

The large shells of *Cucullaea labiata* are approximately quadrate, strongly inflated, with the posterior area strongly truncate, and inequivalve, the left valve overlapping the right. They are covered with a thick, velvety periostracum. Externally, the shells are sculptured with numerous flat, radial ribs, and fine commarginal striae. Umbones are orthogyrate, almost median, separated by the broad ligamental area. The ligament is amphidetic and duplivincular, with a few chevron-shaped grooves.

The hinge teeth of adults are differentiated into a central series of small, transverse denticles and a distally placed series of elongate, pseudolateral teeth, arranged nearly parallel to the ligament. These latter teeth are the major locking mechanism of the shell and are responsible for valve alignment (Morton 1981).

The adductor muscles are of unequal size, with the posterior at least twice the size of the anterior; both are divided into quick (striated) and slow (smooth) muscle blocks (Fig. 6.3B). The pedal retractor muscles are similarly unequal. The shell interior forms a myophoric flange (a built out ridge or buttress), at the position of the anterior edge of the posterior adductor muscle. This structure is the position of attachment of the posterior adductor muscle and functions to reduce the length of the posterior adductor and the effect of shear upon it, necessitated by the extreme posterior truncation of *Cucullaea* species (Morton 1981).

The investigations of Heath (1941) and Morton (1981) of the internal anatomy indicated that the overall structure is similar to that of the Arcidae. The large, flat, transparent mantle is without fusion or siphons, with the mantle edge attached to shell valves along the pallial line. The mantle surface lacks glandular development and the posterior margin is devoid of sensory papillae or tentacles, features found in arcid species. Morton (1981) suggests that unlike the Arcidae, *Cucullaea* has both the inhalant and exhalant currents situated posteriorly. The mantle cavity contains the small, anteriorly pointing foot, thin labial palps and the gills (ctenidia). The foot musculature includes anterior and posterior pedal retractors and anterior pedal protractors. The ventral surface of the foot has a long byssal groove and a small byssal gland, which is presumed not to function in adults.

The alimentary system includes the thick-walled, convoluted, tube-like oesophagus and unmodified stomach, both of which have internal longitudinal ridges. The stomach has a crystalline style. The convoluted intestine is surrounded in part by the ventricle. The heart is more or less double.

Cucullaea labiata has a broad distribution around northern Australia, and is recorded from Shark Bay, Western Australia, to New South Wales. Animals live at depths to at least 200 m, burrowing in sand. In life, the shell valves of *Cucullaea* gape widely and Morton (1981) has suggested that the position in the sand is anterior end down.

The Cucullaeidae are represented in the Recent fauna by a single species, *Cucullaea labiata* (Fig. 6.3), which is distributed throughout the Indo-West Pacific, including Australia (Nicol 1950). A number of junior synonyms of *C. labiata* are found in the literature, including *Cucullaea conamera* and *Cucullaea vaga.* The family was represented by many species worldwide during the Jurassic and Cretaceous, declining in the Early Eocene, in both number of species and the breadth of their distribution (Nicol 1950). *Cucullaea* has been recorded from the Late Palaeocene through to the Late Pliocene of southern Australia (T. Darragh personal communication).

Family Noetiidae

Noetiids are small to medium-sized (up to 40 mm) marine bivalves, characterised by stout inflated shells and a taxodont hinge line. They are distinguished from the Arcidae and Cucullaeidae by having the ligament restricted to only part of the cardinal area.

Distributional records are the only information available on the few Australian members of the family: Iredale (1939) recorded five species from Queensland localities, and Iredale & McMichael (1962) recorded one of these species from New South Wales.

The subfamily and generic systematics and nomenclature of the family are very confused. Newell (1969b) recognised four extant genera, *Noetia* and *Sheldonella* (subfamily Noetiinae) and *Striarca* and *Arcopsis* (subfamily Striarcinae); species of *Sheldonella, Striarca* and *Arcopsis* have been recorded from Australia. Ward & Blackwelder (1987) consider *Arcopsis* a junior synonym of *Quadrilatera. Noetia* is restricted to the Atlantic and eastern Pacific, but the other genera are represented in the Australian fauna by one or more species. Oliver (1985) considered the lack of definition of the genera proposed in the Newell classification to be a serious problem, and indicated the need for a complete generic revision. Iredale (1939) in a work on Queensland species, introduced a number of new genera, all subsequently placed in synonymy by Newell. Further detailed investigation of some of the taxa proposed by Iredale (1939) is required. For example, *Estellacar* is considered by Oliver (1985) to be monotypic, including only *E. olivacea* from Queensland and the Philippines, and in his opinion it is quite unlike other genera and of uncertain relationship with the Noetiidae. Subsequently however, Oliver (1987), placed *Estellacar* in the Noetiidae and tentatively assigned three species to the genus, including the Queensland species *Estellacar saga.* The genera *Scelidionarca* and *Rectangularca,* neither of which is represented in the Australian fauna, were not included in the Newell classification.

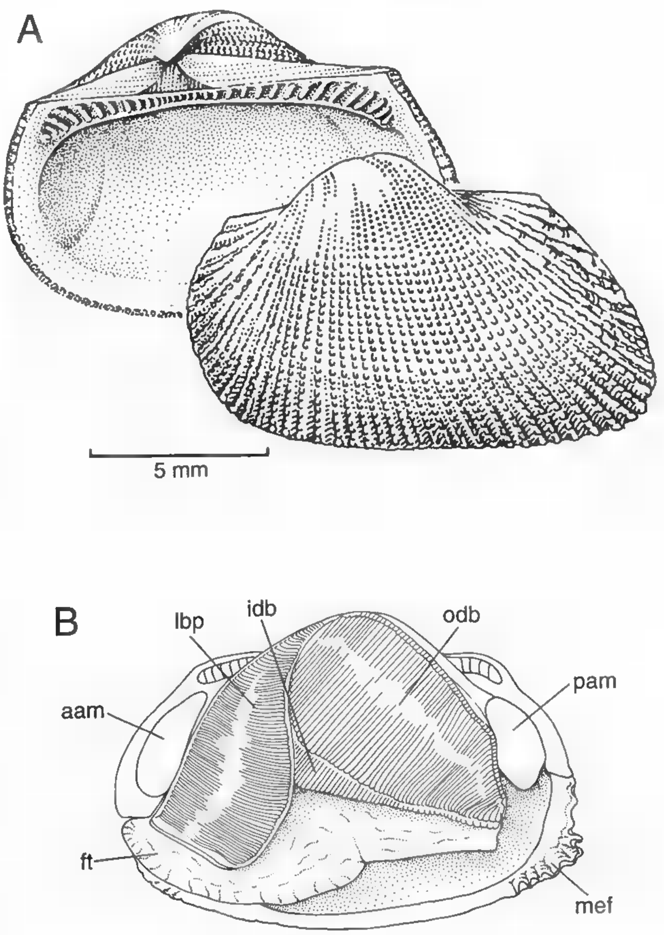

Figure 6.4 Family Noetiidae. A, *Arcopsis* cf. *afra*, shell valves, left valve in internal view, right valve in external view. B, *Estellacar galactodes*, organs of the mantle cavity, left shell valve and mantle lobe removed. **aam**, anterior adductor muscle; **ft**, foot; **idb**, inner demibranch of ctenidium; **lbp**, labial palp; **mef**, mantle edge folds; **odb**, outer demibranch of ctenidium; **pam**, posterior adductor muscle. (B, after Oliver 1987) [R. Plant]

Shells are small and equivalve, with a taxodont hinge (Fig. 6.4A), similar to that present in Arcidae. The shape of *Sheldonella* is obliquely ovate, that of *Striarca* and *Arcopsis* stout, inflated and approximately rectangular. External sculpture is variable, with well-defined radial ribs in *Sheldonella*, or with numerous fine radial striae in *Striarca* and *Acropsis* species. The ligament is duplivincular, the bands forming vertical striations with multiple strips of the elastic layer embedded in the fibrous layer, which is in contact with the shell. The ligament is restricted to only part of the cardinal area, with the remainder bare. In *Arcopsis* the ligament is restricted to a small diamond-shaped area immediately below the umbones. The periostracum is dense, brown and fibrous.

Information on soft-parts is based on non-Australian material. Heath (1941) reported on two species from the Atlantic and eastern Pacific, and Oliver (1985) reported on two species from Hong Kong, one of which, *Striarca symmetrica*, is recorded from northern Australia. Oliver (1987) reported on *Estellacar galactodes* from China (Fig. 6.4B). These works indicate that the overall structure of the soft parts is similar to that of the Arcidae. The flat, glandular mantle is without fusion or siphons, the lobes are apposed along the mantle edge except in the area of inhalant and exhalant apertures. Mantle lobes are attached to the shell valves along the pallial line, peripheral to which is the mantle edge. The mantle edge bears two or three cup-shaped ocelli (eye spots) in the anterior-dorsal region. The labial palps are of moderate size and the stomach is the Type III of Purchon (1957). Heath (1941) reported the Atlantic species *Arcopsis adamsi* as having a single pericardium and ventricle. In *S. symmetrica*, the adductor muscles are subequal, and the posterior pedal retractors are well developed and also act as byssal retractors, whereas the anterior pedal retractors are very small. In *Estellacar galactodes*, the labial palps are very large and ridged and the pedal retractors are small and approximately equal in size. The foot is reported as elongate or compressed and bears a ventral byssal groove. Abdominal sense organs are present.

Australian noetiid species are restricted to the northern tropical fauna, and include *Estellacar saga*, *Arcopsis pellita*, *A. bivia*, *Sheldonella repenta* and *S. venustopsis*. These animals typically live in the intertidal and shallow sub-littoral, attached by a narrow byssus to the underside of rocks (Iredale 1939; Stanley 1970; Oliver 1985).

A specimen of *Arcopsis* has been recorded from Australia from the Late Eocene (T. Darragh personal communication).

Superfamily LIMOPSOIDEA

Limopsoideans are marine bivalves with small to medium-sized equivalve shells, which are orbicular to obliquely ovate in shape. Externally the shell is often sculptured with radial ribs. The hinge is heavy and taxodont, extending along the dorsal margin, however, some philobryids are edentulous. Most limopsoideans are isomyarian, although some philobryids are monomyarian. The mantle margins are open and siphons are absent. The ctenidia are filibranch and eleutherorhabdic. The foot is always present and has a byssal groove, though the byssus is not always present in the adult. Limopsoideans can be distinguished from arcoideans by the shape of the shell, which is usually orbicular to obliquely ovate, rather flat and without an umbonal keel; the taxodont hinge, when present, is usually curved.

Recent authors such as Tevesz (1977) and Dell (1990) consider the Limopsoidea to include the families Limopsidae, Glycymerididae and Philobryidae. The latter family was only tentatively included in the superfamily by Newell (1969b).

The limopsoidean families can be distinguished as follows. Limopsidae have medium-sized shells with a taxodont hinge and a non-striated, short ligament which is restricted mainly to the central triangular resilifer. Glycymerididae have medium-sized shells, the hinge taxodont with an elongate cardinal area and one or more chevron grooves; the ligament is duplivinicular. Philobryidae are minute to small shells; the hinge, may be taxodont, or the valves may be edentulous, and the ligament is partly or wholly internal.

Literature on the Australian members of the superfamily is largely restricted to distributional data on particular species.

Limopsoideans were included in the earliest systematic accounts of the Australian molluscan fauna. Lamarck (1818–1822) and Smith (1885) recorded and described species based on Australian specimens. Subsequently, the southern Australian fauna was extensively documented at a local level by a number of authors: southern Western Australia by Hedley (1915), South Australia by Cotton (1961) and Ludbrook & Gowlett-Holmes (1989), Victoria by Macpherson & Gabriel (1962), Tasmania by May (1923) and New South Wales by Iredale & McMichael (1962). The northern Australian fauna, which includes many broadly distributed Indo-West Pacific species, has not been documented comprehensively. Iredale (1939) reported on the Queensland species, listing four genera of Glycymerididae, all of which were described by the author. Lamprell & Whitehead (1992) record 25 species of Glycymerididae from Australia.

Family Limopsidae

Limopsids are distinguished from other families in the Limopsoidea by the medium-sized, obliquely ovate shells and the short, non-striated ligament which is mainly restricted to a central triangular resilifer.

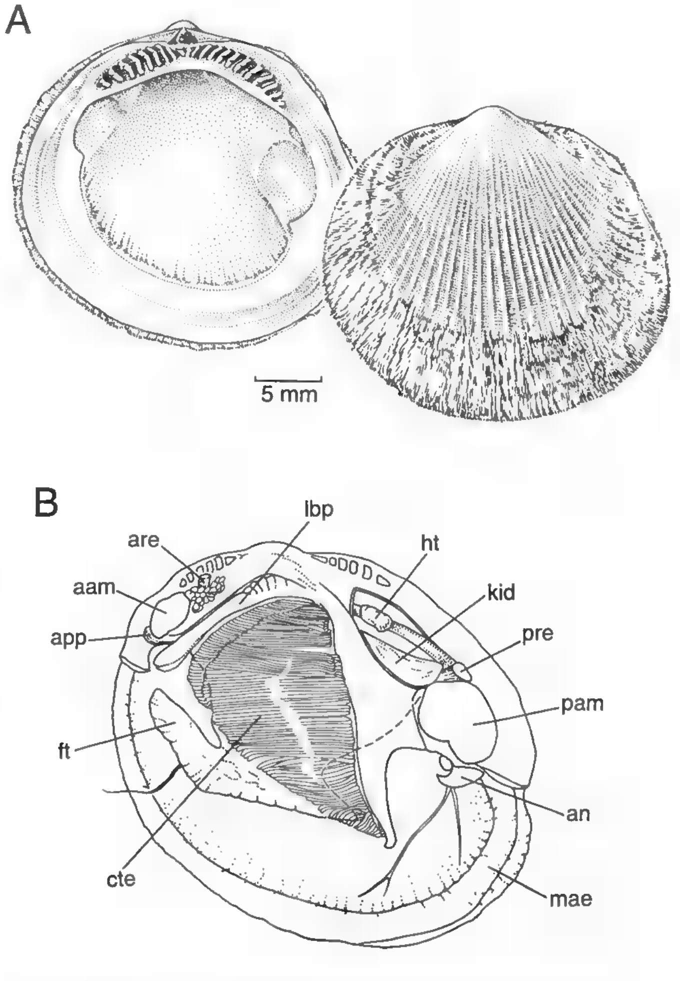

Figure 6.5 Family Limopsidae. A, *Limopsis tenisoni*, shell valves, right valve in internal view, left valve in external view. B, *Limopsis marionensis*, organs of the mantle cavity, left shell valve and mantle lobe removed. **aam**, anterior adductor muscle; **an**, anus; **app**, anterior pedal protractor muscle; **are**, anterior retractor muscle; **cte**, ctenidium; **ft**, foot; **ht**, heart; **kid**, kidney; **lbp**, labial palp; **mae**, mantle edge; **pam**, posterior adductor muscle; **pre**, posterior retractor muscle. (B, after Oliver 1981) [R. Plant]

This small family of marine bivalves is represented in the Australian fauna by a number of subtidal and deeper water species. Australian limopsids have small shells (up to 50 mm), which are obliquely ovate in shape, and have a taxodont hinge.

Limopsid shells are equivalve, triangulate to rotund or obliquely ovate in outline, with valves varying from almost flat to moderately inflated and with umbones approximately central or somewhat anterior to the midline (Fig. 6.5A). The margins close without a byssal gape. Externally the valves are not strongly sculptured and bear fine radial or commarginal striae or narrow low ribs. The exterior is covered with a tufted, silky periostracum, which may extend beyond the shell margin. The taxodont hinge is broad and may be straight or slightly arched, with the teeth arranged in two series on each side of the umbo, and decrease in size or are absent in the area just below the umbo. The ligament is short and restricted to a triangular pit just below the umbo. The remainder of the cardinal area is smooth. The adductor muscle scars are well marked and subequal, with the smaller anterior adductor muscle scar closer to the hinge line.

The anatomy and functional morphology of the family have not been documented comprehensively, and the available detailed accounts are based on Antarctic or Atlantic deep-sea species (Fig. 6.5B; Burne 1920; Knudsen 1967, 1970; Oliver & Allen 1980b). The more general works of Tevesz (1977) and Oliver (1981) include some data on Australian species. These studies indicate that limopsid anatomy does not differ significantly from the typical arcoid form. The mantle lobes are without fusion or siphon, but mantle edges may be apposed posteriorly to form inhalant and exhalant apertures. The mantle is without tentacles, but may bear ocelli, and is attached to the shell along the pallial line. The mantle cavity contains the elongate foot (with ventral byssal groove), the small labial palps and the gills (ctenidia). The heart has triangular auricles and a squarish ventricle traversed by the rectum. The kidneys are posterior to the ventricle.

Anterior and posterior adductor muscles are sub-equal, and small anterior and posterior pedal retractor muscles are present (Boss 1982).

Oliver & Allan (1980b) reported that deep-water Atlantic species have lecithotrophic development with short lived, non-feeding larvae.

Limopsid species are reported both as infaunal shallow burrowers in soft substrata and as epifaunal forms, byssally attached to coarse substratum particles (Tevesz 1977; Oliver & Allan 1980b).

Tevesz (1977), Oliver (1981) and other recent workers have recognised only two genera for extant species of the family: *Limopsis*, with a cosmopolitan distribution including Australia, and *Empleconia*, a genus restricted to the North Pacific and Bering Sea. Newell (1969b) and other earlier authors included a further two extant genera in the family: *Nipponolimopsis*, a Japanese genus, included as a synonym of *Limopsis* by Tevesz (1977), and *Lissarca*, a genus now included in the Philobryidae (Tevesz 1977). Oliver (1981) proposed a complex classification of the family, placing all species in the genus *Limopsis*, but dividing species into thirteen morphological 'classes' which are further arranged into three functional groups.

Lamy (1912b) reviewed Recent species of the family, in a study based largely on shell morphology, and included a limited number of Australian specimens. The regional accounts listed above for the superfamily provide species lists for the areas documented. Dell (1964) and later authors have recorded extensive variability in a number of shell characters documented in *Limopsis* species.

The family Limopsidae is restricted mainly to the cold waters of the higher latitudes and the deep sea. Most of the species recorded from Australia are distributed in southern Australia at depths of 20–600 m. Four *Limopsis* species are documented for the southern Australian fauna: *Limopsis tenisoni*, *L. forteradiatus*, *L. penelevis*, and *L. erectus*. The northern Australian fauna is poorly known and may include only a few species.

The earliest fossil record of this family in Australia is of *Limopsis* from the Late Palaeocene (T. Darragh personal communication).

Family Glycymerididae

Glycymeridids are marine bivalves with small to medium-sized (up to 100 mm in length), heavy shells, usually orbicular in shape, with an arched taxodont hinge line and a duplivinicular ligament.

Shells are heavy, equivalve, equilateral and more or less circular in outline (Fig. 6.6). The valves are not inflated and the ventral margin is without a gape; the interior margins are crenulate. The external sculpture varies from almost smooth, bearing only fine radial and commarginal striae as in *Glycymeris* species, to radial with numerous, well-defined radial riblets as in *Melaxinaea*, to having several strong, sometimes quite high, radial ribs as in *Tucetona*. In most species the external shell surface is covered by a thick, velvety periostracum.

The taxodont hinge is broad and arched, with numerous either straight or chevron-shaped teeth arranged in two series on each side of the umbo. Teeth are larger in the middle area of each series. The ligament is external and of the duplivincular type, and may be in a series of chevron-shaped grooves, extending along the dorsal area above the hinge teeth. The adductor muscle scars are well marked and subequal. In some species a myophoric flange develops on the anterior edge of the posterior adductor muscle.

The anatomy and functional morphology of the family have not been well documented. Pelseneer (1911) examined specimens, including *Tucetona auriflua* (as *Pectunculus auriflus*) which he illustrated. Heath (1941) included five glycymeridid species in his anatomical studies of the family Arcidae. The Heath study was based on Atlantic and eastern Pacific specimens with the exception of the Philippines specimens of *Glycymeris pectiniformis*. Thomas (1975) provided some general information on the family, based on Atlantic species. Anatomical studies of Australian members of the family have not yet been undertaken.

The available studies indicate that glycymeridid anatomy (Fig. 6.6C) does not differ significantly from that typical of the Arcoidea. The mantle lobes are without fusion or siphon, but mantle edges may be apposed posteriorly to form inhalant and exhalant apertures. The mantle is without tentacles but may bear ocelli (eye spots) on the posterior border, and is attached to the shell along the pallial line. The mantle cavity contains the large, ventrally grooved foot, the labial palps and the gills (ctenidia). The heart has paired auricles and

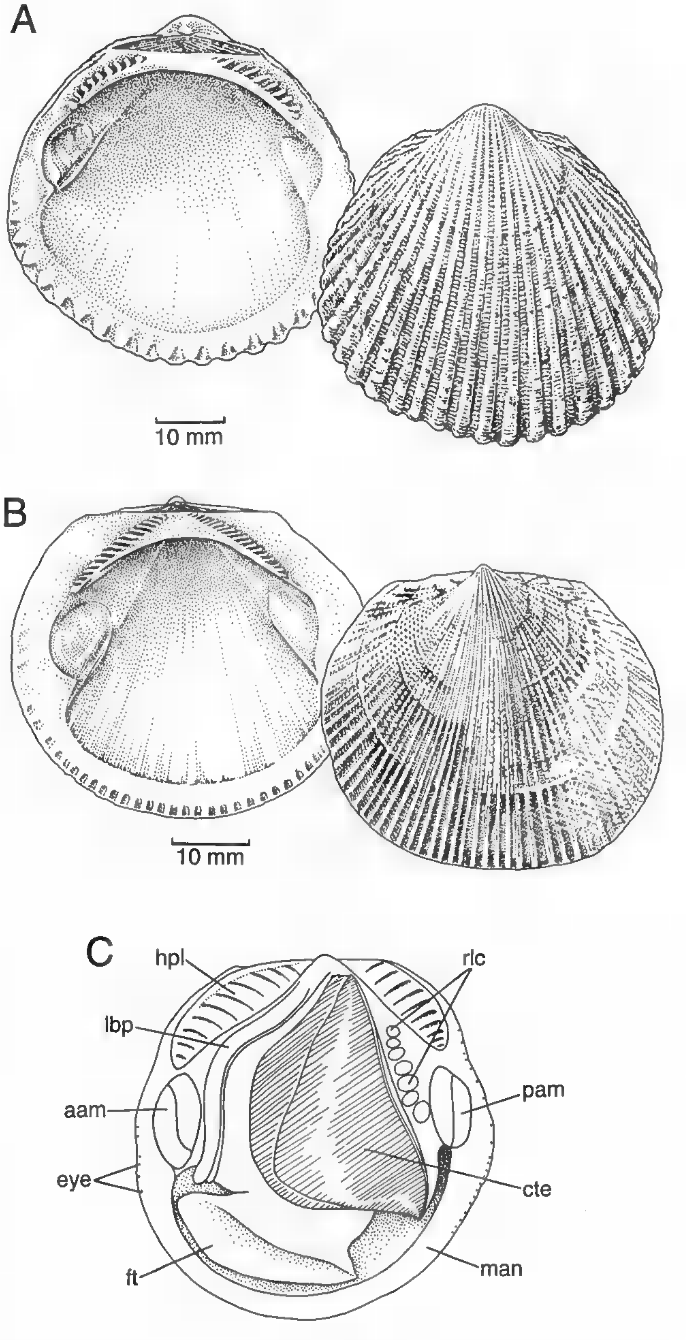

Figure 6.6 Family Glycymerididae. A, B, shell valves, left valve in internal view, right valve in external view: A, *Tucetona hoylei*; B, *Melaxinaea vitrea*. C, *Tucetona auriflua*, organs of the mantle cavity, left shell valve and mantle lobe removed. **aam**, anterior adductor muscle; **cte**, ctenidium; **eye**, 'eyes'; **ft**, foot; **hpl**, hinge plate; **lbp**, labial palp; **man**, mantle; **pam**, posterior adductor muscle; **rlc**, renal concretions. (C, after Pelseneer 1911) [R. Plant]

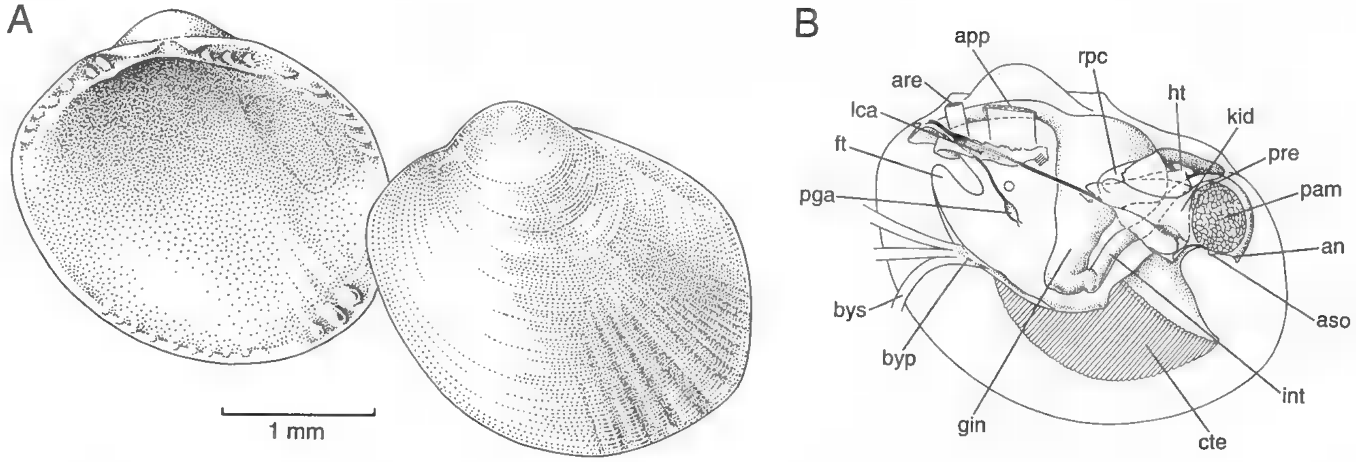

Figure 6.7 Family Philobryidae. **A**, *Lissarca rubricata*, shell valves, right valve in internal view, left valve in external view. **B**, *Lissarca notorcadensis* organs of mantle cavity, left shell valve and mantle lobe removed. **an**, anus; **app**, anterior pedal protractor muscle; **are**, anterior retractor muscle; **aso**, abdominal sense organ; **byp**, byssal papilla; **bys**, byssus; **cte**, ctenidium; **ft**, foot; **gin**, gastro-intestine; **ht**, heart; **int**, intestine; **kid**, kidney; **lca**, labial caecum; **pam**, posterior adductor muscle; **pga**, pedal ganglia; **pre**, posterior retractor muscle; **rpc**, renopericardial duct. (B, after Burne 1920) [R.Plant]

a large, lobulated ventricle traversed by the rectum. The kidneys are large, subtriangular and separate. Anterior and posterior adductor muscles are sub-equal, and anterior and posterior pedal retractor muscles are well developed (Boss 1982). All glycymerids lack a byssus in the adult and appear to lose the byssal cavity. The heart, which surrounds the rectum, has paired auricles and a large ventricle. The kidneys are large, separate, subtriangular and located on each side of the pedal retractors.

Glycymeridids are shallow burrowers in subtidal, sandy bottom environments. Thomas (1975) documented Atlantic species of *Glycymeris* as being slow and inefficient burrowers that move around extensively at night. *In situ* these glycymeridids are usually just covered by the sediment, with the postero-ventral margin exposed at the sediment surface. Large populations of glycymeridids are found in such habitats and the shells are often washed up in large numbers along sandy beaches.

No comprehensive definitive classification of the family is available. The most recent work, which is adopted here, is that of Matsukama (1986), who proposed a classification for the Japanese members of the family. All extant species are included in three genera: *Glycymeris*, *Tucetona* and *Melaxinaea*. Each of these genera has Australian representatives.

Lamy (1912a) reviewed Recent glycymeridid species in a study based largely on shell morphology and included data on a limited number of Australian specimens. For regional accounts of the group see those listed for the superfamily. The southern Australian temperate fauna includes several endemic species: *Glycymeris striatularis*, *G. radians*, *Tucetona broadfooti* and *T. flabellata*. The northern Australian tropical fauna is considerably more diverse, and most of the species have a broad Indo-West Pacific distribution, including *Glycymeris reevei*, *G. crebreliratus*, *Tucetona auriflua*. *Glycymeris dampierensis* and *G. persimilis* are endemic to Western Australia.

The first fossil record of the family in Australia is of *Tucetona* in the Late Eocene (T. Darragh personal communication).

Family Philobryidae

Philobryids are marine bivalves with very small (to length 10 mm) obliquely ovate shells; they are found from intertidal areas to depths of 1000 m. The hinge is very distinctive and differs significantly from other extant groups of the Arcoida. The ligament is internal, situated in a ligamental pit located below the umbones and usually between two rows of transverse denticles. The genera *Cratis* and *Lissarca* each bear two short series of taxodont teeth below the denticles and also on each side of the ligamental pit, but the genera *Philobrya* and *Cosa* are edentulous.

Philobryid shells are small, obliquely ovate to quadrate, moderately inflated, equivalve, very inequilateral with umbones in front of the midline (Fig. 6.7A). The prodissoconch may form a cap-like structure below and around the umbo. A byssal notch may be formed in the antero-ventral margin of the shell. External shell sculpture is variable, ranging from well-defined radial ribs and/or distinct commarginal striae or ridges, to almost smooth.

The anatomy and functional morphology have not been well documented, but Burne (1920) described three Antarctic species *Philobrya sublaevis* (as *Philobrya limoides*), *Lissarca notorcadensis* and *Adacnarca nitens*. Tevesz (1977) provided limited information on three Australian species, *Philobrya modiolus*, *P. crenatulifera* and *Lissarca rhomboidalis*, and Morton (1978) reported on the New Zealand species, *Philobrya munita*.

Philobryids are dimyarian or monomyarian, and in the latter case the anterior adductor muscle is reduced or lost in the adult. Similarly the posterior pedal retractor muscle is developed and the anterior muscle reduced.

The mantle lacks ventral fusion and siphons are not present (Fig. 6.7B). The outer mantle fold may bear pallial eyes or ocelli that are covered by the overhanging periostracum. The gills are characterised by short, stout filaments connected by a few strong interfilamentary junctures (Tevesz 1977). The labial palps are small and ribbon-like. The foot is present, laterally compressed, with a deep ventral byssal groove, and has a small anterior 'toe' and large posterior 'heel', separated by the byssus. The heart has two auricles that may or may not be united, and a single ventricle. The rectum passes through the ventricle in some species or under the heart in others (Morton 1978). The kidney and urogenital openings are separate in some species, but not in others (Morton 1978).

Sexes are separate and large yolky eggs are produced. Philobryids are viviparous, and the young are attached to the byssus (Morton 1978) or the gills (Tevesz 1977) of the parent during incubation. Fertilisation is presumed to be internal (Morton 1978).

Information on Australian species is limited to distributional data (see those works under the superfamily), some systematic and nomenclatural information provided by Bergmans (1970), and some ecological data provided by Tevesz (1977).

Tevesz (1977) redefined the family to include nine genera. Eight of these are in the Recent fauna, four of which occur in Australia: *Cosa*, *Cratis*, *Lissarca* and *Philobrya*. The family is most common and widely distributed in the Southern Hemisphere. Tevesz (1977) confirmed the Philobryidae as part of the Arcoida, suggesting that the family was derived from the Limopsidae. Nicol (1966) had suggested that philobryids be included in the Mytiloidea. Keen (1969a) only tentatively placed the family in the

Limopsoidea and excluded *Lissarca*, which Newell (1969b) in the same publication, placed in the Limopsidae. Tevesz (1977) reported on three Australian species, *Philobrya modiolus*, *P. crenatulifera* and *Lissarca rhomboidalis*, at depths of 0–1 m in Pirates Bay, Eaglehawk Neck, Tasmania. These species live attached by the byssus to brown or red algae.

The fossil record of this family in Australia includes *Cosa* from the Early Oligocene into the Miocene, and *Lissarca* from the Late Eocene (T. Darragh personal communication).

Order PTERIOIDA

Members of the Pterioida are generally inequivalve, inequilateral or nearly equilateral, heteromyarian or monomyarian. The ligament has fibrous portions extending from one valve to the other and is usually extended by a secondary fusion layer though it may be alivincular, multivincular or elongate opisthodetic. There is no mantle fusion ventral to the exhalant area and no mantle septum. The shell has a simple-prismatic, calcitic outer layer, a nacreous aragonitic inner layer and lacks foliated calcitic or crossed-lamellar aragonitic ultrastucture. There is no pallial sinus. The animals are fixed to the substratum by a byssus through a notch in the right valve, mostly into adult life. The gills are filibranch or eulamellibranch. Fossils are known from the Ordovician to Recent.

The classification of the Pteriomorphia was revised by Waller (1978) who discussed the formation of the ligament, and revised views on polarities of ligament form. Waller argued that the form that occurs in the order Pterioida, with fibrous calcification extending across the hinge line, is more advanced than that of, for example, *Pecten*.

Yonge (1968), in discussing the evolution of the 'Pteriacea', postulated that byssal attachment to hard surfaces is primitive and that, secondarily, some forms have become byssally attached in soft substrata. Some pterioids living in soft substrata have lost the byssus and others live without a byssus, burrowed into sponges and algae. Pterioids are almost alone among heteromyarians in making this reversal to infaunal life. There is a tendency to elongation in the Pteriidae (*Electroma*, certain *Pteria*), but it is well developed in the Isognomonidae, Malleidae and Pinnidae, and the adaptations for a secondary infaunal life seem best developed in the last two families. Many subtidal hard substrata are characterised by substantial water currents, but without violent wave action, and by intense competition from modular (colonial) animals for access to the water column. These conditions would tend favour an extension away from the substratum of the pallial chamber and ctenidia. This may have pre-adapted these molluscs for a return to soft sediment, byssally attached with the posterior shell protruding from the sediment. An understanding of the adaptations of Pterioida will be facilitated by further study of the subtidal conditions under which some of them live.

The order comprises two suborders each with one superfamily, the Pteriina with the superfamily Pterioidea, and the Pinnina with the superfamily Pinnoidea. Worldwide there are about 100 species (Boss 1982), most in warm, shallow waters.

Superfamily PTERIOIDEA

Shells of the superfamily Pterioidea are inequivalve and inequilateral, with the right valve usually less convex than the left, markedly sloping in the anterior direction at least in juveniles, and have the umbones situated anteriorly. The ligament is external, located posterior to the umbones, but is otherwise variable. In the extant groups it is alivincular or multivincular. The shell has an outer prismatic (calcitic) layer and middle and inner nacreous (aragonitic) layers; one valve bears one or two denticles that fit into depressions on the other valve; the pallial line is discontinuous anteriorly. There is a byssal notch in the right valve at least in the juvenile stages and pterioideans are characteristically byssate throughout life.

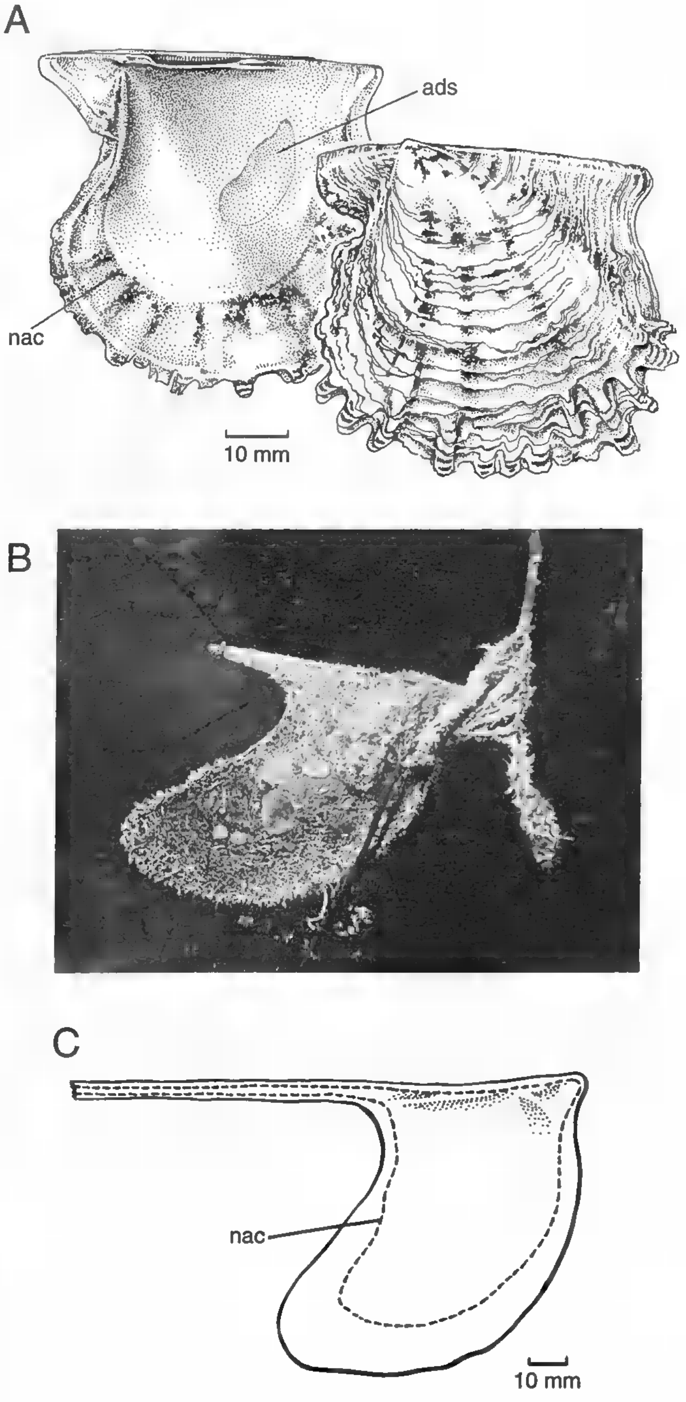

Figure 6.8 Family Pteriidae. **A**, *Pinctada fucata*, shell valves, right valve in internal view, left valve in external view, showing position of adductor muscle scar and outer edge of nacreous layer. **B**, *Pteria penguin*, from Broadhurst Reef, off Townsville in 8 m of water attached to a black coral. **C**, *Pteria penguin*, left shell valve in internal view. **ads**, adductor muscle scar; **nac**, edge of nacreous layer.
[A, R. Plant; B, Australian Istitute of Marine Science; C, R. Evans]

Fossils are known from the Ordovician to the Recent. The superfamily is represented by four extant families, Pteriidae, Malleidae, Isognomonidae and Pulvinitidae; all are represented in the Australian fauna. Newell (1965) introduced the suborder Pteriina containing only the superfamily Pterioida (Pteriacea).

Family Pteriidae

The family Pteriidae includes pearl oysters, wing shells and winged oysters. Their shells are obliquely ovate to almost circular, usually with a triangular wing-like projection bordering each end of the straight hinge line. Because of their economic importance, pearl oysters have been much studied, with emphasis on problems in their culture.

The shells are subequivalve to strongly inequivalve, usually lying on the right valve which is less concave than the left. They are inequilateral, with the umbones placed well towards the anterior end; the anterior auricle is smaller and has a byssal notch beneath it in the right valve. A shallow, obtusely triangular ligament pit is directed posteriorly from the umbo in each valve; dentition is variable, teeth (when present) are usually short and transverse near the umbo and elongate in a longitudinal direction posteriorly. Although dimyarian in juvenile stages, pteriids are monomyarian as adults, having only the large posterior adductor muscle. The pallial line is commonly discontinuous anteriorly. The interior is nacreous and exterior sculpture is variable, relatively smooth forms predominating.

Pteriids approach a (secondary) radial symmetry, with the ctenidium encircling the centrally positioned posterior adductor. The pearl oysters, *Pinctada* species, have thick shells. Other taxa have thin shells and the wing shells, *Electroma* species, are much more delicate. Some pteriids are cryptically coloured and live attached to plants.

The Pteriidae are a predominantly tropical and subtropical, exclusively continental shelf group especially abundant in the Indo-Pacific including Australia. They live in a variety of habitats, sometimes in large gregarious clusters. *Pinctada fucata* (Fig. 6.8A) occurs in fairly muddy environments attached to seagrasses or clumps of dead shells; *Pinctada margaritifera*, the black-lipped pearl shell, is attached to boulders, coral, *etc*; and *Pinctada maxima*, the giant gold-lipped pearl shell, lives on shelly bottoms or attached to rock. Several species of *Electroma* and *Pteria* are noted for their occurrence attached to other sessile organisms (Pls 10.5, 11.1). *Electroma zebra* may be epizoic on hydroids and other colonial animals, *Electroma georgiana* in southern Australia is commonly found on seagrasses and algae, *Pteria penguin* (Fig. 6.8B, C) on a variety of surfaces including hydroids and black corals, and *Pinctada lata* on sea whips and gorgonians. Most occur at depths ranging from low tide to 30–40 m. *Pteria* species rarely attach to scleractinian corals, but most members of this genus more commonly are attached to gorgonians, antipatharians and *Millepora* species. The relationship of certain pteriids with deep-water antipatharians and gorgonians needs further study (Morton 1983c citing R. Roberston). Three pteriid species have been reported by Morton (1983b) as occurring in mangroves in the Caribbean, but none is recorded in this habitat in the Indo-Pacific and Australia.

Many bivalves and indeed some gastropods can produce pearls (see for example, Lauckner 1983), but certain pteriids are outstanding in this respect. *Pinctada maxima* was the basis for the fishery off Broome, Western Australia, for mother-of-pearl from the 1880s to the end of the 1950s (and there is still some demand for mother-of-pearl), and it now produces especially large cultured pearls. Pearls have been cultured in Australian waters since 1949 (Edwards 1983). Growth rates, techniques for culture, disease, genetics, the formation of shell and mother-of-pearl and especially reproduction are well documented. *Pinctada albina*, *P. margaritifera* and *P. fucata* are hermaphrodites with a general tendency to protandry, less marked in *P. fucata* (Tranter 1958a, 1958b, 1958c, 1958d, 1959; Sastry 1979). Tranter (1958c) suggested that sex change is responsive to food reserves in the body. *Pinctada albina* and *P. fucata* reach sexual maturity in the first year. *Pinctada albina* exhibits some gonadal activity throughout the year, but with a maximum in summer. It has a prolonged spawning season with an autumn peak. The heaviest spatfall occurs in winter. As in the other species, there are minor spawnings outside the main spawning period and spawning is often incomplete with phagocytosis of unspent gonadal products. *Pinctada margaritifera* matures in its second year; breeding occurs predominantly in summer and winter, with less activity in between. *Pinctada fucata* shows predominantly summer and autumn spawning, but there are spatfalls throughout the year.

Heavy metal concentrations in *Pinctada margaritifera* in northern Queensland were reported by Klumpp & Burdon-Jones (1982). Diseases and parasites are discussed by Lauckner (1983). Larval cestodes have been described from wild pearl oysters (there is still doubt as to whether they can contribute to the formation of pearls), as well as trematodes (which clearly can be involved in pearl formation) and sporozoans. Various *Pinctada* species are intermediate hosts of *Sulcascaris sulcata* and larvae of other nematodes. The shells are bored by spionid polychaetes, causing pearly excrescences like 'veins' on the inside of the shell, and by clionid sponges. A protistan parasite is believed to be the cause of mass mortalities of *Pinctada maxima* in northern Australia (Wolf & Sprague 1978), as is a similar organism in *P. margaritifera* in the Red Sea (Nasr 1982). *Pinctada maxima* in Japan has been reported to be bored by burrowing bivalves. Pinnotherid crabs, which attach to the gills of many bivalves, have been reported in *P. maxima* from Torres Strait (Dix 1973); they do some damage to gills and palps. Shrimps (Pontoniinae) commonly live in the mantle cavity (Zann 1980; Bruce 1981). Tumours and other abnormalities have been reported.

Pearlfish (*Onuxodon margaritiferae*, Carapidae) shelter inside the mantle cavity of *Pinctada* and *Pteria* by day and feed outside at night (Zann 1980). Pearl oysters, like many other bivalves, are preyed on by pyramidellid gastropods.

The family is known from the Triassic to the Recent. *Pteria* and *Pinctada* are both represented in the Cainozoic of south-eastern Australia, with *Pinctada* from the Late Pleistocene Glanville formation near Adelaide.

Extant pteriid genera are *Pteria* (Triassic to Recent), *Electroma* (Late Cretaceous to Recent) and *Pinctada* (= *Margaritifera*) (Miocene to Recent). Australia has about eight species of *Electroma*, nine of *Pinctada* and 15 of *Pteria* (K. Lamprell personal communication). The Australian pearl oysters, genus *Pinctada*, were revised by Hynd (1955) who described six species and provided a key. There are no comprehensive keys for other Australian pteriids, but Fischer-Piette (1982) gives a comprehensive bibliography and geographic distributions of *Pteria* species, many of which he synonymised such that in Australia only three are valid. There are partial treatments of Australian pteriids in Cotton (1961), Ludbrook (1984) and Macpherson & Gabriel (1962).

Family Malleidae

Members of the family Malleidae (= Vulsellidae) vary in shape, but are usually elongate; extension of the hinge line into 'wings' gives some *Malleus* species the name hammer oysters (Fig. 6.9A). Yonge (1968) has described the form and habit of several malleids including *Malleus malleus* from Australian waters; this is a most useful source of anatomical details. There is little other published work on Australian malleids.

The shells are subequivalve or inequivalve, with or without a byssus and the valve margins commonly gape or are irregularly notched posteriorly. The hinge is simple, with or without teeth, but has a triangular ligamental area which is internal to external, and partly or almost wholly occupied by a median triangular pit which in some genera has a strongly convex, protruding lower margin. The adults are monomyarian.

Malleid shells have no pallial line. The inner surface of the shell has a proximal nacreous area, within which lies the relatively small visceropedal mass, and a distal prismatic area as in the Pinnidae. As in pinnids, the mantle carrying the ctenidia is capable of great extension and withdrawal (by the pallial retractor muscle, with which is associated a ridge in the shell) and is able to make rapid repair if the shell is damaged. In species having them, the 'wings', like the posterior extension, are non-nacreous. There is a wide inhalant region along anterior and distal surfaces. A promyal chamber (Fig. 6.9C) allows water to pass posteriorly between the adductor and the posterior byssal retractor and permits a greater pumping rate and more effective cleaning of the shell. *Isognomon isognomon*, an isognomonid which is similar in many ways, lacks this. In *Vulsella spongiarum* from southern Australia, there is a marked increase in dorso-ventral lengthening and lateral flattening with age (Roberts 1984). Comparison of young with older *Malleus* shows this tendency to an even greater extent (Yonge 1968).

The foot in *Malleus* species is uniquely divided into two portions (Fig. 6.9C; Yonge 1968): the more distal bears the byssal opening, but the proximal and longer one, which Yonge terms the accessory foot, is concerned with cleaning of the lower regions of the inhalant chamber. It appears to be an adaptation to a vertical posture and the danger of sediment and debris accumulating in the restricted antero-dorsal space. The ctenidia are filibranch (Yonge 1968) or pseudolamellibranch (Purchon 1977).

The sponge fingers, *Vulsella* species (for example, Fig. 6.9B), live embedded in sponges, often in considerable numbers (Pl. 10.4). Roberts (1984) found *Vulsella spongiarum* living in a species of *Dysidea* in Princess Royal Harbour, Western Australia, at densities of *ca.* 1800 per 200 g dry weight of sponge, or a biomass *ca.* 1260 g per 200 g dry weight of sponge. The species proved to be dioecious (one hermaphrodite in over 200 specimens) and maintained a relatively high index of gonad activity throughout the 12 month study period.

Apart from brief remarks by Yonge (1968), little has been written about breeding, life cycles or population dynamics in *Malleus* species, but a good deal about form and habit. Some species are known to live attached to reefs and pilings and to be epibiotic on other animals, whilst others are to varying degrees infaunal. *Malleus regula* (Fig. 6.9C) lacks the 'hammer-head'. It is reported to be epibyssate on coral (Morton 1983c) or rocks (Seilacher 1982a) and to attach in intertidal crevices (Purchon 1977). Large and dense beds occur in association with the isognomonid *Isognomon isognomon* (Fig. 6.10A), attached to mud-covered intertidal rock (Yonge 1968). *Malleus malleus* is byssate, but has been reported to occur attached to debris in clean sandy bottoms, whereas *M. albus* (which can be abundant on mud flats or muddy sand flats in northern Australia; Fig. 6.9A) is found unattached in softer mud or muddy sand, anchored when adult only by its long hinge extensions and the crenulations of the shell. Yonge (1968) argued that these three represent a progressive adaptation to soft-bottom dwelling, the more truly infaunal forms having larger wings which act as an anchor. Seilacher (1982a), however, argued that *M. malleus* and *M. albus* are adapted for lying free on the surface of soft sediments and are not truly infaunal, thus the wings

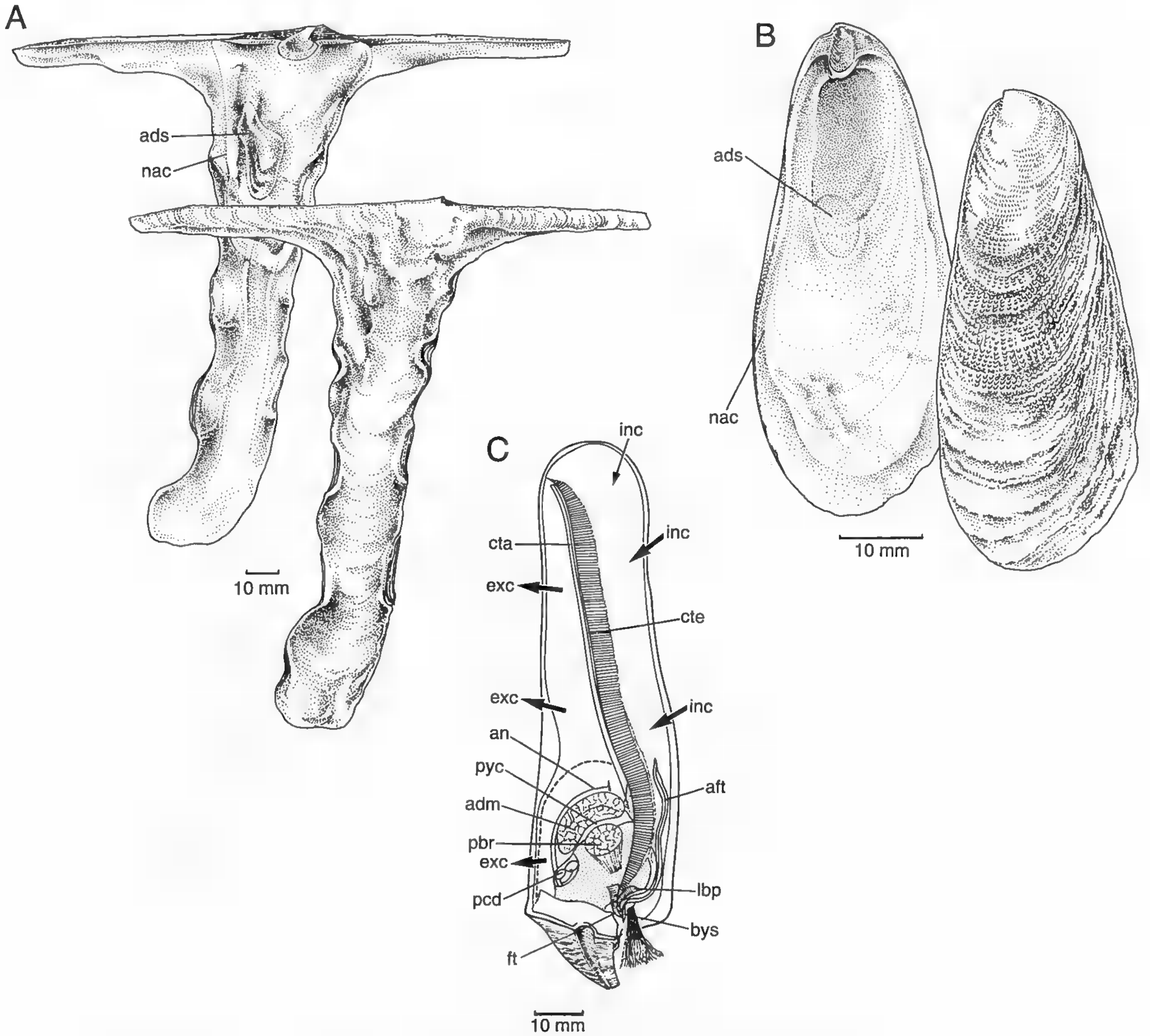

Figure 6.9 Family Malleidae. A, B, shell valves: A, *Malleus albus*, left valve in internal view, right valve in external view; B, *Vulsella spongiarum*, left valve in internal view, right valve in external view. C, *Malleus regula*, internal anatomy, left shell valve and gonad removed. **aft**, accessory foot; **adm**, adductor muscle; **ads**, adductor muscle scar; **an**, anus; **bys**, byssus; **cta**, ctenidial axis; **cte**, ctenidium; **exc**, exhalant current; **ft**, foot; **inc**, inhalant current; **lbp**, labial palp; **nac**, outer edge of nacreous layer; **pbr**, posterior byssal retractor muscle; **pcd**, pericardium; **pyc**, promyal chamber. (C, after Yonge 1968) [A, B, R. Plant; C, R. Evans]

would be of little value. With present knowledge it is probably best to view the wings, together with the ventral extension, as an effective set of adaptations either to epibyssate life in a strong current or to infaunal or semi-infaunal existence. The southern Australian *M. meridianus*, with substantial wings, is well adapted to life on subtidal hard substrata. Although it is reported to occur on soft-bottoms (Shepherd & Sprigg 1976; Ludbrook 1984), it also occurs epizoically on *Pinna* and on colonial animals, and is abundant (densities up to 167 per m^2) on the pilings of certain jetties in South Australia. The great ventral extension of the shell enables passage of currents through the mantle cavity at some distance above the point of attachment, an advantage either in sediment or in competition with colonial suspension-feeding animals. (*Malleus meridianus* is clearly more successful in competitive situations than oysters and mussels, which are characteristic epifaunal bivalves in the intertidal zones of the world). The relationship between form and habit in the Malleidae is an interesting topic for further study.

The family is known from the Jurassic to Recent. *Vulsella* is represented in the Australian Cainozoic by the Late Eocene species *V. laevigata* (Darragh & Kendrick 1980).

There are no comprehensive keys to this family, but some Australian Malleidae are treated by Macpherson & Gabriel (1962), Hertlein & Cox (1969a) and Ludbrook (1984). Comprehensive bibliographies and details of distributions are given by Fischer-Piette (1977, 1978). Extant genera are *Malleus* which is Recent, in the Indo-Pacific including Australia, and in the Mediterranean; and the cosmopolitan, Late Cretaceous to Recent, *Vulsella* (Hertlein & Cox 1969a).

Family Isognomonidae

Isognomonids are distinguished from malleids by the multivincular ligament, which gives them the common name toothed pearl shells, but the elongate forms especially, such as *Isognomon isognomon*, are strikingly similar to malleids. Yonge's 1968 study is the only detailed account available of the biology of Australian species.

The shells are subequivalve to strongly inequivalve, highly to moderately inequilateral, and vary in shape from round to slender-elongate. They are usually compressed, the left valve more strongly convex in inequivalve forms, the commissure plane or undulating. The hinge line is straight, without teeth in the adult, but has short perpendicular ligament pits; the ligamental area is external and usually flat and the ligamental grooves reach and indent its lower margin. The formation of the ligament was discussed by Yonge (1968). Some shells have an anterior byssal gape affecting both valves; there may be a posterior wing, but only rarely is an anterior auricle present. Isognomonids are monomyarian. The pallial line is commonly discontinuous, broken up into small pits. Shell structure is similar to that of pteriids, with a nacreous interior and a drab prismatic outer layer which is smooth, commarginally lamellose or irregularly undulating; radial ornament is absent. Extant isognomonids have much thinner shells than most fossil species.

In *Isognomon (Melina) ephippium*, hinge teeth are present in the earliest growth stages, but soon become obsolete. Beginning with one, the number of ligamental grooves steadily increases during growth.

The rounded, oyster-like *Isognomon ephippium* (Fig. 6.10C) is typically monomyarian in form, the ctenidia encircling the single adductor alongside which is arranged the visceropedal mass. The nacreous layer is relatively large, but there is a broad prismatic layer distal to it. A byssal notch occurs in the right valve upon which the animal lies in a manner similar to pteriids. *Isognomon isognomon* (Fig. 6.10A, B) is elongate, attached in an erect posture and has a very similar mode of life to *Malleus regula* with which it is sympatric. Yonge (1968) compared the anatomy of the two species. Unlike *M. regula*, *I. isognomon* lacks a pallial

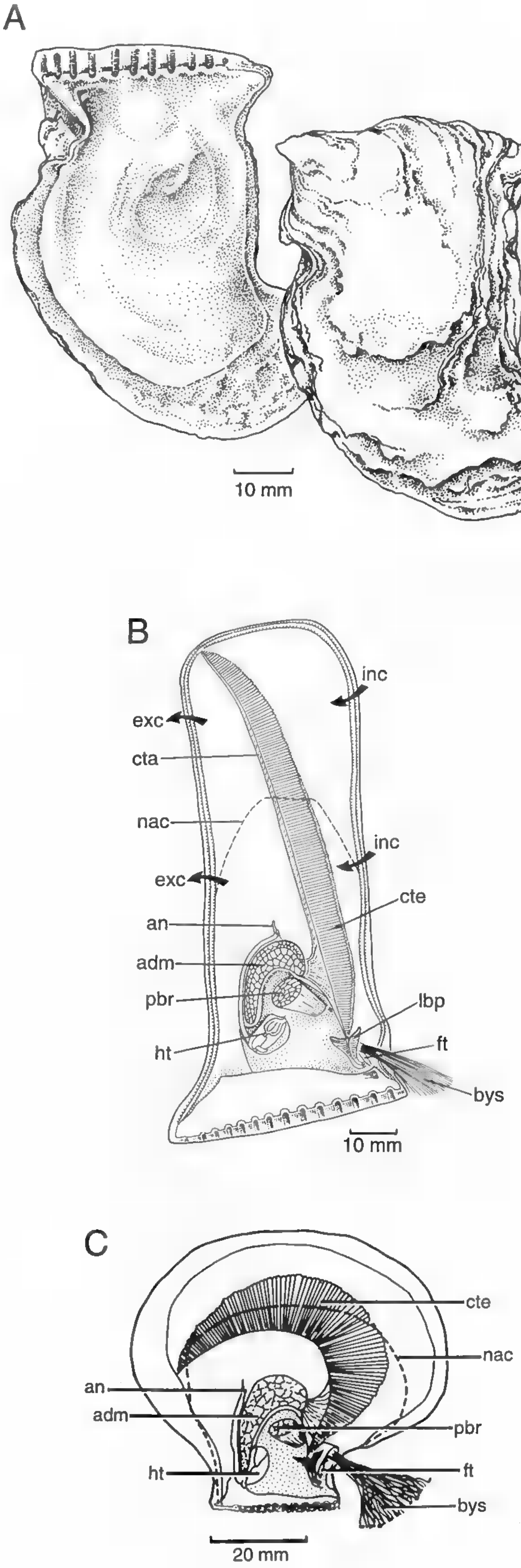

Figure 6.10 Family Isognomonidae. **A**, *Isognomon isognomon*, shell valves of a gnarled or bent specimen, left valve in internal view, right valve in external view. **B**, **C**, internal anatomy, showing the multivincular ('toothed') ligament: **B**, *Isognomon isognomon*, left shell valve and gonad removed; **C**, *Isognomon (Melina) ephippium*, left shell valve removed. **adm**, adductor muscle; **an**, anus; **bys**, byssus; **cta**, ctenidial axis; **cte**, ctenidium; **exc**, exhalant current; **ft**, foot; **ht**, heart; **inc**, inhalant current; **lbp**, labial palp; **nac**, boundary of nacreous layer; **pbr**, posterior byssal retractor muscle. (B, C, after Yonge 1968) [A, B, R. Plant; C, R. Evans]

retractor, a promyal chamber and an accessory appendage to the foot. The foot is primarily concerned with byssal attachment, but large enough to have a possible cleaning function. The arrangement of pedal retractors is similar to that in pinnids and malleids. The ctenidia are non-plicate and more typically filibranch than in *Malleus*.

Isognomonids are generally intertidal although some are subtidal; they often live in sheltered, muddy areas. *Isognomon ephippium* is commonly found attached by the massive byssus to mangrove roots and rocky surfaces in tropical Australia and *I. isognomon* and *Isognomon* cf. *vitrea* are also reported from mangroves (Morton 1983b). Morton (1983c) listed both *I. isognomon* and *I. ephippium* as coral-associates.

Isognomon alatus in the Gulf of Mexico and the Caribbean, is morphologically similar to *I. ephippium*, and may live on hard substrata or in sediments (where it assumes a more elongate growth form). It is tolerant of a range of temperatures, salinities and amounts of suspended matter, and is perhaps stimulated to spawn by a decrease in salinity associated with the onset of the wet season (Siung 1980).

Isognomon ephippium can serve as intermediate host for the nematode *Sulcascaris sulcata* (Lauckner 1983).

The Isognomonidae are known from Late Permian to Recent; they appear to have arisen from the Bakevelliidae in the Triassic, losing the *Pteria*-like form characteristic of typical genera of that family.

Extant genera (all represented in Australia) include *Isognomon* (includes *Melina*; Late Triassic-Recent, cosmopolitan) and *Crenatula* (commensal in sponges, Late Tertiary-Recent, Indo-Pacific-Australia-western South America) (Cox 1969b). Fischer-Piette (1976) gave an extensive bibliography and records of distributions.

Family Pulvinitidae

Pulvinitids have medium-sized shells, which are ovate to almost circular or triangular, compressed and without 'wings'. Externally they are lamellose and oyster-like. The hinge lacks teeth, but there is a wide ligamental area in each valve bearing a series of narrow, elongate ligamental pits perpendicular to the hinge line. The right valve is flat or slightly concave, with a circular foramen for the byssus below the middle of the ligamental area. The left valve is slightly convex, with a circular, radially striated byssal (pedal) retractor scar opposite the foramen of the right valve; in the extant *Foramelina* this is larger than the single adductor scar located in the middle of each valve. The inside of the shell is nacreous. In *Foramelina* a suture leads from the foramen to the anterior extremity of the ligamental platform, suggesting that the foramen was derived from a byssal sinus.

The Australian *Foramelina exempla*, named by Hedley (1914), is the type and sole species of the genus (see Fig. 6.11) . Prior to Hedley's discovery, this family was known only from fossils (Late Jurassic to Recent; Cox 1969c). *Foramelina exempla* was described from Victoria 'South from Gabo Island (100 to 250 fathoms)' (Macpherson & Gabriel 1962) and is known from New South Wales (Fischer-Piette 1976).

Superfamily PINNOIDEA

The suborder Pinnina was proposed by Waller (1978) for this superfamily containing the single Family Pinnidae.

Family Pinnidae

Pinnids are called pen shells, fan shells or wing shells, and in South Australia they are known as razor fish because of the sharp posterior margin.

Pinnids are heteromyarian and non-pleurothetic; the shell has an outer prismatic calcite layer differing slightly in ultrastructural detail from that of the suborder Pteriina (Waller 1978); the ligament is elongate opisthodetic. The family is characterised by a unique, dorsal pallial organ, and by the triangular shell shape associated with partial to almost complete burial in the substratum (Pl. 11.2).

Figure 6.11 Family Pulvinitidae. *Foramelina exempla*, right valve in external and internal view (in part), showing hinge and foramen. (After Macpherson & Gabriel 1962 and Cox 1969c) [R. Evans]

The family in the Indo-Pacific was reviewed (and a key given) by Rosewater, in 1961, who recognised three Recent genera, *Pinna*, *Streptopinna* and *Atrina*, with seven Recent species in Australia. Subsequently, Scheltema (1983) recognised an eighth species. The unique adaptations of the Pinnidae have attracted attention elsewhere, but in Australia only taxonomic work was available until more recent research on other aspects of their biology (Butler & Brewster 1979; Butler & Keough 1981; Scheltema 1983; Roberts 1984; Butler 1987).

Pinnids are mostly equivalve. The umbones are at or near the anterior end of a long hinge margin; there is a long narrow gape ventrally near the anterior end for the byssus. The anterior adductor is relatively small and is situated in the anterior angle of the shell, the posterior adductor is large and situated at or slightly anterior to the mid-length. The middle and inner nacreous layers reach as far as the posterior adductor muscle (Fig. 6.12C, D). The shell valves lack hinge teeth and are united along the dorsal length by a ligament, the anterior part of which is a dark, non-elastic primary ligament; the posterior (or secondary ligament) is a fusion of the outer prismatic shell layer. The shell gapes posteriorly and postero-ventrally, but the posterior adductor muscle can effect complete closure. Shell structure has been well studied (Yonge 1953; Cuif, Dauphin, Denis, Gaspard & Keller 1983). In some taxa, the posterior part is very flexible but in others (for example, *Atrina vexillum*) the shells are massive; Seilacher (1982b) discussed some details of the flexion of the shell in *Pinna bicolor*. Externally, the shell may be smooth or lamellose (Fig. 6.12D), but in some species (for example, *Atrina tasmanica*; Fig. 6.12C) it is covered by sub-tubular spines. In certain species these spines vary between individuals and are more prominent in young individuals.

Most species have large shells. The Mediterranean *Pinna nobilis* reaches a shell length of 800 mm, and in Australia, large *P. bicolor* shells are 350–400 mm long and *Atrina vexillum*, 250–300 mm.

The normal habit is deeply rooted with the pointed, anterior end downwards in sand or mud, attached by a byssus to stones and shell fragments, with the posterior gape at or above the surface of the sediment (Fig. 6.12A, B). Pinnids sometimes live embedded amongst massive epifauna, for example *Atrina vexillum*, on coral reefs.

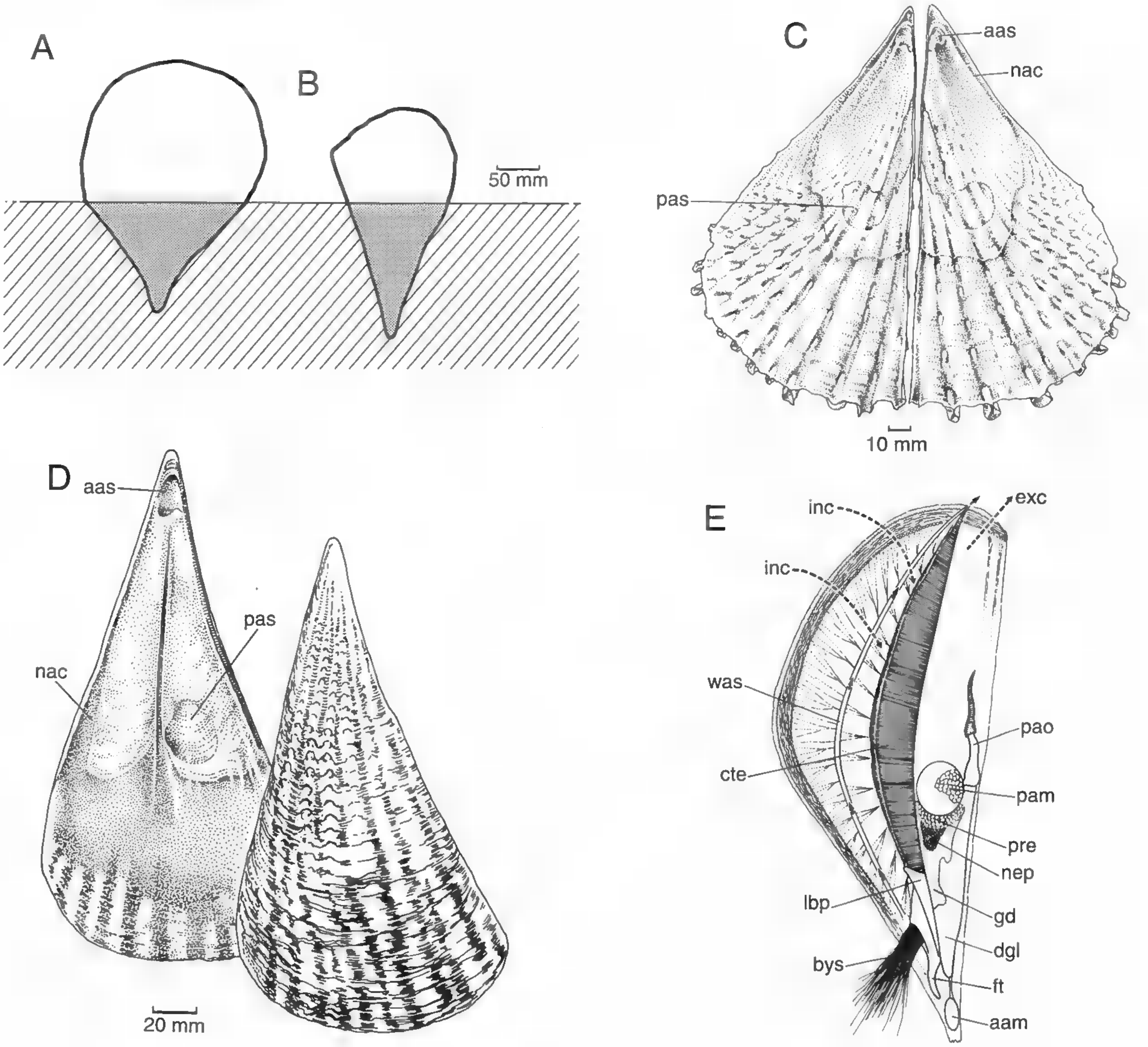

Figure 6.12 Family Pinnidae. **A**, **B**, pinnids in normal position in sediment: **A**, *Atrina vexillum*; **B**, *Pinna bicolor*. **C**, **D**, shell valves: **C**, *Atrina tasmanica*, right and left valves, in internal view; **D**, *Pinna bicolor*, right valve in internal view, left valve in external view; *Pinna* and *Atrina* are distinguished by the nacreous area which has two lobes with a median suture in *Pinna*, but a single lobe in *Atrina*. **E**, *Pinna bicolor*, internal anatomy, right shell valve removed. **aam**, anterior adductor muscle; **aas**, anterior adductor muscle scar; **bys**, byssus; **cte**, ctenidium; **dgl**, digestive gland; **exc**, exhalant current; **ft**, foot; **gd**, gonad; **inc**, inhalant current; **lbp**, labial palp; **nac**, boundary of nacreous layer; **nep**, 'nephridium'; **pam**, posterior adductor muscle; **pas**, posterior adductor muscle scar; **pao**, pallial organ; **pre**, posterior retractor muscle; **was**, waste canals. [A, B, E, R. Evans; C, D, R. Plant]

The foot is small, but a powerful posterior byssal retractor muscle, and a reported ability to 'jet' water from the anterior end of the shell, allow the animal to burrow into the sediment as it grows and give it some ability to re-adjust its position.

Branched, paired pallial retractor muscles enable the mantle and ctenidia to be withdrawn to the level of the posterior adductor muscle when the animal is disturbed. Almost half the shell of *P. bicolor* can be broken off and will regenerate rapidly. The whole mantle behind the posterior adductor is free of the shell; there is no pallial line. Living in soft-bottoms, lacking siphons and gaping upwards, pinnids are vulnerable to accumulation of sediment and debris in both chambers of the mantle cavity. Most bivalves lack a significant cleaning system in the exhalant chamber, but pinnids have a unique, dorsal pallial organ (Yonge 1953) which serves to eject broken shell fragments or other material from the exhalant chamber (Fig. 6.12E). It is made turgid by blood pressure and moved by intrinsic muscles. The ventral, inhalant chamber is cleaned by a pair of ciliated, gutter-like waste canals; ventral, ciliated rejection tracts are present in other bivalves, but their degree of development is unique to this family. These can carry not only pseudofaeces, but also remarkably large particles of sand or shell to the posterior margin where they are carried away by the exhalant current or ejected by abrupt closure of the shell.

Rosewater (1961) discussed the 'organs of Will' – eye-like or glandular spots in the mantle margin, of unconfirmed function. Gill structure appears to be close to the eulamellibranch condition, but the details are still unclear (Yonge 1953; Purchon 1977; Owen 1978).

A 'nephridium' lies adjacent to the anterior side of the posterior adductor muscle (Fig. 6.12E), and stores dark granular concretions which have been studied in *Pinna nobilis* (Lucas & Hignette 1983). The nature of a pre-oral, unpaired pallial gland is discussed by Yonge (1953); the function of the gland is unclear, but may be excretory.

Pinnids occur intertidally and subtidally down to considerable depths. Intertidal *Pinna bicolor* remain closed while the tide is out. Subtidal animals appear to be continuously open and pumping, day and night, unless disturbed.

Reproductive cycles have been described only for *Pinna bicolor* which is dioecious (Roberts 1984; Butler 1987). In South Australia, gonads ripen in early summer. In Western Australia, ripe gonads were found over a longer period – summer to late autumn. The planktotrophic veliger larvae can be identified at least to the family (Ota 1961; Rosewater 1961; Booth 1979; Scheltema & Williams 1983).

Butler & Keough (1981) and Butler (1987) found that recruitment of *Pinna bicolor* varied spatially even over small distances, and between years at one place. The juveniles of *P. bicolor* grow rapidly, reaching sexual maturity within a year or two, but thereafter suffer low natural mortality and may live for well over 10 years. The variation in recruitment of young to the population appears to be buffered by the longevity of the adults.

Predators include starfish and boring gastropods; their importance decreases as the shell grows. Larval cestodes, trematodes, nematodes and ciliates have been reported from pinnids (Lauckner 1983). Shells often are bored extensively by sponges and polychaetes. Since Aristotle's time, pinnotherid crabs (pea crabs) have been known to live in pinnids (Rosewater 1961). Various commensal pontoniine shrimps are widely reported in the Indo-Pacific and in tropical Australian waters (Zann 1980). Page (1983) reported a pinnotherid from *Atrina zelandica* in New Zealand, but no commensals have been found in *Pinna* in South Australia although pea crabs are common in scallops which co-occur with *Pinna bicolor*.

The community of organisms living attached to the shells of *Pinna bicolor* has been studied as a 'model' system for testing ecological theory (Kay & Keough 1981; Keough & Butler 1983; Keough 1984a, 1984b) and as a tool in pollution monitoring (Ward & Young 1983).

Pinnids are collected in many countries for food. In Polynesia at least, the large shell of *Atrina vexillum* has a variety of uses. The byssal threads of the Mediterranean *Pinna nobilis* have long been prized for clothing and the shells as curios. In Australia, there is limited collection of pinnids for bait and food. There are proposals for commercial exploitation, but species with long life and variable recruitment may not sustain intensive fishing, as illustrated by *Pinna nobilis* which is now threatened over most of its range (Butler, Vicente & de Gaulejac 1994).

Rosewater (1961) discussed the biogeography of the Pinnidae in detail. The family is tropical and subtropical. In Australia, only *Atrina (Servatrina) tasmanica* (Fig. 6.12C) is confined to temperate waters (South Australia, Victoria, Tasmania and New South Wales). Other Australian species have wide distributions in the Indo-West Pacific, for example, *P. bicolor* extends in Australia from the tropics to the gulfs and embayments of South Australia and Western Australia. The wide distributions of many species are to be expected, as pinnid larvae can be dispersed across oceans even though the postlarval, benthic stages are found only on the continental shelves (Scheltema & Williams 1983).

Pinnid shells do not fossilise well. External shell characters vary greatly in this family and are insufficient on their own for the recognition of species. This makes the taxonomy of fossils difficult. Nevertheless, the patchy record extends far back to the Palaeozoic and pinnids have changed little since then; of the extant genera, *Pinna* appeared during the Late Carboniferous, *Atrina* in the Middle Jurassic and *Streptopinna* probably during the Late Tertiary (Cox & Hertlein 1969a). Rosewater (1961) gave details of the fossil record of the extant species.

Order LIMOIDA

Limoids are monomyarian, non-pleurothetic Pteriomophia, with an outer layer of calcitic fibrous-homogeneous ultrastructure and an inner layer of simple crossed-lamellar aragonite. The ligament is alivincular with the fibrous resilium almost or entirely uninterrupted by medial lamellar material.

Waller (1978) proposed ordinal status for the group and discussed (*inter alia*) the evolution of the ligament in the Pteriomorphia. Limoids are recorded from the Carboniferous, and perhaps as far back as the Ordovician (Waller 1978), to Recent.

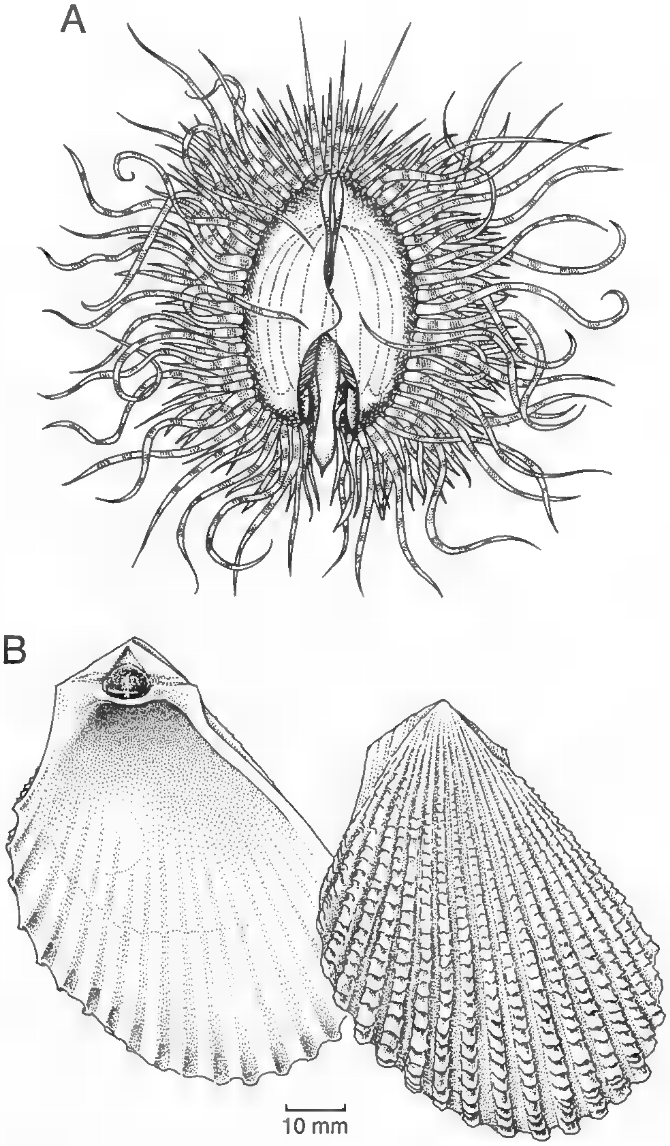

Figure 6.13 Family Limidae. **A**, *Limaria fragilis* in life. **B**, *Lima lima*, shell valves, left valve in internal view, right valve in external view. (A, after Morton 1983c) [A, R. Evans; B, R. Plant]

Superfamily LIMOIDEA

The diagnostic characters are those of the order. The superfamily comprises the single family, Limidae.

Family Limidae

Limids are commonly called file shells. The shells are equivalve, ovate, orbicular or subtrigonal, and are most commonly higher than long, many forms being somewhat extended obliquely in an antero-ventral direction. They are familiar shells throughout Australia and well studied as fossils, but there has been limited work on extant limids here.

The hinge has two unequal or reduced auricles and a triangular cardinal area with a shallow triangular ligament pit in both valves; it is edentulous or has weak teeth of taxodont type. The umbones are well separated. Limids are monomyarian, with only obscure adductor scars in most forms. The shell has an outer calcitic layer and middle and inner layers of non-nacreous aragonite; it gapes widely or narrowly at the margin which is smooth or crenulate. The surface is smooth or with radial ornament; commarginal ornament is very rare (Fig. 6.13B).

The species that swim (for example, *Limaria fragilis*) are lightly constructed, have long sticky tentacles projecting from the edge of the mantle (Fig. 6.13A) and swim by rapidly opening and closing the valves rather like scallops. Unlike scallops, however, they swim with the sagittal plane vertical rather than horizontal, and swimming is aided by a rowing action of the tentacles. Baldwin & Opie (1978), Baldwin & Lee (1979) and Baldwin & Morris (1983) have shown that in the slow, sustained swimming of *Limaria fragilis*, aerobic metabolism is much more important than in the fast but briefer bursts of swimming characteristic of, for example, scallops or the Mediterranean *Lima hians* (Gade 1981).

Baldwin & Opie (1978) described briefly the structure of the adductor muscle in *Limaria fragilis*; there is no indication of a catch muscle. The gill of *Lima hians* is eulamellibranch (Owen 1978). Purchon (1977) discussed various details of feeding and digestion in limids, though not specifically in Australian taxa. Although it is generally considered that bivalve digestion is confined to the stomach and digestive diverticula, there is evidence of digestion in the midgut of *Lima* as well as in *Mya* of the Myidae. The stomach of *Limaria fragilis* was described by Purchon (1957).

Limids are widespread in tropical and temperate waters. They typically live on reefs (Pls 11.3, 11.4) where they are attached by a byssus to the substratum or are free-swimming and hide under rocks or coral (Morton 1983c). Some species spin a nest containing a latticework of byssal threads or mucus and shell fragments. An Australian species, *Lima lima*, lives in aggregations in association with sponges, either in cavities in large sponges or on sponge-covered rocks or overhangs of dead coral, from low tide level to 30 m, on medium-to-high energy coasts. Another, *Limaria orientalis*, lives in large aggregations in nests made of mucus in fine silty sand and mud, from 5–20 m deep on low-to-medium energy coasts (Ludbrook 1984). *Limatula strangei* and *Limaria fragilis* (Fig. 6.13A) live under rocks and coral and are free-swimming.

Although limids are predominantly shelf bivalves, some occur in deep water on the continental slopes (Allen 1983).

Lauckner (1983) records the presence of allocoel turbellarians in the mantle cavity and on the gills of *Limaria orientalis*, which also harbours a stage of a digenetic trematode. Burrowing ectoprocts have been reported from limids.

The family is known from the Late Carboniferous to the Recent. Some species of *Limatula*, despite their conservative morphology and Mesozoic (Triassic) origins, apparently have been widely distributed throughout the world and speciated or subspeciated quite late in geological time (Fleming 1978). Fleming (1978) suggested that the ecology of certain Australian species would repay study. Buonaiuto (1977a, 1977b) has revised the Australian Tertiary species of *Limatula* and the Tertiary composite species, *Lima bassi.*

Extant genera, according to Cox & Hertlein (1969b), are: *Lima* (Jurassic-Recent, cosmopolitan; includes *Austrolima*), *Acesta* (Late Jurassic-Recent, cosmopolitan; now in cold waters or at bathyal depth), *Ctenoides* (Late Jurassic-Recent, cosmopolitan), *Divarilima* (Pliocene-Recent, Eastern Australia- New Zealand- Kermadec Island), *Limaria* (Eocene-Recent, cosmopolitan; includes *Submantellum*, *Promantellum*), *Limatula* (Triassic-Recent, cosmopolitan; includes *Stabilima* as a subgenus) and *Limea* (Middle Triassic-Recent, cosmopolitan; includes as subgenera *Escalima*, *Gemellima*, *Isolimea* and *Notolimea*).

Order OSTREOIDA

The shapes of ostreoid shells vary greatly between and, in many cases, within species. The symmetry of the shell, which reflects that of the internal organs, is primarily affected by the pleurothetic habit adopted by many species, most forms being attached to the substratum for at least part of their lives by a byssus or by cementation (Yonge 1979). The ostreoid shell typically consists of non-nacreous foliated calcite, though some forms have an external layer of simple prismatic calcite on one or both valves.

Ostreoids are anisomyarian or monomyarian, with the anterior adductor muscle reduced or absent and the posterior adductor muscle lying proximal to the simple, non-sinuate pallial line. The monomyarian forms may have evolved independently from dimyarian ancestors in the Ostreoidea, Plicatuloidea and in the stock ancestral to the Pectinoidea and Anomioidea (Waller 1978). The ligament of ostreoids is either alivincular, consisting of a single structure with lamellar layers both anterior and posterior to the fibrous resilial layer, or multivincular with repeated similar segments.

The marginal folds of the mantle are generally furnished with tentacles and the mantle lobes may be fused postero-ventrally, demarcating a postero-dorsal exhalant aperture. There is no ventral fusion, but the mantle folds may be apposed to form a temporary inhalant aperture.

The order Ostreoida appears to have originated in the Early Palaeozoic, undergoing further differentiation during the mid-Palaeozoic separating the suborders Ostreina and Pectinina. Members of the superfamily Halobioidea, cosmopolitan in the Middle Triassic, have features common to the ancestral stock of these suborders (Campbell 1994).

Suborder OSTREINA

The shell shape of members of the suborder Ostreina is variable between and within species. The animals rest on either the left or right valve according to their taxonomic group and typically, at the end of their larval phase, cement to the substratum by the action of the shell glands in the mantle folds edging the 'lower' mantle lobe. The extent of the area of shell attachment in the mature animal may vary with the species and also with the topography of the substratum and the extent of the available substratum area. Some forms may fall from their attachment as they become heavier; they cannot then re-attach.

The adult animals of this suborder lack a byssal notch. In many species the outer layer of both shell valves consists of simple prismatic calcite. In some species there is also a non-nacreous, crossed-lamellar layer of aragonite. The ligament is either alivincular or irregularly multivincular.

The mantle is typically edged with three folds. The edges of one or both of the inner folds bear series of extensible tentacles but not photoreceptors. The innermost fold forms a mantle-curtain of greater or lesser width. The gills are either eleutherorhabdic or synaptorhabdic. The foot is reduced at all stages and is absent after metamorphosis, as is the byssal gland.

Members of the suborder Ostreina are recorded from the Late Triassic to the Recent. By the Early Mesozoic they had adopted a pleurothetic habit and early obligate cementation, the foot had atrophied and they had differentiated into groups which gave rise to the superfamilies Ostreoidea, Dimyoidea and Plicatuloidea (Waller 1978).

Superfamily OSTREOIDEA

Within and between the taxa of the superfamily Ostreoidea shell shape is extremely to moderately variable. Most groups have an inequivalve shell and are cemented to the substratum by shell material secreted by the mantle margins of the left valve. However, some groups have shells which, after a period of cementation, become detached and lie free. There is no byssus or byssal notch in the shells of any of these groups. Ostreoidean shells are calcitic, with the right valve consisting of simple prismatic and foliated layers and the left valve having thick outer foliated layers. Such weak, foliated shells are found only in these and a few other groups of epifaunal bivalves. Pockets of crumbly chalky calcite, formed between the denser shell layers of some ostreoideans, may be effective in absorbing energy when the animal is attacked by predators (Currey & Taylor 1974). The myostraca of the adductor and other muscles that attach to the shell consist of prismatic aragonite.

Ostreoideans are monomyarian. The pallial line is obscure and not impressed. Both anterior pallial muscles and anterior gill elevator or Quenstedt muscles are present. In the adult the dorsal hinge of the shell is edentulous. There is no lamellar section interrupting the

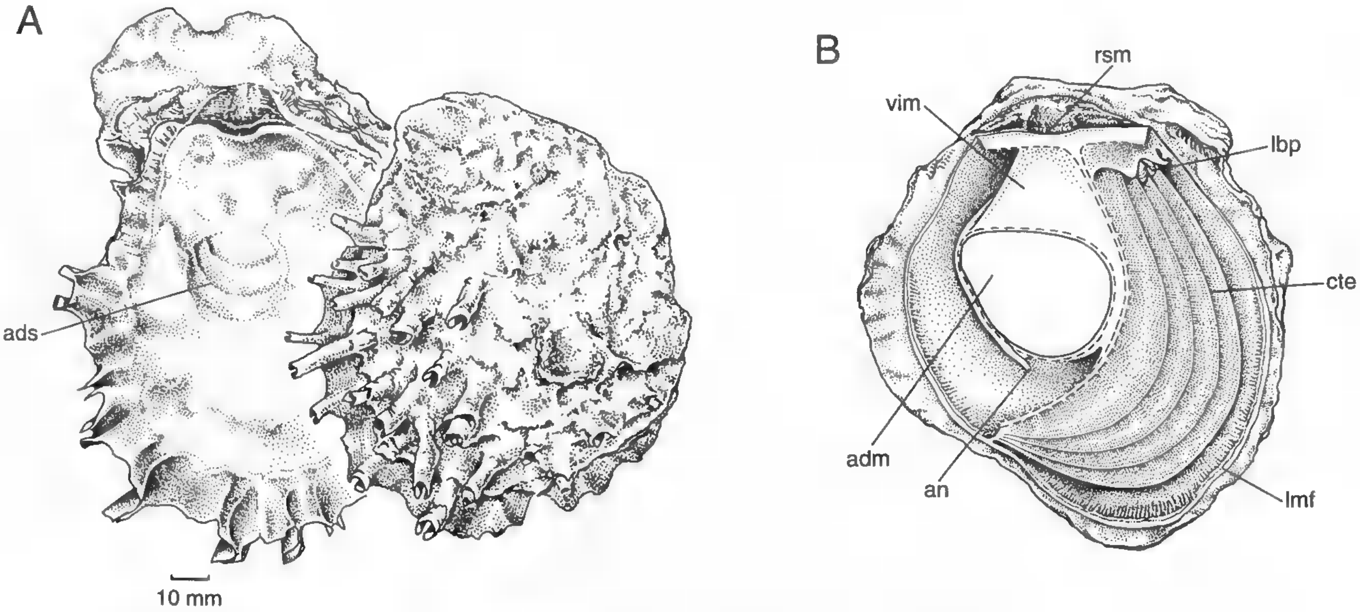

Figure 6.14 Family Gryphaeidae, subfamily Pycnodonteinae. *Hyotissa hyotis*: A, shell valves, left valve in internal view, right valve in external view; **B**, organs of the mantle cavity, right shell valve and mantle lobe removed. **adm**, adductor muscle; **ads**, adductor muscle scar; **an**, anus; **cte**, ctenidium; **lbp**, labial palps; **lmf**, left mantle folds; **rsm**, resilium; **vim**, visceral mass to left of promyal passage. [R. Plant]

fibrous resilium between the shell valves. Lamellar tensilia extend both anteriorly and posteriorly to the resilium, which is attached within a central socket on the hinge line of each valve.

The innermost folds of the mantle are fused to one another and to the posterior tips of the gills postero-ventrally. The gills are eulamellibranchiate, with those of most groups being heterorhabdic and synaptorhabdic. Usually the tips of the ascending filaments of the external demibranchs are fused with the mantle, and those of the inner demibranchs are fused with the visceral mass and, more posteriorly, with one another. The gills thus separate the incurrent infrabranchial from the excurrent suprabranchial chamber. The labial palps are simple in form. Both the foot and byssus are absent after metamorphosis.

The heart consists of two auricles which, to different extents in different forms, are joined medially to one another and dorsally to the ventral wall of the ventricle. Most members of this superfamily are alternating protandric hermaphrodites.

Ostreoideans occur in both marine and estuarine habitats and most are inhabitants of shallow waters. Many forms aggregate to form intertidal or subtidal reefs. The most recent revision of the Australian oysters was published by Thomson in 1954.

Arising in the Late Triassic and persisting to the present (Stenzel 1971), this superfamily seems to have been derived from a dimyarian and possibly non-pleurothetic ancestor (Waller 1978). The family Chondrodontidae arose during the Early Cretaceous, to become extinct during the Late Cretaceous. The Lithiotidae, tentatively regarded as ostreoidean, lived only during the Early Jurassic period. All extant oysters belong to the families Ostreidae and Gryphaeidae.

Family Gryphaeidae

The shell valves of gryphaeid oysters range from being very unequal to subequal. The left valve may bear a deep posterior radial groove or this may be absent, reduced to a flexure or obscured. The substratum-attachment area varies from very small to large. Because of increasing weight and/or because of the weakening of the shell by burrowing organisms, large heavy specimens may eventually fall from the hard substratum to lie free. The left umbonal recess is generally shallow except in the extinct Exogyrinae and may be filled with solid shelly material. The commissural shelf is wide and well defined. In general the chomata, located on both valves anterior and posterior to the ligament, vary from short to long and are vermiculate or anastomosing. The prismatic shell layer in these oysters is thin in most forms and absent in a few. Patches or even layers of softer material are present between denser, more vitreous layers. This soft shell material may be chalky as in the genus *Neopycnodonte* or, more typically, cellular as in species of the genus *Hyotissa*.

The prodissoconch hinge consists of an uninterrupted alternating series of equal-sized tooth precursors with corresponding sockets on the opposite valve (Ranson 1960). The ligamental area of the left valve is not high except in the extinct Exogyrinae.

The adductor muscle is orbicular in cross section, and is located closer to the hinge than to the ventral shell margin. The ventral edge of the left valve and that of the right valve which fits into it are raised above the general surface of the substratum and the interior 'floor' of the valve.

The history of the Gryphaeidae extends from the Late Triassic to the Recent (Stenzel 1971). The only extant subfamily is the Pycnodonteinae. The subfamilies Gryphaeinae and Exogyrinae are extinct, the former having survived from the Late Triassic to the Late Jurassic and the latter from the Middle Jurassic to the Miocene. Skwarko (1974) recorded representatives of both of these subfamilies from the Middle Jurassic of Western Australia.

Subfamily Pycnodonteinae

The shell, in general, has a circular outline and, in size, varies from being small with very unequal valves (*Neopycnodonte* spp.) to large with subequal valves (some species of *Hyotissa*). Many forms have radially undulate or ribbed shells. The ribs are very strong and acute in most specimens of *H. hyotis*, bearing strong scales, which in the juvenile stage may be folded into hollow spines. The left umbonal cavity is deep in the forms that have a very concave left and an opercular right valve (for example, *N. cochlear*) but may be shallow and filled with solid shell material in more equivalved shells such as those of *H. hyotis*.

The shell structure varies from thin, fragile and semi-translucent layers alternating with thick, chalky, cellular layers in *Neopycnodonte* species, to solid, opaque and dense layers alternating with coarsely cellular layers in species of *Hyotissa* (Fig. 6.14A). Fluid-filled cavities may be formed between the shell layers. The chomata, if present, may be short or long and are confined to patches anterior and posterior to the ligament on both valves. One of these patches may be absent or obscure. The ventral edge of the circular adductor muscle scar is raised from the general internal surface of the valve, whereas the dorsal edge is generally indented into it.

Apart from the posterior exhalant channel, gryphaeid oysters have additional exhalant passages anterior to the adductor muscle. These are termed promyal passages and may be extensive, extending dorsally almost to the pallial isthmus along the hinge line. In some forms, such as *Hyotissa hyotis* the epithelium covering the interior of the mantle lobes and that covering the viscera is darkly pigmented, even dense black (Fig. 6.14B). The gills of most forms are moderately to darkly pigmented.

The outer labial palps are fused medially to form a hood over the mouth. The intestine is arranged in a Z-shape and does not form a loop around the stomach. The rectum passes through the pericardium and, generally, through the ventricle of the heart. Its distal section is free of attachment to the adductor muscle. The gonad is orange to cream, and fertilisation is external.

Gryphaeid oysters are euryhaline and stenohaline. They are generally not aggregative and reef forming, though dense populations of *Hyotissa* species may occur on subtidal surfaces or under intertidal rocks and dead coral slabs of coral and rock reefs in tropical and sub-tropical waters.

A few widespread Indo-West Pacific species of the genus *Hyotissa* , including *H. hyotis* (Pl. 12.2) and *H. numisma*, are present in Australian tropical and subtropical waters. One species of the genus *Neopycnodonte*, known from Queensland and northern Western Australian waters, is much more rare.

Apparently having arisen in the Early Cretaceous, this is the only gryphaeid subfamily that has persisted to the Recent (Stenzel 1971). The oldest Australian records of the subfamily may be those based on the Late Cretaceous specimens of *Pycnodonte*, from Western Australia (Etheridge 1913; Feldtmann 1963; Darragh & Kendrick 1991).

Family Ostreidae

Ostreid shells exhibit a moderate range in shape and size, both of which are typically variable within species. The shells are rounded to narrowly and elongately ovate in outline and are usually flattened and inequilateral. They are usually not equivalve, having a more concave left valve and a more flattened right valve. In most forms the extent of the attachment area greatly influences the shape of the shell. Ostreids have a small to large area over which the left valve is cemented to the substratum by shell material. In the genus *Ostrea*, the secretion of the cement by the mantle folds has been shown to be preceded by the production of non-calcareous cements produced firstly by the foot of the pediveliger and then by the mantle edge of the dissoconch stage (Harper 1991).

Ostreid shells do not have a posterior radial groove and the shell margins are variably plicate (Fig. 6.15A–F). The umbones are generally inconspicuous and eroded, with the left umbonal cavity more or less well developed. Chomata are present on the commissural shelves around the anterior, ventral and posterior edges of most forms. Hollow chambers and chalky layers are present in the shells of many forms but cellular shell structure is completely absent in this group. The pallial line may be absent or poorly marked. The adductor muscle is kidney-shaped, oval or crescentic in cross-section and is located in the posterior area of the body (Fig. 6.15F). The ostreid hinge is edentate in the post-metamorphic stage but the prodissoconch has four nearly equal teeth precursors and sockets separated by a median gap (Ranson 1960). The ligament is either alivincular or irregularly multivincular, with a resilial socket which is generally trigonal.

The gills are plicate, heterorhabdic and synaptorhabdic, with some degree of inter-lamellar fusion and development of inter-filamental junctions. The major typhlosole of the stomach has a long extension into the food-sorting caecum (*i.e.* stomach of Type III according to Purchon 1958). The style-sac is fused with the midgut and the intestine is strongly recurved. The rectum is dorsal and the rim of the anus may be simple or may bear a papilla or an extensible flap. Pericardial glands are located in the walls of the auricles and the pericardium. The ventricle is more-or-less medially divided by an internal septum and neither it nor the pericardial cavity is traversed by the rectum.

The kidneys are situated laterally but are joined together posteriorly. Each joins to the gonads anteriorly. Each reno-pericardial apex is long and is located on the inner side of the outer nephridial lobe. Ostreids are gonochoristic and some, at least, first become mature as males. Some groups have been shown to undergo sex reversal annually or more often. Incubation of eggs and/or larvae occurs only in some groups. Only the non-incubatory groups have a promyal exhalant passage on the right side of the body dorsal to the adductor muscle.

This family, which arose during the Late Triassic and persists up to the present (Stenzel 1971), consists of the subfamilies Ostreinae, Lophinae and Crassostreinae (Torigoe 1981).

Subfamily Ostreinae

The shells of this subfamily are generally circular to triangular in outline and are small to medium in size. The southern Australian flat oyster, *Ostrea angasi* (Fig. 6.15A), reaches about 180 mm in greatest diameter. The margins of the subequal valves are generally undulating, the radial ribbing is generally subdued and the upper right valve is more or less convex. The shells are attached to a hard substratum when young, though sometimes only to very small pieces of shell, or other such objects, which may disintegrate later. Oysters attached to rock boulders and other more substantial substrata may also fall when they become large and heavy.

External growth scales, particularly those of the right valve, are often very wide and close, although in some habitats these might be eroded. Internally, the left valve is usually only shallowly indented under the hinge line. The chomata are in a single row, with simple pustules on the right valve generally inserting into corresponding sockets on the opposite valve. They are generally present at least on the antero-dorsal section, less often on the postero-dorsal section but sometimes may be present around the whole extent of the shell margin. Older shells may sometimes lack chomata. Ostreine shells are generally thick and friable and are lamellose, with inter-lamellar cavities commonly being formed, particularly in the left valve. Such cavities are filled with fluid or with chalky deposits.

The adductor muscle is located in an approximately central position (Fig. 6.15A). No ostreine species has a promyal passage dorsal to the adductor muscle and so there is only one route available for the outflow of the exhalant current. The outer labial palps are fused medially for a short distance and thus form a hood which overlaps the thick edge of the lower lip and the inner or lower palps. Although water can escape along their length, suitable particulate matter selected by the extensively ridged and ciliated areas of the opposed surfaces of the labial palps is passed into the mouth (Gilmour 1974). The pseudofaeces of unwanted particles bound by mucus are discarded from the tips of the palps and are disposed of antero-ventrally.

The intestine forms a wide loop on the left side of the stomach, as in the Crassostreinae (Torigoe 1981). The anal end of the rectum is free of the adductor muscle for a short distance and the anal rim may be plain or bear a short, simple, median papilla posteriorly.

During spawning, sperm are voided from the males, together with the exhalant water current. Ova are passed through the ostia of the female's gills into the infrabranchial chamber. Here the ova are fertilised by sperm entering with the inhalant water flow. The eggs remain in the inhalant chamber until incubation has progressed to the prodissoconch stage, when the larvae are expelled.

Most ostreine species inhabit temperate and relatively clear waters of approximately oceanic salinities. They are generally subtidal, the southern Australian *Ostrea angasi* occurring in depths of up to about 200 m. They lie free on soft substrata or are cemented to dead and living shells and their fragments, to rocks or to dead coral. The Indo-West Pacific species, *O. tuberculata*, attaches underneath or within crevices of living coral colonies.

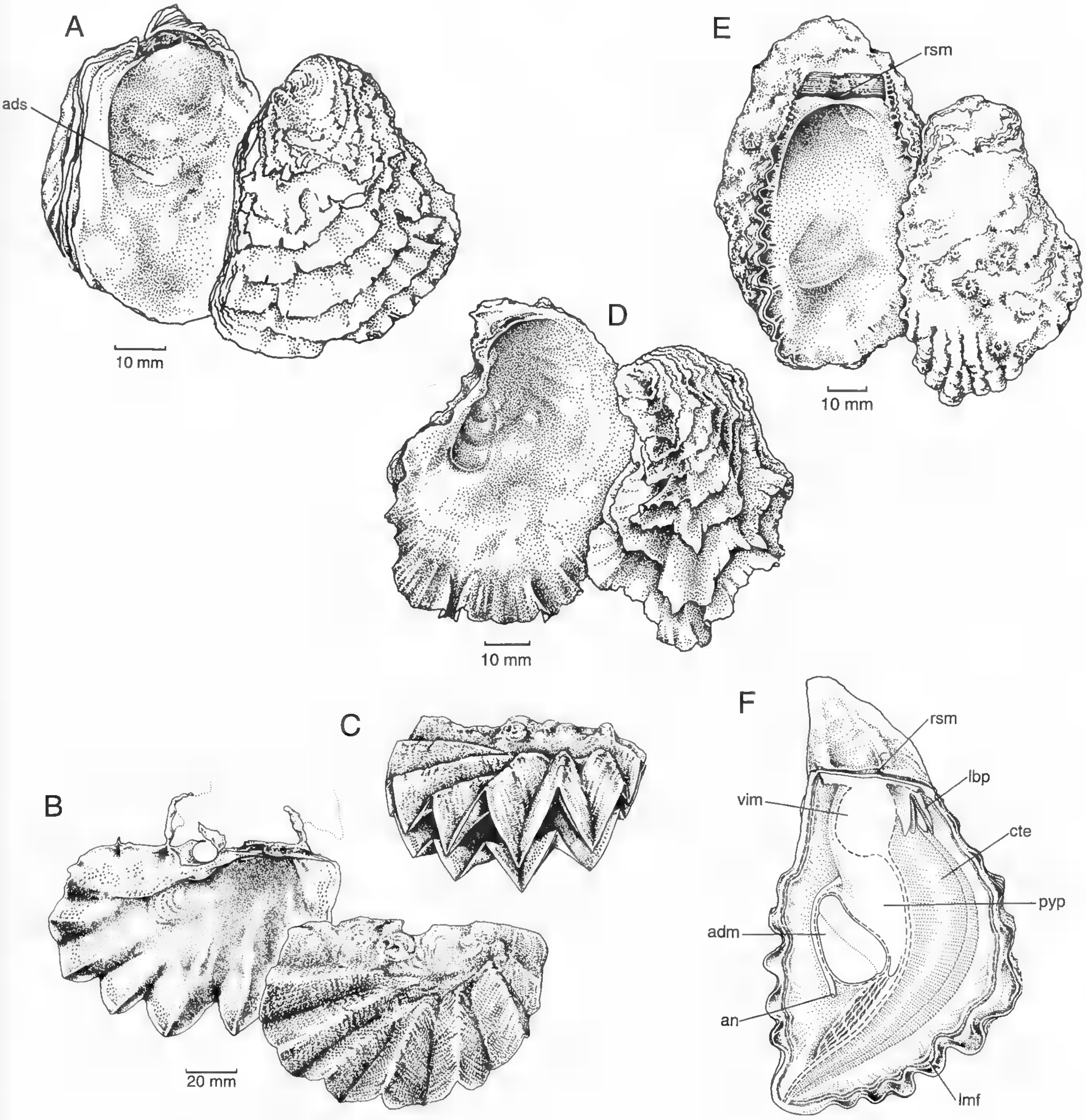

Figure 6.15 Family Ostreidae. **A**, subfamily Ostreinae, *Ostrea angasi*, shell valves, left valve in internal view, right valve in external view. **B**, **C**, subfamily Lophinae, *Lopha cristagalli*: **B**, shell valves, left valve in internal view, right valve in external view; **C**, paired shell valves showing the typical zigzag commissure. **D–F**, subfamily Crassostreinae: **D**, *Crassostrea gigas*, shell valves, left valve in internal view, right valve in external view; **E**, *Saccostrea cuccullata*, shell valves, left valve in internal view, right valve in external view; **F**, *Saccostrea commercialis*, organs of mantle cavity, right shell valve and mantle lobe removed. **adm**, adductor muscle; **ads**, adductor muscle scar; **an**, anus; **cte**, ctenidium; **lbp**, labial palps; **lmf**, left mantle folds; **pyp**, promyal passage; **rsm**, resilium; **vim**, visceral mass.[R. Plant]

Since the voyages of the early European explorers of Australia and the early period of European settlement, there have been fisheries based upon naturally occurring populations of the flat oyster, *O. angasi*, particularly in Victoria and South Australia. Farming of this species is now being initiated in New South Wales, Tasmania, Victoria, South Australia and Western Australia.

With a fossil record extending from the Late Cretaceous (Stenzel 1971), this subfamily is represented in the fossil record of Australia by Pliocene species. In the extant Australian fauna it is represented by species of the genus *Ostrea*, of both the tropical Indo-West Pacific and the temperate southern Australian faunas. One of the latter group, *O. angasi*, is recorded from the fossil fauna of the calcaranites of the Roe Plain (Ludbrook 1978), now regarded as of Late Pliocene age (G.W. Kendrick personal communication). The extinct species, *O. arenicola* (= *O. sturtiana*), has also been recorded from the Pliocene of southern Australia.

Subfamily Lophinae

The shape of lophine oysters is very variable between and within species. They tend to be circular to triangular in outline, and most are almost equivalve in convexity (Fig. 6.15B, C). The left shell valves may have a small or large attachment area which, in some forms, is surrounded by shelly outgrowths or claspers (Fig. 6.15B). These are best developed on oysters attached to gorgonians, mangrove roots, ropes, *etc*. Such ecomorphs are also those in which the shell margins are more acutely folded, with correspondingly well-developed and acutely angled radial ribs. The commissural folds and corresponding ribs are very few in the genus *Lopha* (Fig. 6.15B, C), but the sharp to shallow folds or undulations and their corresponding ribs are generally more numerous in the genera *Dendostrea* and *Alectryonella*.

Pustular chomata are usually present in one or more rows on the lips of one or both shell valves. The capacity of the interior cavity of lophine oysters tends to be small relative to the outer dimensions of the shell. There are few if any cavities between the layers of the shell valves, and these are never filled with chalky inclusions. Lophine shells are generally thin but solid and those of the genus *Dendostrea* are usually strongly lamellose. The external shell surface of the tropical genus *Lopha* is sculptured with fine vermiculose pustules but not with growth lamellae. The lustrous internal shell layers include patches of the unique 'fingerprint' structure in the widespread Indo-West Pacific coral-associated oyster genus *Alectryonella*.

There is no promyal exhalant passage present in any lophine species. The pseudofaecal rejection system terminates anteriorly or antero-ventrally. The intestine does not loop beside the stomach but is bent in a Z-shape (Torigoe 1981), as in the Gryphaeidae. The anal rim of most species supports a large flap, which is leaf-shaped in some species. Fertilisation in lophine species is internal and the eggs are incubated as in the sub-family Ostreinae.

Lophine species live mainly in tropical waters, with very few ranging into temperate seas. They are all subtidal. Species of *Dendostrea* are commonly attached to rocks, dead coral, live gorgonians, floating buoys and other similar substrata and may have a covering of sponge. Oysters of the species *Lopha cristagalli* (Fig. 6.15B, C; Pl. 12.1) are typically attached to dead coral and to one another and, almost always, are sponge-covered. Large clumps often fall from their hard substratum. *Alectryonella plicatula* is almost invariably embedded in living massive corals, with only its ventral lips exposed.

The most notable of the Australasian species of this subfamily belong to the genera *Lopha*, *Alectryonella* and *Dendostrea*. The first two of these genera seem to be mono-specific, with a tropical Indo-West Pacific distribution that includes the northern waters of Australia. *Dendostrea* is more diverse and more widespread, with its tropical species seeming to be more tolerant of cooler waters than are those of ostreine genera. No lophine species has supported a commercial fishery.

The fossil record of this extant subfamily extends from the Late Triassic to the Recent (Stenzel 1971).

Subfamily Crassostreinae

The crassostreine oysters exhibit an extreme degree of intra-specific variation in shell shape and sculpture. They are inequilateral and in general their outline is trapezoid – being higher than long. The axis of shell growth is curved to the posterior in most species and to the anterior in a few. The shell is inequivalve with a less convex, upper, right valve which may even be opercular in form, and a much more convex left valve (Fig. 6.15D, E). This valve is cemented to a hard substratum over an area which varies in extent between and within species. The upstanding portion of this lower valve is usually radially ribbed, as is the upper valve of some species. Most species have well marked growth lamellae which, in some juveniles of some species such as *Saccostrea echinata*, are upraised and folded to form hollow tubes. The left valve usually has some degree of development of an umbonal cavity, well marked in the genus *Saccostrea* (Fig. 6.15E). This cavity is most definitely developed by closely packed individuals, particularly of *S. cucullata*. In such oysters the left valve may even become tubular in shape and the right valve may be almost circular, covering the small aperture like an operculum.

In most species the interior of the commissural shelf of one shell valve usually bears well-marked pustular or elongate chomata, with corresponding depressions on the opposite valve. The extent to which the chomata extend ventrally from the hinge varies between and within species. Members of the genus *Crassostrea* do not develop chomata, in contrast to the species currently referred to the genus *Saccostrea*. Shells of crassostreine oysters are generally solid, although the growing shell margins may be fragile and lamellose distal to the line of chomata on the commissural shelf. In most species there is some development of shallow fluid-filled or chalk-filled cavities, particularly within the lower valve.

In all crassostreine oysters, a promyal passage is present between the right mantle lobe and the visceral mass, and dorsal to the heart and adductor muscle. This passage provides a route, other than that ventral to the adductor muscle, for the exhalant current to flow from the suprabranchial chamber to the exterior. The pseudofaecal rejection system within the inhalant pallial cavity generally terminates antero-ventrally. The adductor muscle tends to be narrower than that in other oysters and is located closer to the posterior margin (Fig. 6.15F). The colour of the adductor muscle scars varies between valves, between species and, to a small extent, within species.

The series of tentacles on the middle and innermost mantle folds are generally well developed. The depth of the colour of the gills varies between species and also varies, at least in the black-lip oyster, *S. echinata*, with the degree of exposure to light. The cardiac auricles of the various taxa are joined to one another medially to different extents.

The outer labial palps are usually only narrowly fused together medially. After leaving the stomach, the intestine forms a ventral hairpin loop which is accommodated in the visceral pouch. It then runs dorsally to form a wide loop around the left side of the stomach (Torigoe 1981). The rectum emerges from the visceral mass to run posteriorly to the heart and adductor muscle. It is attached to the posterior and postero-ventral face of this muscle except at the distal tip (Fig. 6.15F). There the anus is surrounded by a simple lip.

Crassostreine oysters are not incubatory. The sperm are voided with the exhalant current but the ova of at least some species pass through the pores or ostia of the gills into the inhalant pallial cavity before being expelled by a sudden clapping of the valves. Fertilisation occurs externally.

Crassostreines tend to be gregarious (Pls 11.5, 11.6) and may aggregate to form intertidal or subtidal reefs. The spat of *Saccostrea* species seem to settle over a wide intertidal area. Subsequently there is usually a high mortality of the juveniles. This is often caused by such physical factors as heat and desiccation above and by predation by fishes, gastropods, *etc.* below the optimal intertidal area. The shells of crassostreine oysters living close to a muddy bottom are commonly infected by mudworms which cause mud blisters to form between the layers of the shell, so weakening it and leaving the oyster open to predation.

Research effort on crassostreine oysters has been and still is high, partly because of the high commercial value of their 'meat' and shell.

Recent genetic research has affirmed a close relationship between the Sydney rock oyster *S. commercialis*, common and extensively farmed in more sheltered habitats along Australia's eastern coasts, and the New Zealand species *S. glomerata* (Buroker, Hershberger & Chew 1979; Anderson & Adlard 1994). A genetic survey of all Indo-West Pacific species of this group would allow the degree of this relationship to be assessed more accurately.

A similar study is needed to determine the status of the coral rock oysters, generally grouped under the name *S. cucullata*. According to Stenzel (1971), this is the type species of the genus *Saccostrea*. The taxon is widespread on the oceanic coasts of the Indo-West Pacific region but is not generally suitable for farming due to its habitat requirements and growth form. In Australia this taxon has been known under the names of *Saccostrea* (formerly *Crassostrea) amasa* and *tuberculata*.

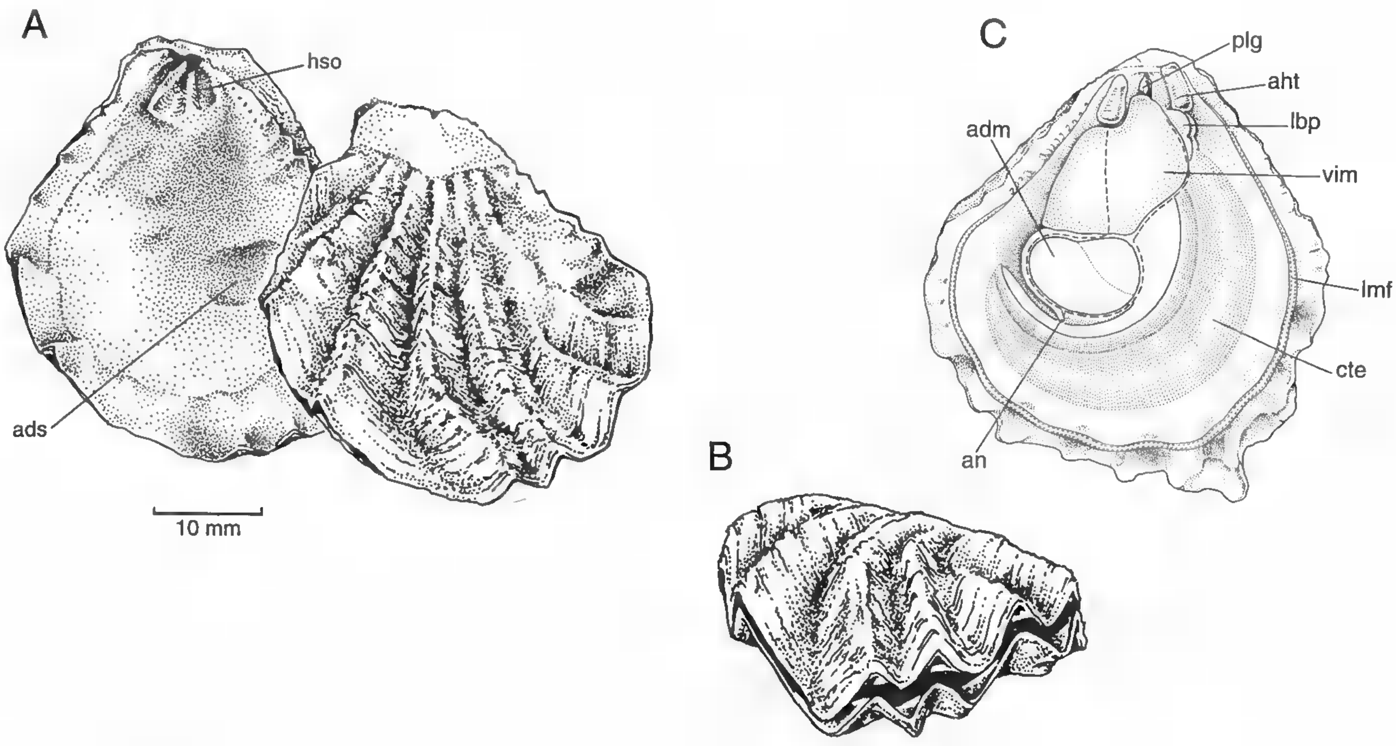

Figure 6.16 Family Plicatulidae. A, B, *Plicatula chinensis*: A, shell valves, right valve in internal view, left valve in external view; **B**, paired shell valves showing the zigzag commissure. C, *Plicatula* sp., organs of the mantle cavity, right shell valve and mantle lobe removed. **adm**, adductor muscle; **ads**, adductor muscle scar; **aht**, anterior hinge tooth; **an**, anus; **cte**, ctenidium; **hso**, hinge socket; **lbp**, labial palps; **lmf**, left mantle folds; **plg**, primary ligament; **vim**, visceral mass. [R. Plant]

Long-established farms of the Sydney rock-oyster (*Saccostrea commercialis*) along the New South Wales coast have had to cope with disease and pollution, as well as biological and economic competition from the introduced and essentially subtidal Pacific oyster, *Crassostrea gigas*. The value of subtidal culture of both of these species is being compared with that from farms using intertidal techniques, such as those employed in recent years with the more tropical black-lip oyster, *S. echinata*, and more traditionally with members of the *S. commercialis* complex in New South Wales, Queensland and Western Australia. Farming of *C. gigas* is carried out in Tasmania, Victoria and South Australia where native crassostreine oysters are sparse or absent.

This diverse and very widespread extant subfamily has a fossil record going back to the Early Cretaceous (Stenzel 1971).

Superfamily PLICATULOIDEA

Plicatuloideans are monomyarian ostreinans with filibranch gills. They cement themselves to hard substrata by the right shell valve. The interior surfaces of the valves are covered by a layer of crossed lamellar aragonite which extends well outside the pallial line. The ligamental resilium is fibrous and, unlike that of dimyoideans, is split between the valves. The ligament lacks extensions of lamellar material along the opposed surfaces of the hinge line anterior and posterior to the resilium.

Waller (1978) separated dimyariids from this superfamily, into which Yonge (1975) had placed them, and allied both groups with the oysters in the suborder Ostreina. The superfamily Plicatuloidea as presently defined is known to have been extant during the Triassic, and may have been represented by the extinct family Terquemiidae, even as early as the Early Permian. That family persisted to the Late Jurassic and, perhaps, even into the Cretaceous (Cox 1969d). The only other family, the Plicatulidae, is known from the Middle Triassic to the present (Cox & Hertlein 1969c). Feldtmann (1963) recorded a species of *Plicatula* from the Late Cretaceous of the Perth Basin of Western Australia, but Darragh & Kendrick (1980) considered this to belong to the genus *Atreta*, of ambiguous family placement (see Hodges 1991). Also from Western Australia, Darragh & Kendrick (1991) recorded *Atreta* specimens from the Late Cretaceous of the Carnarvon Basin, but the same authors (1980) had recorded Eocene specimens of *Plicatula* from the Pallinup Siltstone. Tate (1898) and Chapman (1922) published on Miocene plicatulid occurrences from south-eastern Australia.

Family Plicatulidae

The right shell valves of plicatulids are cemented more or less extensively to a hard substratum by shell material and so the form of the shell tends to be somewhat irregular. The valves do not develop auricles in front of or behind the short hinge line. The valves are, in general, strongly folded or plicate (Fig. 6.16). The shell structure is generally as in the family Spondylidae (Kennedy, Taylor & Hall 1969). The hinge consists of strongly interlocking secondary teeth and sockets on short, deep hinge plates in both valves. These teeth function in maintaining the correct alignment of the valves.

The ligament consists of a deeply V-shaped, central, transverse, aragonitic, primary ligament with its outer layers fused to each side of the resilium. Due to the growth of the dorsal margin of the pallium which comes to arch over the primary ligament, a secondary ligament is secreted which simply joins the valves dorsally. The primary ligament becomes internal between the secondary teeth, and ventral to the secondary ligament.

The inner and middle folds of the mantle are much simpler than is usual among ostreoideans. The inner fold is narrow and bears small tentacles. There are no eyes on the middle fold. The gills are not plicate, and they lack inter-lamellar junctions. They are thus simpler than those of some other ostreoideans. The gill ciliation is of Atkins' (1937) Type B(1a) (Yonge 1975) but the ascending limb of the inner demibranch is absent in some taxa. The labial palps are small, with the outer pair fused medially to form a hood over the mouth (Fig. 6.16C). The foot is absent in plicatulids. The kidneys are united medially and have a long duct. The sexes are separate.

All plicatulid species are marine and most live in shallow water. The few living species of this family belong to the genus *Plicatula*, with most of these being of Indo-West Pacific distribution extending to the northern coasts of Australia. The relationships of the variable species are poorly understood, however currently recognised members of the Australian plicatulid fauna include the species *Plicatula australis*, *P. muricata* and *P. chinensis*. These species have been recorded at depths between the intertidal zone and about 200 m, with *P. chinensis* appearing to be the most tolerant of temperate waters.

Superfamily DIMYOIDEA

These small anisomyarian, filibranchiate ostreines are cemented by the right valve to hard substrata. Their shells lack a simple prismatic calcitic outer layer. The fibrous resilium is continuous between the valves, is surrounded dorsally by the hinge plate and the lamellar ligament, and is inwardly bowed. The layer of crossed lamellar aragonite lining the interior of the valves rarely extends distally to the pallial line.

This superfamily, consisting of only one family, is known to have existed from the Late Triassic to the present (Hodges 1991).

Family Dimyidae

Dimyid shells are generally subcircular in outline (Fig. 6.17A) and are cemented to a hard substratum by shell material secreted by the folds edging the right mantle lobe. The extent of the area of attachment varies with the species to a larger extent than is usual in cemented forms, with some attaching to small, soon outgrown, shell fragments. The hinge line is short and there is no development of anterior or posterior auricles. Secondary teeth develop only on the right valve, and even these may be absent in some species.

The primary ligament is bow-shaped and transverse, with the resilium being completely fibrous and continuous between the valves. Dorsal to it is an uninterrupted, relatively long, secondary, external, longitudinal ligament. It develops by a bridging and fusing of the anterior and posterior parts of the muscular dorsal pallial isthmus, and is partly responsible for successful valve alignment.

As their name indicates, these ostreoids are dimyarian, with the anterior adductor muscle being much smaller and more dorsally situated than is the posterior adductor. This latter is divided into two distinct sections (Fig. 6.17B) - the more posterior section being composed of smooth muscle fibres as is the anterior adductor muscle. The more anterior section of the posterior adductor muscle is composed of striated muscle fibres. At the shell/muscle interface of the posterior adductor muscle the two sections are generally juxtaposed to produce a more or less bilobed posterior adductor muscle scar. The foot is completely absent in dimyids.

The inner and middle folds of the mantle are simple, with a narrow inner fold bearing small tentacles. There are no eyes on the middle fold.

The gills are very simple. Each demibranch consists of a single row of unattached descending filaments (Ridewood 1903). There are food grooves along the gill axes of the eastern Australian *Dimya corrugata* and the smaller Caribbean *Basilomya goreaui*, with the tips of the inner demibranchs adherent to one another according to Yonge (1978). The gill ciliation is similar to that of Atkins' (1937) Type B(2b) but no rejection currents were observed on the ventral margins by Yonge (1975, 1978). The palps are well developed though lacking sorting folds (Yonge 1978) and the outer pair form a hood dorsal to the mouth. Presumably the sorting of entrapped particles occurs only on the gill surfaces.

The heart of the dimyid species examined by Yonge (1978) is not well developed and the non-muscular ventricle is traversed by the rectum. By contrast, the kidneys are large, with their fused dorsal section communicating with the pericardium and their lateral sections opening ventrally to the pallial cavity. Both of these species are hermaphroditic, with both sperm and eggs developing in the same follicles of the dorso-lateral gonads. The eggs of these species are large and yolky.

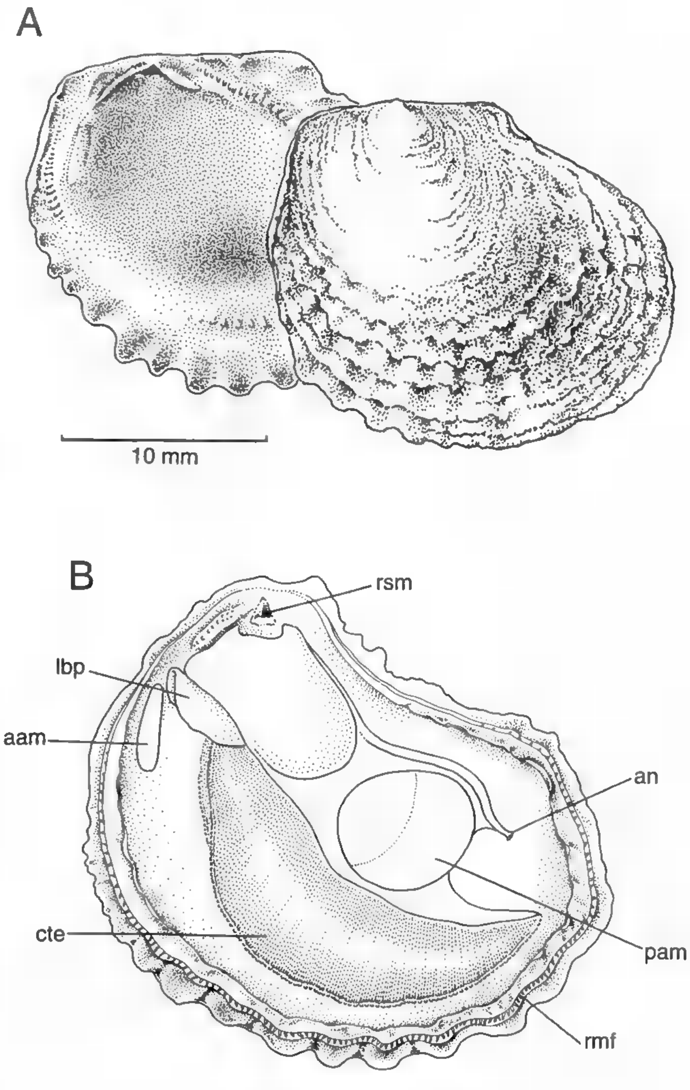

Figure 6.17 Family Dimyidae. *Dimya corrugata*: **A**, shell valves, right valve in internal view, left valve in external view. **B**, organs of the mantle cavity, left shell valve and mantle lobe removed. **aam**, anterior adductor muscle; **an**, anus; **cte**, ctenidium; **lbp**, labial palps; **pam**, posterior adductor muscle; **rmf**, right mantle folds; **rsm**, resilium. [R. Plant]

Yonge (1975) placed the family Dimyidae with the Plicatulidae in his new superfamily Plicatuloidea on the basis of the similarity of their hinges and primary and secondary ligaments. However Waller (1978) separated these two groups at the superfamily level, and placed them both, with the oysters, in the suborder Ostreina.

All dimyid species are marine and most live in deep water. Most living species are inhabitants of the Pacific Ocean, although the genus *Dimya* also occurs in the Indian Ocean and the Caribbean. The genera *Basilomya* and *Dimyella* also occur in Atlantic waters. There are two or three forms of *Dimya* that live attached to small shelly fragments, to one another or to other living molluscs in the deeper waters of the Continental Shelf off eastern and western Australia. For the eastern Australian species, *Dimya corrugata*, Iredale (1936) erected the genus *Dimyarina*. The biology and the extent of the geographical distribution of the Australian taxa require further investigation, as does the relationship of these forms to those of the central Indo-West Pacific.

The family Dimyidae, the only family within the Dimyoidea, arose during the Late Triassic (Hodges 1991) and has persisted to the Recent, although only a few small species are now extant (Cox & Hertlein 1969d). The Australian fossil record of this family may extend from the Late Cretaceous, should Feldtmann's (1963) record of *Plicatula* (= *Atreta* according to Darragh & Kendrick 1980) from the Perth Basin of Western Australia prove to be a dimyid (see Hodges 1991).

Suborder PECTININA

Those ostreoids that are grouped within the sub-order Pectinina are pleurothetic on either the right or the left valve and are cemented, byssate or free. A byssal notch is usually present on the right valve, at least in the early stages. They are monomyarian, with a posterior adductor muscle lying within the area demarcated by the simple, non-sinuate pallial line.

In most forms the shell has an outer layer of simple prismatic calcite, present in at least one valve but usually in both. A foliated calcitic layer is usually dominant and a crossed-lamellar aragonitic layer is variously developed. The ligament is alivincular, with a lamellar section variously developed and ranging from absent to hypertrophied.

There is no ventral fusion of the mantle lobes. Their margins are tentaculate, with the innermost fold forming a pallial curtain. The gills are eleutherorhabdic and a foot is present at all stages.

Before the Late Palaeozoic, the Pectinina had differentiated from the ostreine forms, retaining the foot, though adopting the pleurothetic habit (Waller 1978). The suborder is composed of the extant superfamilies Pectinoidea and Anomioidea, and the extinct superfamilies Aviculopectinoidea and Monotoidea (= Buchioidea) and two other extinct families of unknown superfamilial affinity. These extinct superfamilies originated in the Mid- to Late Palaeozoic; the Monotoidea survived until the Late Cretaceous. Although Waller reported that the Aviculopectinoidea persisted only into the Triassic, Skwarko (1967) has recorded the presence of an aviculopectinid in the Early Cretaceous of the Gibson Desert of Western Australia. The characteristics and relationships of these superfamilies have been described by Waller (1978, 1984, 1991).

Superfamily PECTINOIDEA

Pectinoideans may be pleurothetic on the right valve, and byssate, cemented or free. If cemented, they are attached, temporarally or permanently, to the substratum by shell material secreted by the marginal folds of the right mantle lobe (for example, the spondylids and species that have been placed in the pectinid genus *Hinnites*). Most pectinoidean shells are inequivalve and consist of a disk having a more or less circular outline and one or two sets of auricles. A byssal notch on the lower valve is commonly present throughout life.

An outer layer of simple calcitic prisms is limited to the right valve of the shell or is absent, and a foliated calcitic layer is usually dominant. Internally there is an aragonitic crossed-lamellar layer that is of variable extent and is not nacreous. The median portion of the ligament, the resilium, is hypertrophied and extends even below the hinge line so that its active portion is approximately triangular in section and pyramidal in shape. This resilium is lamellar centrally and fibrous laterally (Waller 1991). Anteriorly and posteriorly to the resilium the bands of fibrous ligament are attached to each shell valve within a groove or fossa.

The anterior adductor muscle is absent and the posterior adductor is correspondingly enlarged. Both the inner fold (or pallial curtain) and the middle fold of the pallium are edged with one or more series of tentacles. Usually the middle fold also bears a series of pallial eyes. The foot is often byssate, at least during the juvenile stage.

The superfamily Pectinoidea comprises the extant families Pectinidae, Propeamussiidae, Spondylidae and Entoliidae (= Syncyclonemidae), which exhibit a remarkably diverse range of habitats and life styles.

Pectinoideans appear to have arisen in the Ordovician. By the period from the Early Carboniferous to the Cretaceous the group had diverged into the four extant families. The Triassic genus *Pleuronectites* has a well-developed ctenolium (see below) and a resilium of the pectinoidean type and is considered to be the oldest known member of the superfamily Pectinoidea (Waller 1984).

Family Pectinidae

The shells of this large family, commonly known as scallops, are of small to medium size. The shell valves typically consist of a disk that is circular to oval in outline and is almost equilateral (Fig. 6.18A–G). The shell is either equivalve or, if inequivalve, often with the right valve more convex. The shell margins are usually completely or almost completely closed. The hinge line is usually lengthened by an anterior and posterior set of auricles. A noticeable ventral migration of the hinge line and byssal notch occurs in those byssally attached forms in which the shell is confined within cavities, such as the coral-dwelling *Pedum spondyloideum* (Pls 12.3, 12.4). In such forms there is often a wide shell gape.

The shell may be free, byssate when young or throughout life, or with obligate cementation in adults (for example, species grouped under the generic name *Hinnites*). There is a byssal notch below the right auricle edged ventrally with a series of teeth which is known as a ctenolium. Such a ctenolium is limited to and universal within the family Pectinidae and is, except in species of the genus *Juxtamusium*, located only on the right valve. It seems to have as its most important function the maintenance of the separation of byssal thread bundles in order to increase their spread. This would increase the amount of torque necessary to break the byssal attachment. As the shell grows the proximal (more dorsal) ctenolial teeth are overgrown by the advancing edge of the fasciole with which the byssal notch, advancing ventrally, is back-filled. New teeth form distally (ventrally). However, in older animals of some species, the formation of new teeth ceases and the ctenolium eventually disappears. This situation occurs mainly in cemented or in strongly swimming forms. However, it also occurs in some less strongly swimming species which form a weak byssus that can be readily detached if danger threatens. A pseudo-ctenolium is formed from the external sculpture on the edge of the right side of the byssal gape in some species of *Delectopecten* and in coarsely sculptured forms of *Cryptopecten vesiculosus* (Waller 1984).

Scallops range in size from small species to those reaching about 300 mm (the largest free-living scallop) or 500 mm (*Hinnites* group) in length. The southern Australian species, *Pecten fumatus* (= *alba*; Fig. 6.18B; Pl. 13.1), reaches 110 mm in diameter, and *Equichlamys bifrons* can grow to 135 mm (Pls 5, 13.2). The maximum size of a species may vary between populations. Doughboy scallops, *Mimachlamys asperrima* (Pl. 13.3), grow to no more than 80 mm in diameter in Bass Strait but may reach more than 100 mm in the populations in the D'Entrecasteaux Channel of Tasmania (see Young & Martin 1989).

Scallop shells may be nearly smooth or have radial ribs or folds and/or commarginal lamellae. It is thought that the ability of scallops to form often-elaborate sculpture may have given them a selective advantage as predator pressure increased. The shells are usually thin and light and are composed mainly of lathic calcite. A simple prismatic calcitic foliated layer is present externally in all species, though usually only in the early stages of development. An exception is the Indo-West Pacific species *'Chlamys' coruscans* in which the outer layer of the left valve is also composed of lathic calcite. The inner layer of pectinid shells is sub-nacreous or porcellaneous and is usually formed, at least proximally to the pallial line, of a thin layer of aragonite. Prismatic aragonitic myostraca are present. The ctenolium is, in all cases, composed of lathic calcite, and this layer is strongest in strongly byssate forms (Waller 1991).

A straight hinge line with taxodont teeth is present in very young shells. Post-larval shells may have two pairs of teeth in each valve, the resilial and dorsal pairs on the right valve interlocking with the infradorsal and supradorsal pairs on the left. The degree of development of these hinge-teeth may vary with the group and extra teeth may be present in some (Waller 1991).

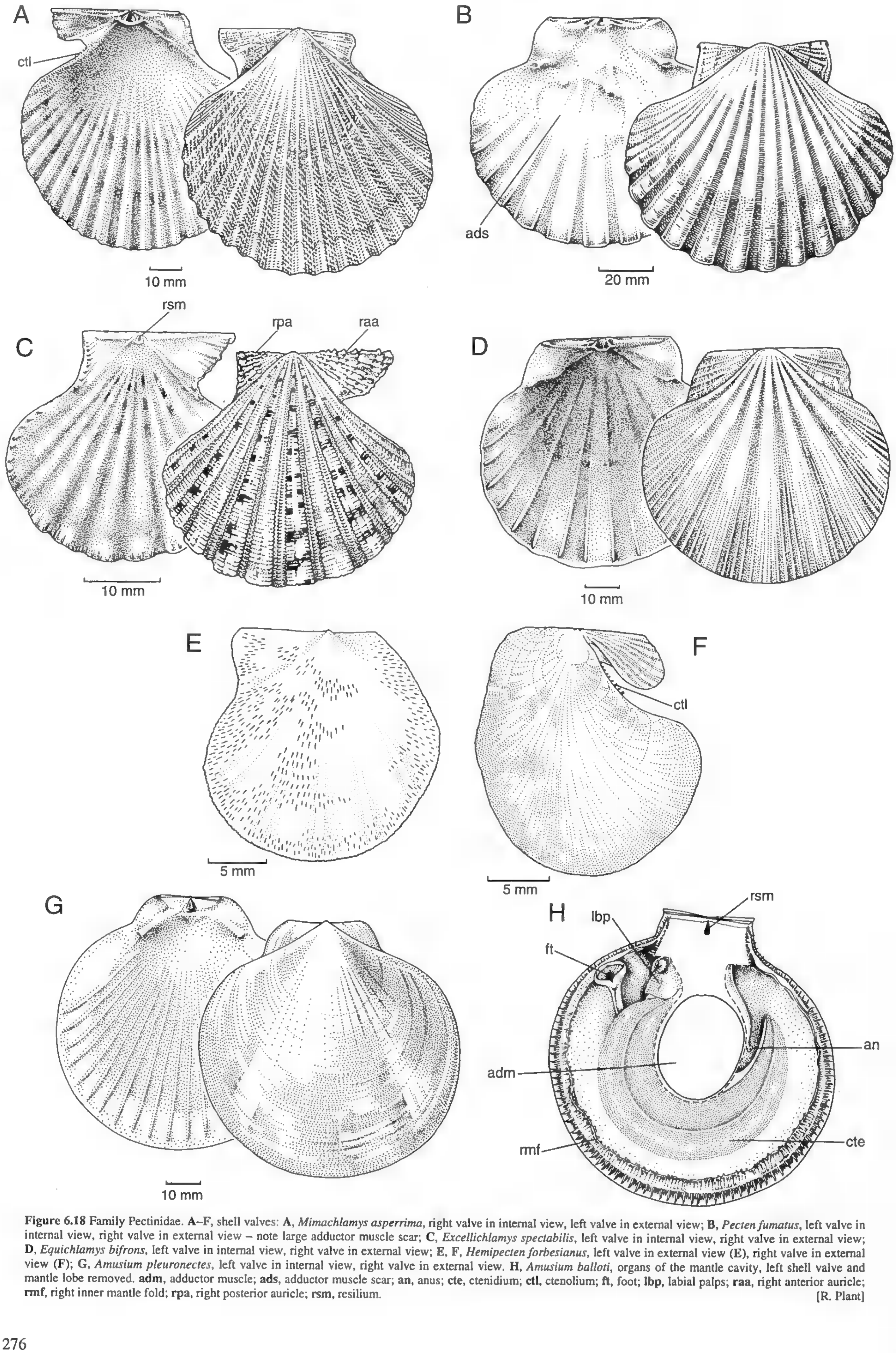

Figure 6.18 Family Pectinidae. **A**–**F**, shell valves: **A**, *Mimachlamys asperrima*, right valve in internal view, left valve in external view; **B**, *Pecten fumatus*, left valve in internal view, right valve in external view – note large adductor muscle scar; **C**, *Excellichlamys spectabilis*, left valve in internal view, right valve in external view; **D**, *Equichlamys bifrons*, left valve in internal view, right valve in external view; **E**, **F**, *Hemipecten forbesianus*, left valve in external view (**E**), right valve in external view (**F**); **G**, *Amusium pleuronectes*, left valve in internal view, right valve in external view. **H**, *Amusium balloti*, organs of the mantle cavity, left shell valve and mantle lobe removed. **adm**, adductor muscle; **ads**, adductor muscle scar; **an**, anus; **cte**, ctenidium; **ctl**, ctenolium; **ft**, foot; **lbp**, labial palps; **raa**, right anterior auricle; **rmf**, right inner mantle fold; **rpa**, right posterior auricle; **rsm**, resilium. [R. Plant]

The ligamental resilium, the ends of which attach to the surfaces of amphidetic triangular pits below the umbones, and the anterior and posterior sections of the interrupted outer fibrous ligament at and just below the hinge line help to control the alignment of the valves.

The striated quick section and the non-striated catch section of the single adductor muscle are variously developed. The attachment scars of each section can usually be discerned on the interior surfaces of the valves (Fig. 6.18B). The left posterior pedal retractor muscle is generally present but is sometimes much reduced. The mantle folds generally bear eyes and guard tentacles (Pls 12.4, 13.1), although these are few or absent in the saucer scallops of the genus *Amusium*. The gills are plicate and heterorhabdic in most forms, with the principle filaments expanded. However, in *Amusium*, the gills are smooth and homorhabdic. The dorsal ends of the ascending lamellae of the outer demibranchs are fastened together by ciliated discs arranged in a longitudinal fashion, and they are usually free of the mantle. The demibranchs are not organically united medially, and are of Atkins'(1937) ciliation Type B(1b) (see Yonge 1975).

Aspects of the internal anatomy are illustrated in Figure 6.18H. The labial palps of pectinids are somewhat trigonal in shape, and the lips are hypertrophied and interdigitate over the mouth. In the European *Pecten maximus* the numerous pores between these lips have been shown to allow the escape of water, and the thick ciliated epithelium on their internal ridges prevents the loss of food particles (Gilmour 1974). The stomach is of Purchon's (1958) Type IV, with its major typhlosole lacking a long tongue and ending near the left pouch, the sorting area of the dorsal hood being well developed and the style sac being united to the mid-gut. The anal end of the rectum is usually free and erectile. Unlike the diet of phytoplankton which is usual for pectinids and similar bivalves, the food of *A. pleuronectes* may include zooplankton as well as phytoplankton (Llana 1986). The foot is of moderate size. It does not function in locomotion but, in at least the juvenile stages of many forms, secretes a byssus. There is a variation in the development of the byssus from the condition present in the southern Australian *P. fumatus* which has a fine byssus for only a short time after settlement, to that in strongly and almost permanently byssate forms such as some species of the genera *Chlamys*, *Mimachlamys*, *Leptopecten* and *Delectopecten*. The free end of the foot is funnel-shaped or bent and functions efficiently in cleaning the inhalant pallial cavity (Fig. 6.18H).

The left auricle of the heart is usually smaller than the right. The median ventricle is traversed by the rectum and both anterior and posterior aortae are present. Pericardial glands are located in the walls of the auricles and the pericardium. The kidneys are located anterior to the auricles and are joined to one another. The pectinid nervous system is unusually concentrated, perhaps in connection with the functioning of the elaborate and efficient sense organs. The cerebral ganglia are small and are connected to the pedal ganglia. The visceral ganglia are fused to form an often-asymmetrical complex.

Most pectinid species are gonochoristic (for example, *Mimachlamys asperrima*, *Equichlamys bifrons* and *Amusium balloti*) but some are functional hermaphrodites (for example, *P. fumatus* and *A. pleuronectes*). The timing and duration of the spawning and settlement periods may vary within a species' range, as in *P. fumatus* (Sause, Gwyther & Burgess 1987), probably reflecting environmental differences. The eggs of *E. bifrons* are 120 µm in diameter and the pediveligers range in size from 160 to 175 µm. The fecundity of *A. pleuronectes* has been shown to vary with body size (Dredge 1981). In a number of scallop species, including *A. balloti* (Joll & Caputi 1995), there is a seasonal change, which is related to the reproductive cycle, in the weight of the adductor muscle. This muscle appears to act as a reserve of nutrients used in the development of the gonads. Studies on the castration by bucephalid trematodes of larger females of *Pecten* in southern Australia and of both species of *Amusium* represented in the northern Australian fauna have been summarised by Young & Martin (1989).

The duration of the period of larval development from the time of fertilisation to metamorphosis and spatfall may vary with the temperature (for example, 16–31 days in *P. fumatus*). The larval life span of other Australian scallop species, where known, falls within these limits. The post-larval rate of growth is also strongly affected by environmental conditions. The life span of *P. fumatus* has been recorded (as *Notovola meridionalis*) to reach 14 years (Fairbridge 1953). The reliability of the technique of ageing individuals of *A. balloti*, using the shell-pigment rings deposited daily, has been proven by marking experiments (Joll 1988).

Predators on *Pecten* species include the whelks *Fusinus australasia* in Tasmania and *Bedeva hanleyi* in Western Australia, octopuses in New South Wales, and starfish like *Coscinasterias calamaria* in Tasmania and possibly in Victoria and Western Australia. The shell of some species may be covered by a symbiotic sponge, like that on *M. asperrima* in South Australia, which may protect the scallop against starfish predation (Chernoff 1987).

Studies on infection of the adductor muscle of southern Australian *Pecten* and northern Australian *Amusium* species by larval nematodes have been summarised by Young & Martin (1989). It is thought that turtles may be the final hosts of the species of *Sulcascaris* that infects *A. balloti*, and that elasmobranch fishes may be the final hosts of the *Echinocephalus* species that infect *A. balloti* and *Pecten* species (Sanders 1966; Sanders & Lester 1981; McShane & Lester 1984). Boring of the shell of *Pecten* species by the mudworm *Polydora websteri*, recorded in Tasmania by Dix (1981), may result in the weakening of the shell structure.

Pectinids may be cemented to a hard substratum in the post-juvenile stage (*Hinnites* species) or may be firmly byssally attached to rocks, *etc.* (some species of *Chlamys* and *Mimachlamys*), to kelp or pilings (*Leptopecten* species) or to deep-sea living and non-living hard substrata (*Delectopecten* species). There are less strongly byssally attached forms that can detach the byssus from the foot and swim away when danger threatens (for example, some species of *Aequipecten*, *Argopecten*, *Decatopecten*, *Mimachlamys* and *Chlamys*). Some forms, such as *Pedum spondyloideum*, are byssally attached to and embedded in living coral (Pls 12.3, 12.4) or are attached, like *Hemipecten forbesianus*, by a fine byssus beneath colonies of living coral. Actively swimming forms such as species of *Amusium* may form dense aggregations. Other less actively swimming forms may normally nestle in the soft substratum, as do *P. fumatus* and *E. bifrons*.

The depth range inhabited by this family is great, extending from the shallow subtidal zone (*E. bifrons* from depths of 2–40 m) to depths of approximately 7000 m (non-Australian species of *Hyalopecten*). In addition, the climatic range that they inhabit is great, extending from the tropics (including many northern Australian forms) to the polar regions (for example, *Adamussium colbecki* in the Antarctic).

The Australian 'true' scallop, *Pecten fumatus*, is distributed in southern waters (Pl. 13.1; Woodburn 1990). This species is now dredged commercially in Tasmania and Victoria, though it was formerly also dredged in New South Wales, South Australia and Western Australia. It has been shown that considerable mortality in these scallops is associated with injuries caused by the dredging gear and the methods used in the fishery. In addition, considerable changes in their habitat have been caused by repeated disturbance of the sediment. Over-fishing may also have caused a general decline in these fisheries. The less-popular doughboy scallop *Mimachlamys asperrima* and the queen scallop *E. bifrons* are both distributed in southern Australian waters and were formerly (and occasionally still are) fished in Tasmanian waters. The saucer scallop *Amusium balloti*, distributed in northern Australian waters south to Esperance in Western Australia but only to a lower latitude in New South Wales, is trawled in Western Australia and Queensland. The related species *A. pleuronectes*, living off the coast of northern Australia, is trawled in the waters of the Northern Territory and the Kimberley region of Western Australia, although it is less popular because of its smaller size.

Pectinids are cosmopolitan in distribution but the group is best represented in the warm seas of the Indo-West Pacific and Eastern Pacific-Caribbean Regions. A widely diverse Australian fauna includes species of the genera *Pecten*, *Mimachlamys*, *Decatopecten*, *Semipallium*, *Pedum*, *Amusium* and others.

A number of new pectinid genera were proposed by Iredale (1929, 1939) and by Cotton (1930). Several of these were accepted as valid taxa by Hertlein (1969), generally as subgenera, but Iredale's (1929) genus, *Mimachlamys* was placed into the synonymy of *Chlamys*. However, it is now accorded generic rank and, in fact, is not closely related to *Chlamys* (Waller 1991).

This large extant family has a fossil history going back to the Triassic (Hertlein 1969), probably having arisen from the Entoliidae (Waller 1991). From Western Australia, Skwarko (1974) described a Middle Jurassic species from the Kojarena sandstone, Etheridge (1913) and Feldtmann (1951) described Late Cretaceous species from the Gingin Chalk and Darragh & Kendrick (1991) described a variety of pectinids from the Late Cretaceous of the Carnarvon Basin. Skwarko (1966, 1983) recorded pectinids from the Early and Late Cretaceous, respectively, of the Northern Territory. Oligocene to Early Miocene fossil imprints of *Chlamys* n. sp. aff. *natans* have been taken from cores in the Ross Sea (77°07.62'S, 176°45.61'W). *'Chlamys' natans* is now known to be living in Subantarctic seas near Tierra del Fuego and the Magellan Straits where it is found swimming freely or attached to the shallow-water kelp, *Macrocystis*. A review of the Tertiary pectinid fossils of Australian and New Zealand is currently being carried out by Beu and Darragh.

Some Cretaceous forms that are apparently pectinids, as they have a ctenolium and a limited layer of prismatic calcite on the right valve, differ from other fossil and living pectinids in having an extensive crossed-lamellar aragonitic layer extending well distal to the pallial line. In this they resemble members of the three other extant pectinoidean families.

Family Propeamussiidae

Almost all propeamussiids are free-living, and most have a wide shell gape. A true ctenolium is absent in all extant and Mesozoic species. However a weak pseudo-ctenolial tooth does occur on the leading edge of the fasciole which progressively fills the byssal notch in a West Atlantic species of *Cyclopecten*.

Propeamussiid shells have a relatively fragile microstructure and the degree of development of their sculpture is limited. This restriction in form and structure has perhaps allowed species diversification to occur only in deeper, relatively predator-free, waters. The prismatic calcitic outer layer on the right valve persists throughout life and commonly approaches the disc edge at the byssal notch. Its presence is related to the subdued sculpture of this valve. The innermost layer of crossed-lamellar aragonite extends distally well beyond the pallial line.

There are no hinge teeth in the shells of propeamussiids. The rounded inner ligament layer provides the opening thrust to the shell valves. This layer is bounded anteriorly and posteriorly by an outer ligament layer that maintains the alignment of the valves in the absence of hinge teeth.

There are no pallial eyes on the mantle folds, which also usually lack guard tentacles. The gills are non-plicate and lack inter-lamellar junctions. In contrast to those of the pectinids, the labial lips of propeamussiids are simple. At least some species of deep-water propeamussiids are known to be carnivorous, with small crustaceans having been found in the gut contents of *Propeamussium* species (Knudsen 1967, 1970). Hicks & Marshall (1985) reported that bathyal species of *Parvamussium* from the south-western Pacific and *Propeamussium* from the western Indian Ocean capture male but not female copepods. Luminous spots on the bivalves' mantle margins attract males searching for luminescent females.

Propeamussiids inhabit shallow to deep waters, with the Australian species *Ctenamussium thetidis* having been taken to about 600 m and *Cyclopecten favus* to about 300 m. The few shallow-water species are generally small to very small in size and are cryptic and/or occupy specialised habitats. Most species are probably byssate throughout life, although a few species of *Propeamussium sensu stricto* are presumed to be non-byssate as adults because the byssal notches that they have as juveniles later disappear.

This is an ancient group, according to Waller (1978). The Propeamussiidae appear to have diverged from the main pectinoidean group during the Mesozoic before the differentiation of all other extant groups of pectinoideans. The earliest Australian record appears to be of a Middle Jurassic species of *Propeamussium* from the Newmarracarra limestone of Western Australia (Skwarko 1974).

Family Spondylidae

Spondylids are cemented to the substratum by the right valve (Pl. 12.5). The area of cementation varies mainly with the species. Spondylid shape is, in general, species specific and does not vary within species to the same extent as in ostreids. The attached right valve is usually more convex than the left and does not have a ctenolium. In species of the genus *Spondylus* there is a byssal notch for a short period after settlement, perhaps indicating that the animal is mobile for a time and has the capability of forming a temporary byssus. No such notch ever develops in the eastern Atlantic and Mediterranean genus *Corallospondylus*. Spondylid shells are generally ornamented, sometimes profusely so, with protective lamellae and/or spines (Fig. 6.19A–C).

The shell exterior, along with the edge of the byssal notch, is composed of foliated lathic calcite, as is a narrow edging strip of the shell interior (Fig. 6.19A–D). This strip and the hinge plate are encroached upon by the extensive crossed-lamellar aragonitic middle and inner layers. Spondylids have a strong hinge of interlocking secondary teeth and sockets in both valves. These are important in maintaining the alignment of the valves. An outer ligamental layer of the aragonitic primary ligament is fused to both sides of the sub-umbonal inner resilial layer. This is continuous with the interrupted secondary ligament formed from the periostracum, and is without any tensile strength. It unites the long hinge line anteriorly and posteriorly to the primary ligament.

Aspects of the internal anatomy are illustrated in Figure 6.19E. The inner and middle pallial folds are hypertrophied and bear numerous large tentacles and eyes. The gills are non-plicate and their ciliation is of Atkins'(1937) Type B(1a) (see Yonge 1975). Though not used for locomotion, the foot is retained and is used to clean the inhalant part of the pallial cavity (Yonge 1973).

The lips of spondylids are hypertrophied and elaborately folded so that the lobes interdigitate over the oral grooves and mouth. The pores between these lobes allow the escape of water while particulate matter is retained by the ciliated tracts on the inner surfaces of the lips (Gilmour 1974). Unusual features are that for the greater part, the cerebropleural ganglia are fused with the visceral ganglia (Watson 1930), and the sexes are separate.

Spondylids are primarily tropical in distribution, being most abundant and diverse on rock and coral reefs, usually in situations with strong water flow but with protection from strong wave action. The strong, closely interlocking shells of cemented spondylids armed with spines and scales, and the even longer spines, such as in *Spondylus wrightianus* (Fig. 6.20B) which lies free as an adult, are proof against most predators. However, the southern Australian species *S. tenellus* (Fig. 6.20C), with its relatively fragile shell, is preyed upon by a muricid gastropod that drills fine holes through the exposed part of the right hinge plate.

Australian species belong to the genus *Spondylus*, and are much more diverse in tropical waters, with more than 20 species recorded from the northern Australian coasts. Prominent in the northern Australian spondylid fauna are the attached species *S. violascens*, *S. echinatus*, *S. nicobaricus*, *S. squamosus*, *S. barbatus* and *S. sanguineus*, and the free-living species *S. wrightianus* and *S. victoriae* (see Lamprell 1986). Only a single species (*S. tenellus*; Pl. 12.6) has been recorded from the southern coasts.

This family is represented in the fossil record from the Jurassic to the Recent (Hertlein & Cox 1969b), with the Australian record dating from the Eocene spondylid, *S. gaderopoides*, from southern Australia (Tate 1886; Darragh & Kendrick 1980). Fossils indicate that the cementing habit evolved early in the family's history.

Family Entoliidae

Fossils placed in the genus *Entolium* have been recorded from the Cretaceous of northern and southernparts of Western Australia and of Queensland (Skwarko 1967; Darragh & Kendrick 1991), as well as from Antarctica, New Zealand and many other areas. Long assumed to have become extinct by the end of the Cretaceous (Newell 1969c), Late Pleistocene fossils belonging to this family were found in the New Hebrides. More recently, living species were discovered in the waters of the Caribbean and the Gulf of Mexico and in the Pacific off Hawaii (Waller 1984).

The members of this small family lack a true ctenolium but have a weak pseudo-ctenolium consisting of a tooth on the edge of the byssal notch fasciole.

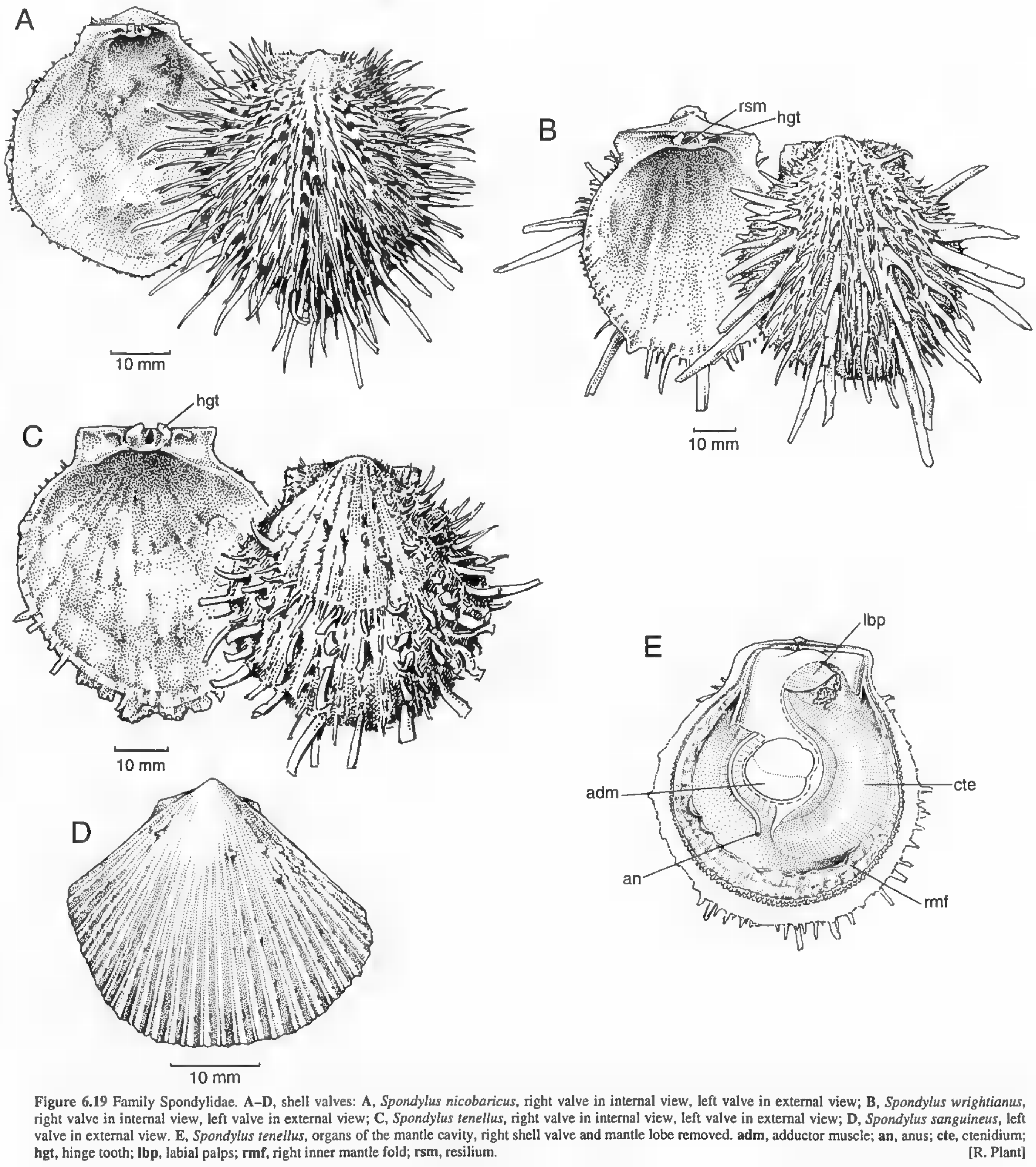

Figure 6.19 Family Spondylidae. A–D, shell valves: **A**, *Spondylus nicobaricus*, right valve in internal view, left valve in external view; **B**, *Spondylus wrightianus*, right valve in internal view, left valve in external view; **C**, *Spondylus tenellus*, right valve in internal view, left valve in external view; **D**, *Spondylus sanguineus*, left valve in external view. **E**, *Spondylus tenellus*, organs of the mantle cavity, right shell valve and mantle lobe removed. **adm**, adductor muscle; **an**, anus; **cte**, ctenidium; **hgt**, hinge tooth; **lbp**, labial palps; **rmf**, right inner mantle fold; **rsm**, resilium. [R. Plant]

The shells do not have a prismatic calcitic layer. The very narrow zone of secretion of lathic calcite produces a thin layer underlying the periostracum. The interior of the shell is lined with an extensive crossed-lamellar aragonitic layer.

Superfamily ANOMIOIDEA

The Anomioidea is an exclusively marine group. Anomioidean fossils are recognised from the Cretaceous to the Recent, but some fossils known from the Permian might also belong to this group (Keen 1969b).

The shells of members of this superfamily are circular to elongate in outline and irregular in shape with attached forms generally conforming to the topography of the substratum. They are compressed laterally, are subequivalve and are generally attached by or at least lie upon the right side. The byssal notch, if present, is without a ctenolium and usually develops into a byssal aperture or foramen. The shell appears lustrous internally. There is a layer of foliated calcite in the left or in both valves with a simple prismatic calcitic outer layer usually present in the right, and rarely in both valves. A non-nacreous complex crossed-lamellar aragonitic layer is usually present internally, proximal to the pallial line.

Anomioideans are more or less edentulous. The ligament is calcified and aragonitic, and is alivincular in all but some Palaeozoic forms. There is a fibrous resilium that has migrated internally due to the coiling of the young shell. The fibrous part of the resilium is continuous between the valves. It lacks lamellar interruptions and is associated with the crural ridges.

Anomioideans are monomyarian, with a posterior adductor muscle lying within the pallial line. This pallial line is obscure, simple and non-sinuous. Only a small section of the adductor is composed of non-striated catch muscle fibres, and adduction is actually achieved by the contraction of a larger byssal retractor muscle. The 'quick' portion of the adductor muscle is responsible for rapid shell closure to achieve pseudofaecal rejection from the posterior region of the mantle cavity. The foot functions in cleaning the mantle cavity, and, in most forms, in producing a byssus which is fine and flexible, or calcified and aragonitic (Kennedy *et al.* 1969).

There is no ventral fusion of the pallium. The innermost pallial fold is edged with series of extensible tentacles forming a pallial curtain. There are no eyes on the pallial folds but, in some groups, there are eyes in the more central part of the mantle. The gills are eleutherorhabdic and some forms have eyes on the first gill filament. The oral lips are simple and the stomach is of Purchon's (1957) Type IV, with a large gastric shield. The major typhlosole lacks a tongue extending into the food-sorting caecum, and the very long crystalline-style sac is separate from the short midgut. Anomioideans lack a definite pericardium so that the ventricle and the auricles are exposed. All species which have been investigated are gonochoristic.

Family Anomiidae

The shells of anomiids are medium to large in size, with subdued sculpture which often reflects the contours of the substratum. They are usually variable in colour. The shells are rounded to ovate in outline, being flat or folded and inequivalve. Except for *Enigmonia* in which an uncalcified byssus is retained, all forms are attached, though not necessarily permanently, by a calcified byssus. Anomiids are pleurothetic on the thinner right valves which are pierced by sub-umbonal byssal notches or foramina (Fig. 6.20). These notches may be small to moderate in size, opening as slits to the dorsal margins, as in *Anomia* and in *Patro*, or they may be very large as in the genus *Monia*. The dorsal margins of the notches are fused without a sutural ridge in *Placunanomia*, but are fused with a ridge in *Pododesmus*. The umbones of the left valves are displaced ventrally by the dorsal overgrowth of the pallial lobes and shell, especially in the more or less inequilateral *Enigmonia*.

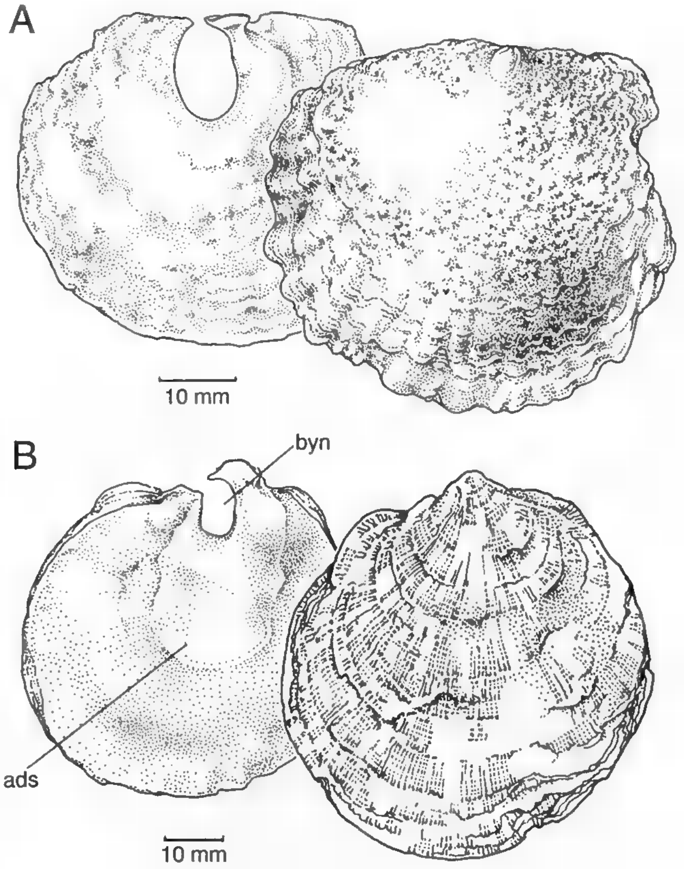

Figure 6.20 Family Anomiidae. Shell valves: **A**, *Monia trigonopsis*, right valve in internal view, left valve in external view; **B**, *Patro australis*, right valve in internal view, left valve in external view. **ads**, area of adductor muscle scars; **byn**, byssal notch. [R. Plant]

The shells of anomiids are delicate and sub-transparent in most forms, with the lower right valve being the thinner (Fig. 6.20). An outer layer of prismatic calcite is rarely present in the left valve, and is often confined to areas near the hinge. There is a prominent layer of foliated calcite, and a proximal inner crossed-lamellar aragonitic layer, which according to Beu (1967) extends up onto the crurum, is absent in some forms. The byssal plug is aragonitic (Beu 1967).

The posterior adductor muscle is relatively small and the right anterior pedal-byssal retractor may be absent. The left anterior pedal retractor muscle attaches with an obscure scar at the posterior end of the resilial scar. The posterior pedal-byssal retractor is usually present and large. It may be divided, with a strong scar or scars on the left valve. The details of these muscles and of their scars on the shell valves distinguish the anomiid genera (Seed & Roberts 1976).

The anomiid hinge is edentate and the valves are joined by an inner fibrous resilium which is supported in the right valve by a chondrophore or crurum. The form of the crurum and the details of the resilial attachment vary generically.

The filibranch gills are asymmetrically disposed in most genera, three demibranchs making contact with the left labial palp and only one with the right palp. They are eleutherorhabdic with their ascending lamellae fused in series or with ciliary junctions. However, in a very few forms the outer demibranchs are unreflected as their ascending lamellae are lacking (Atkins 1937). Hypobranchial glands are present, are very large and separate the ctenidia in *Pododesmus* species. The ctenidia are united along the midline by tissue junctions in some forms, whereas in others ciliary junctions connect the ctenidia anterior to the hypobranchial glands.

Only in *Enigmonia* species is the foot used for locomotion. In most other forms it is used to clean out the pallial cavity.

The gut is, in general, fairly short. Its basic bilateral symmetry is lost to different extents due to the pleurothetic habit. In some forms the lips and palps are much longer on the right side and the mouth is displaced to the right of the midline. The right outer palp curves around the posterior and dorsal surfaces of the byssal retractor muscle and merges with the thin upper lip which folds over the lower lip. This allows the escape of water, which then flows out through the dorsal byssal notch (Gilmour 1974). In other forms the mouth, with its labial palps, is twisted to the right and may be displaced to a more posterior position. In these forms, the anus is usually attached to the right mantle lobe. These modifications are associated with the loss of the right anterior pedal retractor and so with the loss of bilateral symmetry (Yonge 1977, 1980). The crystalline style is long and delicate but well developed. A long, separate style sac extends into the substance of the right mantle lobe in some forms, but in *Patro* the style sac describes a complete circle. The midgut is not coiled, the orifices of the digestive diverticula are scattered, and the anal end of the rectum is free and erectile.

The heart has two auricles, and a ventricle which is dorsal to the rectum. There are pericardial glands in the auricular walls, and there is usually only a single aorta. The renogenital system is very asymmetric, particularly in those forms such as *Anomia* in which lateral compression is marked and in which the visceral mass is concentrated posteriorly. It is larger on the left side where there is a common urinogenital pore. In the more symmetrical *Enigmonia* the left gonad is much larger. In New South Wales, gametogenesis in *Anomia descripta* commences in winter, with a minor spawning peak in summer when the temperature is rising, and a major spawning peak in autumn when a phytoplankton bloom, which is likely to act as a cue, occurs (Hadfield & Anderson 1988). In New Zealand, *A. trigonopsis* spawns in summer (Booth 1983).

The nervous system is asymmetric, with the right cerebropedal connective being longer than the right and the visceral ganglia lying anterior to the adductor muscle. A branchial eye is often present on the first left gill filament. In *Enigmonia* unique pallial eyes are present on the proximal part of the left pallial lobe beneath the semi-transparent left shell valve.

The subfamily Anomiinae contains the genera *Anomia*, *Patro* and *Enigmonia* in which the right valve lacks radial sculpture and the posterior pedal retractor muscle is present, so that three muscle scars are located on the left valve. Indo-West Pacific species of the genera *Patro* and *Enigmonia* are represented in the fauna of the northern Australian coasts. The plug is fused to the substratum only weakly in *Patro* but is firmly fixed in *Anomia descripta*, an endemic Australian species common in eastern Australian estuaries and along the southern coasts of Australia, in weed beds and along rocky shores. *Enigmonia* is limpet-like and has a partially plantar foot with a long flagellum that is protruded through the foramen. It is a motile form moving around upon mangroves and other vegetation, and is tolerant of long periods of emersion (Morton 1976). Its variation in shell colour according to its substratum has been discussed by Sigurdsson & Sundari (1990).

The subfamily Placunanomiinae contains the genus *Monia*; the posterior pedal retractor muscle is lacking and as a consequence of which the left valve has only two muscle scars. The upper scar, the byssal retractor, is usually larger and radially wrinkled, and both valves are radially wrinkled (Beu 1967). The fossil record of this group goes back to the Cretaceous and perhaps even to the Permian. *Monia* occurs from the Pliocene to the present day in southern Australia and New Zealand (Beu 1967). *Monia tatei* is an Australian Pliocene species from south-eastern Australia. The southern Australian *Monia trigonopsis* is a fouling species in Western Australia, where it flourishes inside water-uptake pipes – as do related species in similar habitats in Europe.

Family Placunidae

Placunids have medium to large shells, which may be smooth with wide radial folds, or ornamented with very fine radial ribs crossed by commarginal growth lines or by lamellae or plicae (Fig. 6.21A, B). The shells are circular in outline, are superficially equivalve, and are compressed, particularly in *Placuna*. The valves are of similar thickness, and the umbones are usually marginal.

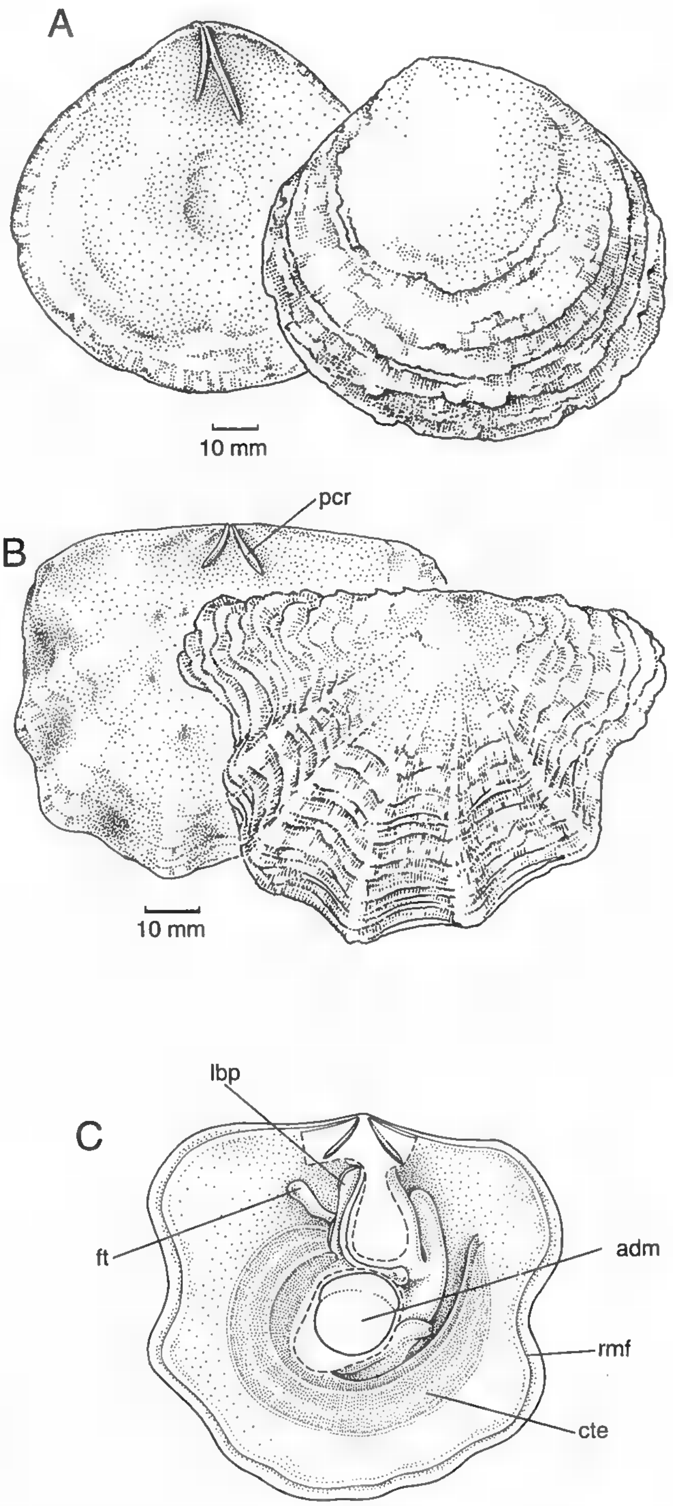

Figure 6.21 Family Placunidae. Shell valves: **A**, *Placuna placenta*, right valve internal view, left valve external view; **B**, *Placuna lobata*, right valve internal view, left valve external view. **C**, *Placuna lobata*, organs of the mantle cavity, left shell valve and mantle lobe removed. **adm**, adductor muscle; **cte**, ctenidium; **ft**, foot; **lbp**, labial palps; **pcr** posterior crural ridge; **rmf**, right mantle folds. [R. Plant]

Except during a brief period following settlement, the shell neither has a byssal notch, nor is it byssally attached. The alivincular primary ligament is internal and attached to the non-stalked crural ridges arranged in an inverted V on the right valve. The primary ligament functions only in providing an opening thrust to the valves. The periostracum is continuous with the secondary dorsal ligament which is concerned with the alignment of the valves, and is formed by the hypertrophied dorsal parts of the pallium (Yonge 1977, 1980).

Prismatic and foliated calcite layers are present in both shell valves of placunids; the inner aragonitic adductor layer is absent in the genus *Placuna*. The pallial line is obscure. There is a single, centrally located, circular aragonitic muscle scar in *Placuna*, and a single weak pedal muscle scar.

The pallial organs of *Placuna lobata* are shown in Figure 6.22C. The filibranch gills are virtually symmetrical and are suspended from the visceral mass on very deep membranes. Food grooves are located on the axes and at the tips of the ascending limbs of both inner and outer demibranchs, conforming to Atkin's (1937a) gill Type B(1a). The symmetrical mantle lobes lack photoreceptors, and have a middle fold, which bears tentacles, and a fairly narrow inner fold. The foot is extensible, long and narrow with an expanded tip; in the adult its sole function is to clean the mantle cavity.

The labial palps are relatively large with many sorting ridges. The stomach is of Purchon's (1957) Type IV. The mid-gut is separate from the style sac, which is long and embedded in the right pallial lobe.

The ventricle of the exposed heart is dorsal to the rectum. The kidneys are connected below the heart; the right kidney is slightly larger than the left. The left gonad does not develop and the right gonad surrounds much of the gut and penetrates the right mantle lobe (Hornell 1909). Fertilisation is external and the larvae are pelagic.

Placunids are all non-motile but free-living, and can rest on either valve. The genus *Placuna* is represented by about five species in the Indo-West Pacific region. All are pleurothetic, either on the left or right valve and lie unattached on shallow muddy banks in the Pacific region. *Placuna placenta*, particularly, has been heavily fished in south and South-East Asian waters for use as window panes or for the manufacture of ornaments.

The family Placunidae apparently originated in the Eocene.

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SUBCLASS PALAEOHETERODONTA

CHAPTER 7

DEFINITION AND GENERAL DESCRIPTION

The subclass Palaeoheterodonta is composed of two very distinct orders, the Trigonioida and the Unionoida (Fig. 7.1). The Trigonioida, an exclusively marine group consisting of the family Trigoniidae, is represented in the Recent fauna by the sole genus *Neotrigonia*. The Unionoida, abundant and diverse in North America, is represented in Australia by only the small family Hyriidae, a group of totally freshwater bivalves. There is some debate as to the taxonomic status of this subclass, but the palaeoheterodonts are united by having prismatonacreous shells that are equivalve and inequilateral, have schizodont hinge dentition, usually a thick periostracum, parivincular and opisthodetic ligaments, two adductor muscles with associated pedal retractors, and predominantly free mantle margins with only poorly developed siphonal apertures. With few exceptions, members of both the Hyriidae and Trigoniidae are dioecious. The hyriids produce parasitic glochidial larvae.

Worldwide the subclass embraces over 1200 living species (Boss 1982) in seven families of the Unionoida and one family of the Trigonioida. The Unionoida is represented in the Australian fauna by the family Hyriidae with 17 species (Smith, B.J. 1992), and the Trigonioida by six species in the family Trigoniidae.

HISTORY OF DISCOVERY

Although freshwater mussels were long recognised as a common and important component of lentic and lotic systems worldwide, the taxonomy of the Unionoida remained relatively obscure until fairly recently. In fact, until Simpson (1900) proposed various genera for the Unionoida, all members were placed in the genus *Unio*. Parodiz & Bonetto (1963) revised the taxonomy of the order and produced a classification approximating the one used today. Tate (1889) listed 27 members of the Unionidae from Australia. McMichael & Hiscock (1958) recognised 17 species of freshwater mussels in Australian waters and placed these in the family Mutelidae. The discovery that *Mutela*, the African type genus for the family, lacks a glochidium (Fryer 1954, 1961), forced the removal of the Australian mussels from this family and their placement in the family Hyriidae (Parodiz & Bonnetto 1963). Walker (1981a) noted 17 species in six genera of Unionoidea in mainland Australian and northern Tasmanian waters. In his 1992 catalogue of the non-marine molluscs of Australia, B.J. Smith included the hyriids and gave details on species, synonyms, type data, locality and distributional data, ecological information, and references.

In 1802, François Péron discovered a fresh shell of a trigoniid on a beach in southern Tasmania (see Fleming 1964). The Trigoniidae, common in the Mesozoic, were thought to be extinct. In 1827 Quoy and Gaimard collected living specimens and demonstrated that a group that otherwise underwent a late Cretaceous extinction, had a living relict population in Australian waters. The history of this group is described by Fleming (1964).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The two palaeoheterodont orders are readily distinguishable on the basis of external shell characters. While both are prismatonacreous, equivalve and inequilateral, sculpture can usually be used to separate the groups.

The hyriids have a typical unionoidean form (Fig. 7.1A) and as such are usually elongate, somewhat dorsally keeled, and reach lengths as great as 150 mm. Shells vary greatly in thickness between species and can range from being so thin as to be almost transparent to several millimetres thick. Radial sculpture is often present, at least on the umbones, although this is often eroded away in adult clams. The shells may also have numerous, closely set commarginal lines or ridges, and as a result of living in acidic waters, often have shells with erosion pits, especially located close to the umbones. The internal nacre is often coloured with tints of brown or purple. The periostracum is thick and darkly coloured.

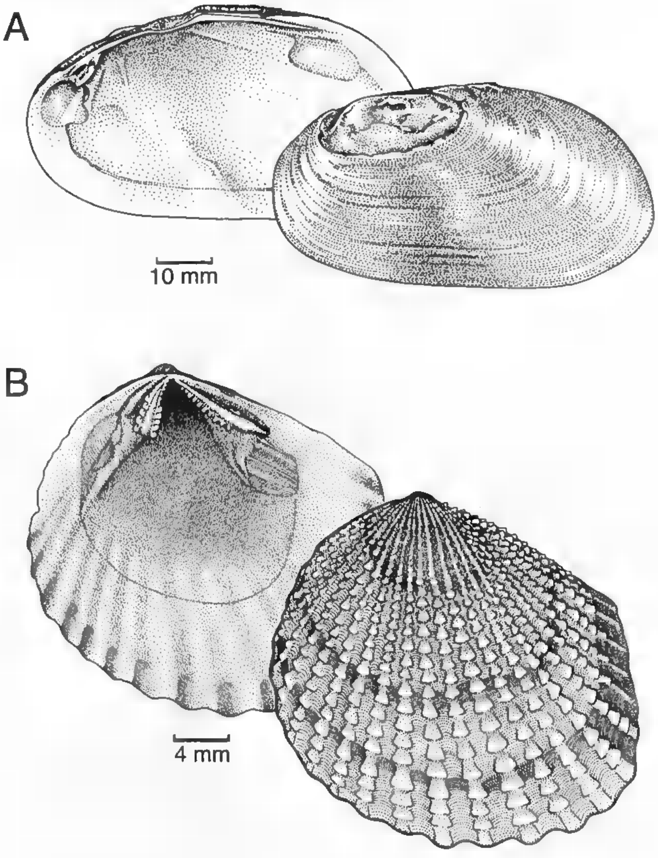

Figure 7.1 Shells of the Palaeoheterodonta. A, Order Unionoida, *Hyridella drapeta*, a common hyriid of coastal southern Queensland, New South Wales and eastern Victoria. B, Order Trigonioida, *Neotrigonia bednalli*, a trigoniid from Western Australia. [A, R. Plant; B, C. Eadie]

The extant trigoniids are generally smaller than hyriids and rarely exceed 40 mm in length. They typically have ovate to subcircular shells that are also prismatonacreous (Fig. 7.1B). The exterior, however, may have radial ribs, scales or truncate spines formed by the distal margins of the outer shell prisms. The thick brown periostracum typically remains intact in these marine bivalves. Internal muscle and pallial scars are well defined in both families.

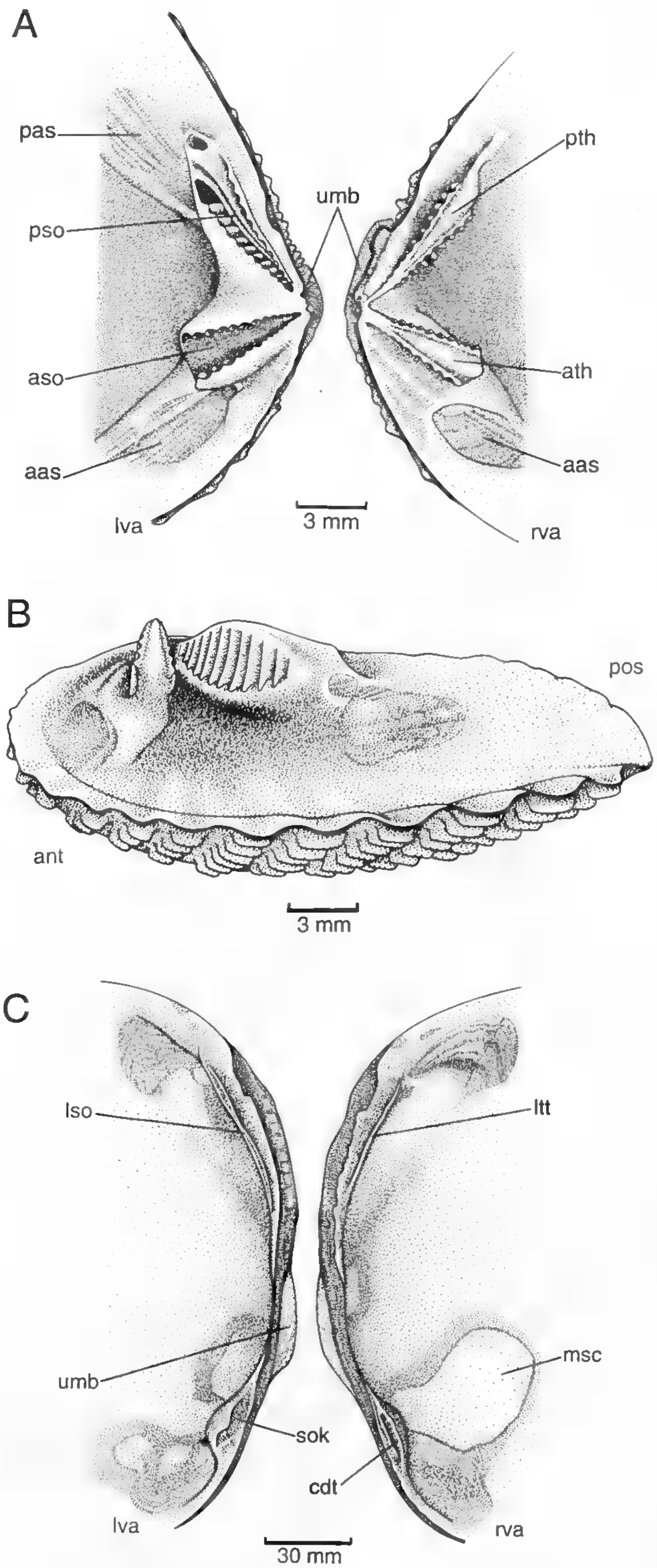

Figure 7.2 Hinge dentition. A, B, *Neotrigonia bednalli*: A, details of left and right valves; B, right valve, oblique view, showing the depth of the hinge teeth. C, *Alathyria condola*, details of left and right valves. **aas**, anterior adductor muscle scar; **ant**, anterior; **aso**, anterior tooth socket; **ath**, anterior tooth; **cdt**, cardinal tooth; **lso**, lateral tooth socket; **ltt**, lateral tooth; **lva**, left valve; **msc**, muscle scar; **pas**, posterior adductor muscle scar; **pos**, posterior; **pso**, posterior tooth socket; **pth**, posterior tooth; **rva**, right valve; **sok**, socket; **umb**, umbo. [C. Eadie]

Palaeoheterodonts are commonly schizodont (Fig. 7.2), although some Unionoida lack hinge teeth altogether. The primary dentition of *Neotrigonia* consists of very large teeth that are involved with alignment of valves (Fig. 7.2A, B). Secondary dentition, which runs transversely on the primary hinge teeth, helps to reduce abrasion that would result from the wide adduction that allows protrusion of the large, muscular foot in the Trigoniidae (Stanley 1977).

Basic shell form, as well as microstructural components of the shell, may be modified by the environment. Water current velocity, temperature, salinity and organic content all may influence the final form of the shell. Environmentally induced variation in the overall shell form of Australian Hyriidae has been described by Walker (1981a).

Body Wall

The mantle hangs free laterally in the palaeoheterodonts and terminates in the three folds typical of bivalves. The only area of fusion of the left and right mantle edges is along the posterior siphonal regions. Here fusion may merely be in the form of a narrow septum that separates the inhalant and exhalant regions. Only rarely in some Unionoida are short siphons developed. The trigoniids typically have a fringe of short tentacles that surrounds the mantle edge (Fig. 7.3). These 'tentacles' elongate along the inhalant aperture where they may function in straining debris, preventing fouling of the mantle cavity and ctenidia, or serve a sensory function.

Locomotion

Palaeoheterodonts are infaunal. Trigoniids, using their muscular foot, are capable of reburial if exhumed from life position (Tevesz 1975). Stanley (1977) has shown that the ornamentation of the shell exterior in the Trigoniidae aids in burial. Trigoniids, like most unionoids, are sedentary as adults and remain buried at about a 45° angle in the sediment with only the posteriormost region of the shell and siphons exposed. All appear capable of repositioning themselves within the substratum to a limited degree and some appear capable of slow burrowing using their compressed, but elongate foot. A byssus is present only in juvenile palaeoheterodonts (Cotton 1961).

Feeding and Digestive System

It is presumed that the palaeoheterodonts are filter-feeders that use their ctenidia to sieve food particles from the inhalant flow of water (Morton 1983). The Trigoniidae have a short oesophagus that leads to a type IV stomach (Purchon 1958). The labial palps (and stomach type) of trigoniids and the Unionoida are similar. Both ctenidia and palps have ciliated tracts that lead to the mouth. The feeding currents produced by cilia of the mantle, ctenidia, labial palps and stomach were described by Avelar & Santos (1991) for a South American hyriid, *Castalia undosa undosa*. In the Trigoniidae the stomach has three large depressions that accommodate the numerous openings from the tubules of the digestive diverticula. Little is known of the digestive physiology or feeding behaviour of these bivalves.

Circulatory System

White (1942) and Morton (1987) have described the trigoniid cardiac system as being of typical bivalve form, consisting of a medial ventricle and associated lateral auricles. Aside from descriptive work and some reports of cardiac function in North American unionids, little is known of the form and function of the palaeoheterodont circulatory system. Because of the relatively large size of these molluscs and the robustness of the cardiac tissue, the mechanisms involved in heart innervation and circulatory flow for members of the Unionidae have been examined (Pecsi 1968; Pujol 1968; Brand 1972, 1976). These are reviewed by Jones (1983).

Respiration

Palaeoheterodonts are suspension-feeders that use their ctenidia as food catchment sieves and hence it is difficult to separate the respiratory functions of the ctenidia from feeding functions. Several different ctenidial arrangements occur in the group. The ctenidia of the Trigoniidae are 'filibranch'. In this gill type the adjacent ctenidial filaments are linked laterally by thin and short cilia. The trigoniid ctenidia are homorhabdic and non-plicate. The individual gill filament of *Neotrigonia* is unique with a rounded apical 'head' that tapers into a stalk-like region towards the remainder of the filament (Fig. 7.4). This structure was first described by Ridewood (1903) and a discussion of its phylogenetic significance is offered by Morton (1987).

The ctenidia of the hyriids are synaptorhabdic with inner and outer demibranch interlamellar septa formed as incomplete water tubes that run in parallel with the filaments. Unionoida have one or both demibranchs in the females modified as marsupia. Only the inner demibranch of hyriids serves such a function and no such modifications are found in the Trigoniidae.

Excretion

Even though the first proof of a filtration function for the bivalve kidney came from a unionid (Picken 1937), the excretory system of palaeoheterodonts has received little attention. Because unionids are freshwater and trigoniids marine, it would be expected that the physiological features of the excretory system of these two groups would differ significantly. Trigoniids are most likely to be osmoconformers, as are many of the marine bivalves studied (Khan, Ashton & Saleuddin 1986).

Freshwater bivalves often live in environments with very low ionic concentrations and face the osmotic problems associated with continuous water influx. To solve these, unionids osmoregulate by producing very dilute urine and actively taking up ions in resorptive kidney tissues. In *Anodonta* (family Unionidae), and probably other freshwater unionids, the ability to produce copious amounts of hypotonic urine is related to the large area of tissue modified as pericardial gland (Andrews 1988). *Anodonta* has a filtration rate of up to 0.34 μm/min/g (Potts 1954). The fine structure of an osmotically stressed North American unionid (*Anodonta* sp.) was examined by Khan *et al.* (1986). Hiscock (1953a, 1953b) examined osmoregulatory capabilities of the Australian unionid *Hyridella australis*.

Brief descriptions of the trigoniid excretory systems are given by White (1942) and Morton (1987). In *Neotrigonia margaritacea*, pericardial gland tissue is evident on the auricles and pericardium. The kidneys proper are fed from renopericardial ducts arising from the postero-ventral margins of the pericardial cavity. Nephridiopores open into the suprabranchial chamber. Potts (1967) suggested that a 'prourine', formed by ultrafiltration across the pericardium and heart tissue, passes into the kidneys for urine production. More recent evidence suggests that 'prourine' is actually formed by ultrafiltration through kidney tissue (Saleuddin, Farrell, Gomot & Khan 1983).

Sense Organs and Nervous System

No information is available on the nervous and sensory systems of Australian palaeoheterodonts. Palaeoheterodonts in general have a typical bivalvian nervous system composed of cerebral, pedal and visceral ganglia and associated connectives.

The osphradial complex of a North American unionid is described by Kraemer (1981). The siphons or siphonal apertures are variably elaborated with short sensory tentacles or papillae.

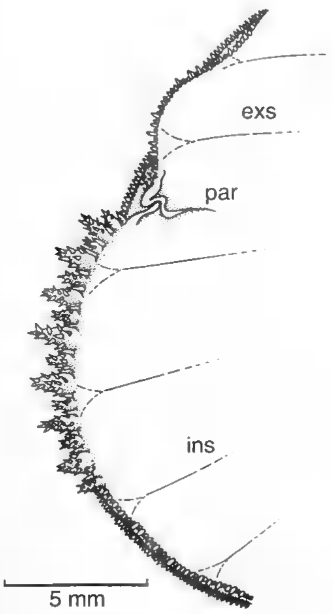

Figure 7.3 Left posterior mantle margin of *Neotrigonia margaritacea* showing the inhalant and exhalant 'siphons'. **exs**, exhalant 'siphon'; **ins**, inhalant 'siphon'; **par**, pallial ridge. (After Morton 1987) [I. Hallam]

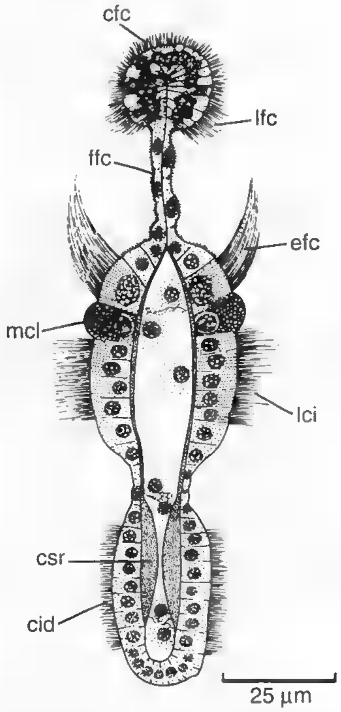

Figure 7.4 A gill filament of *Neotrigonia margaritacea*, in cross-section, showing the arrangement of cilia. **cfc**, coarse frontal cilia; **cid**, ciliated disc; **csr**, chitinous rod; **efc**, eulaterofrontal cilia; **ffc**, fine frontal cilia; **lci**, lateral cilia; **lfc**, long frontal cilia; **mcl**, mucous cell. (After Morton 1987) [I. Hallam]

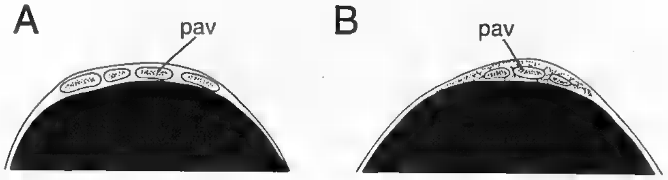

Figure 7.5 Comparative sperm acrosome ultrastructure: **A**, *Neotrigonia* sp.; **B**, *Velesunio* sp. **pav**, proacrosomal vesicles. (After Healy 1989) [I. Hallam]

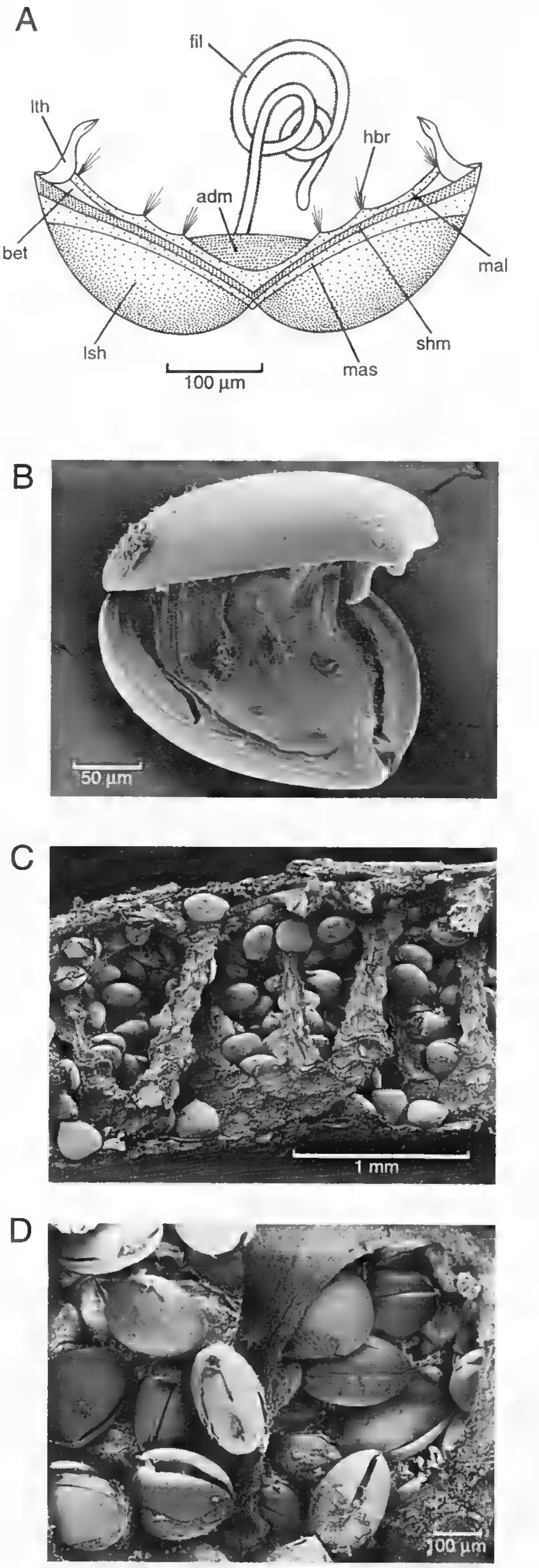

Figure 7.6 Glochidial larvae. **A**, *Velesunio ambiguus*. **B–D**, *Hyridella depressa*: **B**, a gaping glochidium showing larval teeth; **C**, glochidia in the modified gill or gill marsupium; **D**, glochidia nestled in pouches of gill. **adm**, adductor muscle; **bet**, basal expansion of shell; **fil**, filament; **hbr**, sensitive hair brushes; **lsh**, larval shell; **lth**, larval tooth; **mal**, mantle of larva; **mas**, marginated area of shell; **shm**, striation of shell margin. (A, after Parodiz & Bonetto 1963) [A, C. Eadie; B–D, S. Jupiter & M. Byrne]

Reproduction and Development

The Trigonioida and Unionoida are typically dioecious; however, some North American unionids have been reported to be hermaphroditic (Van Der Schalie 1966; Downing, Amyot, Pérusse & Rochon 1989). *Neotrigonia* has external fertilisation and development (Tevesz 1975) whereas unionoids have internal fertilisation and brood their young within a ctenidial marsupium (Fig. 7.6B–D). Because of the complex life cycles of the freshwater mussels, it is likely that there is synchronisation of the various aspects of reproduction to ensure success. Coordination of reproductive events, including gamete production, larval development, glochidial release and parasite-host interactions within the Unionoida are reviewed by Heard (1992).

Healy (1989) recently examined sperm structure in *Neotrigonia* from South Australia and New South Wales, and found that along with Unionoida from Queensland (*Velesunio ambiguus*), trigoniids have a blunt apical cap with up to three acrosomal vesicles (Fig. 7.5). Multiple vesicles, thus far, have only been found in the sperm of *Neotrigonia* and unionoids, lending support to the presumed relationship between these two groups.

The glochidia (Fig. 7.6) of Australian hyriids are poorly known. There have been very few detailed examinations of larval development of any Australian hyriid or trigoniid other than Atkins' (1979) description of the larval form and host relationships of *Hyridella drapeta* from Diamond Creek, Victoria, and Jones, Simpson & Humphrey's (1986) study on the glochidia and reproductive cycles of some hyriids of the Macleay River in northern New South Wales.

Jones *et al.* (1986) found that gametogenesis in *Cucumerunio novaehollandiae* occurred year-round with mature gametes being particularly abundant from January through August. After a nine week brood period, glochidia were released from mid-May through July upstream and from June to August in the lower reaches of Macleay River. Jones *et al.* (1986) suspected that environmental parameters, such as water temperature or water runoff, are responsible for shifts in spawning and the breeding season of the Macleay River population of *C. novaehollandiae.* These same authors found that the brooding period for various species of *Hyridella* in the Macleay River varied from eight to eleven weeks depending upon water temperature. Atkins (1979) found glochidia of *Hyridella drapeta* parasitising fish in coastal Victorian streams throughout the year, but with the highest concentrations in the spring. Studies by Percival (1931), Atkins (1979), and Jones *et al.* (1986) indicate that *Hyridella* is characterised by a long breeding season.

The success of unionids depends upon glochidia using fish, or rarely, tadpoles or salamanders (Howard 1951; Walker 1981a), as intermediate hosts. Various mechanisms are employed by unionids to ensure this success. Some North American unionids modify a portion of the mantle as a lure to attract potential host fish. *Hyridella australis*, in common with many North American unionids (Kat 1984), produces conglutinates of glochidia that form vermiform strands (Jones *et al.* 1986). These presumably resemble worm-like prey and clearly enhance the chances of contact with a 'predatory' host.

The glochidium larvae are usually subtriangular in outline, measuring about 0.3 mm long and 0.2 mm high. The glochidia of *Cucumerunio novaehollandiae* are more rounded in form and are exceptionally small, measuring only 64 × 55 µm (Jones *et al.* 1986). The mid-ventral margin of each larval valve has one or two, usually recurved, attachment teeth (Fig. 7.6A, B). The glochidium has a well-developed adductor muscle that enables the valves to close rapidly. It was previously thought that the glochidia of Australian hyriids show only minor variation in size and form (Walker 1981a), but Jones *et al.* (1986) documented significant variation in the size and shape of Australian glochidia, in particular with regard to larval shell hooks and general shell shape.

NATURAL HISTORY

Life History

Trigoniids presumably have veliger larvae that develop entirely externally in the sea. Hyriids, on the other hand, produce parasitic glochidial larvae that complete their development attached to host fish. Walker (1981a) reported spring and late summer reproductive peaks for *Velesunio ambiguus*. Hyriid glochidia, as noted previously, are typically released in strands of mucus produced by the brooding parent. The larvae remain attached to the mucoid strand by a 'larval thread'. Glochidia attach by the larval teeth to the gills, nares and epithelia of host fish. The larvae are encysted by a thin epithelial layer produced by the fish. In its natural range, *Hyridella drapeta* attaches to blackfish and galaxiids (Atkins 1979). Hiscock (1951) found about 100 glochidia of *Velesunio ambiguus* attached to callop, *Plectoplites ambiguus*. Larvae can exist extramarsupially for up to two weeks. The glochidium remains encysted for up to three weeks before it excysts and falls to the stream bottom as a juvenile mussel. Walker (1981a) listed known host fish of hyriid glochidia from the Murray–Darling catchment.

Ecology

All living trigoniids are restricted to coastal and continental shelf marine Australian waters where they occur in sand or mixed sand-mud substrata to depths of 400 m, although they are most common between 3 and 100 m (Tevesz 1975; Stanley 1984; Darragh 1986). *Neotrigonia margaritacea*, partially buried in the substratum, often has sponge epibionts on the exposed portion of its shell.

Hyriidae are found in most Australian river systems as well as in some lentic environments, such as lakes, billabongs and dams (Smith, B.J. & Kershaw 1979). The distribution of freshwater mussels is regulated by various environmental and biological factors including sediment type (Harman 1972; Salmon & Green 1983), food supply (Pequegnot 1961), bed slope (James 1985), presence of ripples (Cvancara 1970), sedimentation rate (Coon, Eckblad & Trygstad 1977) and presence of appropriate fish hosts (Strayer, Cole, Likens & Buso 1981). They usually prefer stable sandy or muddy bottoms and are rarely found on unstable sand substrata or on exposed hard bottoms. Remarkably, some hyriids are able to withstand long periods of desiccation, usually remaining buried in a coat of mud during drought (Ch'ng-Tan 1968). Williams (1980) reported that a specimen of *Velesunio wilsonii* survived five years 'in a box without water'.

Behaviour

Macpherson & Gabriel (1962) related that a specimen of *Neotrigonia margaritacea* 'leapt overboard, clearing a ledge of four inches' when placed on deck after being collected. The functional morphology of their muscular and glandular foot was described by Gould (1969). The burrowing behaviour of *N. gemma* has been described by Tevesz (1975). *Neotrigonia gemma* typically is found with the posterior valve region just above the sediment surface. An active byssal gland is present in juvenile *N. margaritacea* but is inactive in adults (Gould 1969).

There are few reports that concern living trigoniids. Morton (1987) examined ctenidial current patterns in *Neotrigonia margaritacea*. Stanley (1977, 1978) described the basic functional morphology of *N. margaritacea* based on observations of living laboratory specimens.

Economic Significance

Although they form an important component within the overall ecosystem, hyriids and trigoniids have little direct economic significance. Some hyriids, such as *Velesunio ambiguus*, have been used as a food source by Aboriginal people (Smith, B.J. & Kershaw 1979). Certain unionids have been used as indicator species to monitor inorganic pollution (Havlik & Marking 1987) in North America; as nuclei for cultured pearls in Japan; and historically as 'mother-of-pearl' for production of buttons (Williams 1980). Jones & Walker (1979), Millington & Walker (1983) and Walker (1986) discussed the use of *Velesunio ambiguus* as a monitor of metal pollution. Trigoniids are commonly called brooch clams and, because of their iridescent nacre, are used in jewellery (Abbott & Dance 1982).

BIOGEOGRAPHY & PHYLOGENY

Distribution

The distribution of Trigonioida is restricted. With a single exception (*Neotrigonia novaguineana* from the Late Tertiary of New Guinea; see Darragh 1986), all species of *Neotrigonia* are known only from Australia. They are recorded from many localities along most of the Australian coast-line.

The Unionoida are nearly worldwide in distribution, being absent only from the Antarctic continent, but hyriids are found only in South America and Australasia. The distribution of Australian freshwater mussels is detailed by McMichael & Hiscock (1958), B.J. Smith & Kershaw (1979) and Walker (1981a). Hyriids are dispersed as glochidial larvae by fish and a few crustaceans, and as adults by birds (Cotton 1961). Walker (1981a) reviewed the province concept as it applies to freshwater mussels of Australia. The concept, developed for Australasia by Iredale & Whitley (1938), appears not to hold for Australia where the overlap of species is too great to distinguish specific 'Provinces'. Regional distribution of hyriids is reviewed by Keast (1981). Walker (1981a) determined that hyriid diversity is greatest in south-eastern Australia and New Guinea, and that there are 29 species of freshwater mussels in Australia, New Guinea and New Zealand. Of six genera (with 17 species) of freshwater mussels occurring in Australia, only *Lortiella* (with two species) is unique to Australia. Of the remaining 15 hyriid species of continental Australia and Tasmania, 13 are endemic.

Affinities with other Groups

The palaeontological history of trigoniids was reviewed by Fleming (1964; 1987). The Tertiary fossil beds of Victoria, South Australia and Tasmania have allowed us to chart in some detail the history of Australian trigoniids over the past 60 million years. Trigoniids underwent a wide radiation in the Mesozoic and occurred throughout the world's oceans with a concentration in the Tethyan realm (Stanley 1977). It is likely that the Trigoniidae arose from the Myophoridae (Douville 1912; Newell 1969; Stanley 1977, 1978). McMichael & Hiscock (1958) discussed the phylogeny of Australian hyriids. Fossil material is rare. It does appear, however, that the Velesunioninae, the most primitive living hyriid subfamily, are also the most widely distributed in Australia (Walker 1981a). Ludbrook (1961) described Mesozoic unionids from South Australia.

Affinities within the Taxon

The Trigoniidae are today represented by a small number of species (McMichael 1956; Habe 1985), all restricted to Australian waters. Darragh (1986) suggested that during the Cainozoic the family comprised two genera, *Eotrigonia* and *Neotrigonia* (Fig. 7.7), and supported Cossmann's (1912) suggestion that *Eotrigonia*, with five species all confined to southern Australia, gave rise to *Neotrigonia* in the Oligocene or Early Miocene. *Neotrigonia* contains 10 species, with six extant members (Darragh 1986). *Eotrigonia* in turn probably arose from *Trigonia sensu stricto* in the Late Cretaceous or Early Tertiary.

There is considerable debate over the placement of trigonioids and unionoids within the same subclass. Newell & Boyd (1975) suggested that trigonioids gave rise to unionoids through the now extinct Pachycardiidae. The two orders are united by mainly shell characters. In particular, both have an aragonitic, prismato-nacreous shell and similar (although perhaps not homologous) schizodont dentition. Gould & Jones (1974) suggested that the closest extant relatives of the Trigoniidae are the Unionoida. Morton (1987), supporting the contentions of Newell (1969), noted significant anatomical differences that cast doubt on the assumed relationship. Instead he suggested that the presently accepted Palaeoheterodonta is an 'artificial' grouping and that the Trigoniidae are more closely allied to the Pteriomorpha. Purchon (1978), following a cladistic analysis, argued that the unionoids and trigonioids should not be placed within a separate subclass Palaeoheterodonta, but instead should be relegated to the subclass Heterodonta. Recently Healy (1989) found great similarities in the sperm ultrastructure of *Neotrigonia* and some unionoids, again suggesting a phylogenetic link. The argument remains unresolved.

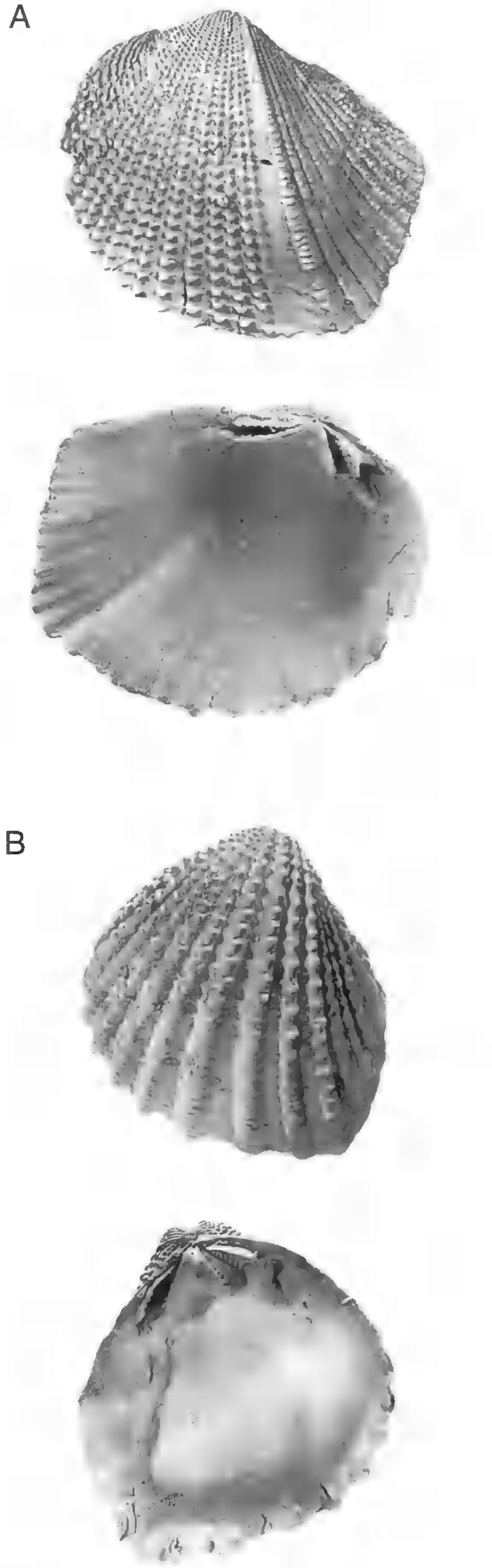

Figure 7.7 Fossil Trigoniidae. A, *Eotrigonia eocenica* of the Late Eocene from Browns Creek Clay, Aldingan Formation, Victoria; **B**, *Neotrigonia medipontea* of the Late Pliocene from the Norwest Bend Formation, South Australia. (From Darragh 1986)

FOSSIL HISTORY

The fossil record of the Trigoniidae is rich and diverse (see Darragh 1986), and that of the Hyriidae is relatively sparse (Walker 1981a). Although the Trigoniidae were widespread and diverse during the Mesozoic, the only genus recorded from the early Cainozoic is *Eotrigonia* among the Trigonioidea, which survived to the late Miocene in southern Australia. Darragh (1986) presented a detailed review, with localities, of Australian Cainozoic trigoniids. Reviews of the fossil Unionoidea of Australia are found in McMichael (1956) and in Ludbrook (1961).

CLASSIFICATION

The Palaeoheterodonta is a mixed group of bivalves composed of the freshwater Unionoidea and the marine Trigonioidea (see Table 7.1). Within the latter, only the family Trigoniidae, represented by the single genus *Neotrigonia* is still extant. The Hyriidae are the only family of Unionoidea in Australia. The much larger family Unionidae, concentrated in North America, as well as the less diverse Margaritiferidae, are both absent from Australian waters. The following classification is after Parodiz & Bonetto (1963), modified by Boss (1982).

Table 7.1 Family classification of extant Palaeoheterodonta. Families indicated by an asterisk have not been recorded from Australia.

Subclass PALAEOHETERODONTA
Order TRIGONIOIDA
    Superfamily TRIGONIOIDEA
        Family Trigoniidae
Order UNIONOIDA
    Superfamily UNIONOIDEA
        Family Margaritiferidae*
        Family Unionidae*
        Family Hyriidae
    Superfamily MUTELOIDEA
        Family Mutelidae*
        Family Mycetopodidae*
        Family Etheridae*

Order TRIGONIOIDA

The order Trigonioida is represented by the single superfamily Trigonioidea. The characters of the order are those of the superfamily. In summary, the shell is ovate to subcircular, with a prominent dorsal keel, often with radial ribs, scales, or spines, and usually a thin brown periostracum; the umbones are mostly directed posteriorly; and the ctenidium is filibranch. All species are marine.

Superfamily TRIGONIOIDEA

Trigonioidean shells are equivalve, and generally trigonal in shape, but ovate or rhomboidal in some groups, with the posterior generally truncate. The posterior slope of the shell is carinate or subcarinate, and may be smooth or sculptured. The ligament is external, short and opisthodetic. The hinge teeth radiate from the umbo (beak). The left valve has generally strong median teeth and the right valve has two slightly weaker teeth. Additional and weaker teeth may be present in both valves. The adductor scars are small, and are situated close to the hinge teeth, in many groups with the anterior scar in each valve bordered on its inner side by a strong buttress. The pallial line is entire and the shells are internally nacreous.

The Trigonioida comprises eight families; only one, the Trigoniidae, has living representatives (Newell & Boyd 1975).

Family Trigoniidae

Shells of the family Trigoniidae are small to large in size (5–200 mm), triangular to subquadrate in outline, and generally are opisthogyrous, but ortho- and prosogyrous in some groups. The posterior area and flank sculpture are differentiated in most genera, with the flanks having commarginal or oblique sculpture and the posterior area, radial sculpture. The left valve has a prominent strongly grooved bifid tooth, and the right valve has two weaker strongly grooved divergent teeth not borne on the hinge plate. The anterior myophorous buttresses are well developed. The pallial line is entire, and the shells are internally nacreous.

The morphology, functional biology and fossil history have been well documented by recent studies (Gould 1969; Gould & Jones 1974; Newell & Boyd 1975; Tevesz 1975; Stanley 1977; Darragh 1986; Morton 1987). There is only one extant genus, *Neotrigonia*, represented by six extant species all of which are restricted to Australia.

The shells of *Neotrigonia* (Fig. 7.8) are ovate to subcircular, rarely subquadrate, equivalve, strongly inequilateral and covered with a brown periostracum. The flank, posterior area and escutcheon are not prominently differentiated and all bear radial ribs. The radial ribs are generally sculptured with strong or weak scales, spines or tubercles, which may become obsolete towards the margin of the shell. The umbones are small to large, orthogyral, not projecting, and bear a discrepant juvenile sculpture of about eight commarginal ribs on the anterior and middle portions of the flank extending from the prodissoconch for about 1.5 mm, and fine radial ribs on the posterior area. This juvenile umbonal sculpture is similar to that on adult specimens of the fossil genera *Trigonia* and *Eotrigonia* which are believed to be ancestral to *Neotrigonia*. The shell structure consists of three aragonite layers, the outer layer prismatic with each prism terminating in a small concentrically striated boss, the middle layer of lenticular nacre and the inner layer of sheet nacre (Taylor, Kennedy & Hall 1969). The hinge is strong with large schizodont teeth interlocked by ridges and grooves. The tooth formula is right valve n01010; anterior and the left valve i0 10. The pallial line is entire. The internal surface of each valve is prominently furrowed, particularly near the margin, which is strongly denticulate and permits the valves to be interlocked.

The anterior and posterior adductor muscles are situated high in the valves immediately beneath the hinge. The posterior adductor muscle is slightly larger and more rounded than the anterior. The muscle scars on the inner surface of the valves are prominent and the anterior scar is flanked by a narrow hinge plate buttress.

The paired pedal retractor muscles are situated internally and dorsally to the adductor muscles, with the anterior retractor inserted on the face of the hinge plate buttress just above the anterior adductor. The paired anterior pedal protractor muscles are located ventrally to the anterior adductor, and the insertion scar is triangular in shape and situated just below the anterior adductor scar. Paired pedal elevator muscles are inserted in deep pits beneath the umbo. The foot is very large and muscular, and capable of strong and sudden movements. It consists of a column-like mass expanding ventrally into an anchor or plough-like extension. In the foot there is a small byssal apparatus which functions in juveniles, but not in adults (Gould 1969).

The mantle is simple with three folds at its margin. The mantle margins are unfused and lack siphons, but inhalant and exhalant openings are formed by the adpression of two pallial ridges on the inner surface of each mantle lobe. The pallial ridges may be distended with blood from the pallial blood vessel to assist in the separation of the inhalant and exhalant currents during feeding. The free edges of the mantle are fringed on each mantle fold by three parallel series of short tentacles or papillae. At the inhalant area of the mantle the tentacles are large and branched to strain and exclude large debris from entering the mantle cavity, and at the exhalant area of the mantle they are small and simple (Gould & Jones 1974; Morton 1987).

The gills or ctenidia consist of equal lath-like filaments (filibranch), with each gill filament alike (homorhabdic). The gill lamellae are non-plicate and extend beyond the visceral mass. Each gill consists of two demibranchs, the outer of which is shorter dorso-ventrally than the inner. The gill ciliation is similar to that of the pseudolamellibranch families (for example, Pteriidae, Limidae, Ostreidae and Pectinidae), but the presence of differentiated ciliary tracts which result in the gill fulfilling a particle sorting role is reminiscent of the Arcoidea and Anomioidea. The gill of *Neotrigonia* therefore represents a unique condition in the Bivalvia (Morton 1987).

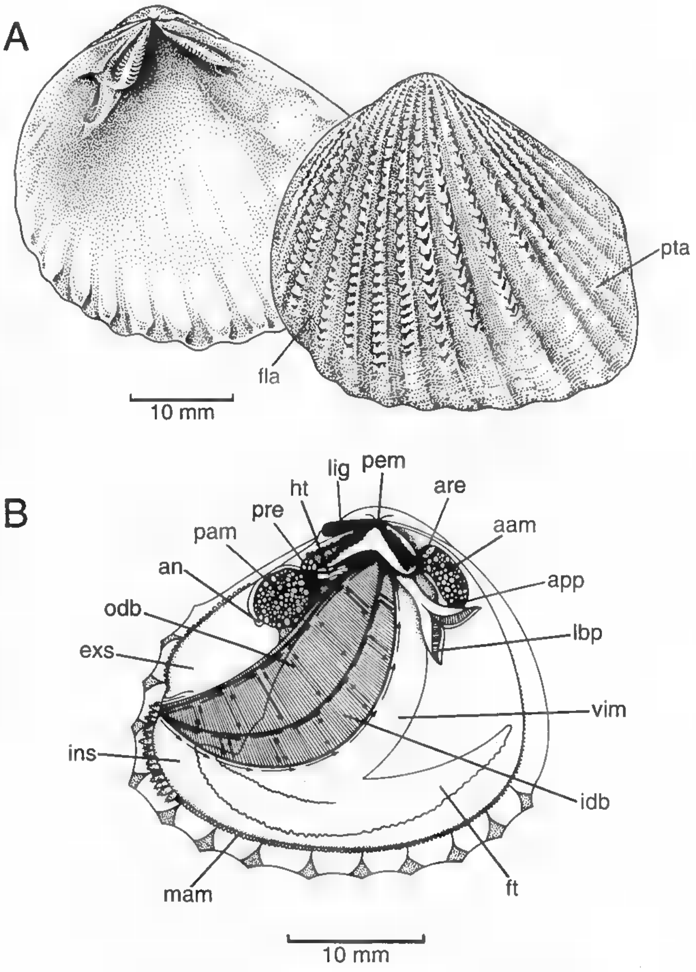

Figure 7.8 Family Trigoniidae. *Neotrigonia margaritacea*: **A**, shell valves, showing the large schizodont teeth which are interlocked by ridges and grooves; **B**, organs of the mantle cavity, viewed from the right side with arrows showing the ciliary currents of the right ctenidium. **aam**, anterior adductor muscle; **an**, anus; **app**, anterior pedal protractor muscle; **are**, anterior retractor muscle; **exs**, exhalant siphon; **fla**, flank; **ft**, foot; **ht**, heart; **idb**, inner demibranch; **ins**, inhalant siphon; **lbp**, labial palp; **lig**, ligament; **mam**, mantle margin; **odb**, outer demibranch; **pam**, posterior adductor muscle; **pem**, pedal elevator muscle; **pre**, posterior retractor muscle; **pta**, posterior area; **vim**, visceral mass. (B, after Morton 1987) [A, R. Plant; B, C. Eadie]

The labial palps are without appendages and only the anteriormost part of the inner demibranch is inserted into the distal oral groove. This arrangement is similar to that in members of the Unionoidea, Pteriomorphia, Heterodonta and Anomalodesmata (Morton 1987).

The oesophagus is short and wide, and opens into the anterior wall of the globular stomach. The stomach is described by Purchon (1957) as belonging to his group IV, which includes the Unionoidea, Pteriomorphia, Heterodonta and Anomalodesmata. The significant characters are the concentration of ducts of the digestive diverticula into three wide embayments, the extreme reduction of the food-sorting caecum, the absence of a well-developed tongue of the major typhlosole, the great development of the dorsal hood and its contained sorting areas, and the great development of the posterior sorting area on the right wall of the stomach. The stomach most closely resembles those of the families Limidae, Pectinidae and Anomiidae of the Pteriomorphia.

The heart is situated in the dorsal mid-line and is traversed by the rectum. It comprises a single ventricle with two wide lateral pouches or bulbs, the posterior of which is very large. The lateral auricles are triangular and very muscular (White 1943; Morton 1987).

The kidneys are paired and elongate with branched sacs, and their apertures discharge ventrally into the suprabranchial part of the mantle cavity. The sexes are separate, the dorsally situated gonads paired. The large eggs are extruded into the mantle cavity through two oviducts opening posterior to the visceral mass above the gills (Tevesz 1975).

Neotrigonia species are highly active, burrowing molluscs which live with the posterior portion of the valves just projecting above the sediment. *Neotrigonia margaritacea* frequently has sponges and other epibionts on the exposed portion of the valves. Watson (1971) observed *N. margaritacea* in the channel system of Western Port, Victoria, where the shells are often scoured out of the sediment by the currents. The muscular foot was used by the animal to right itself and burrow rapidly beneath the sediment. Tevesz (1975) described the rapid burrowing movements of *N. gemma* and *N. margaritacea*, both observed in aquaria. *Neotrigonia* species live in depths ranging from subtidal to 400 m, but are mostly found between three and 100 m.

With the exception of *Neotrigonia novaguineana* from the Late Tertiary of New Guinea, all species of *Neotrigonia* are restricted to Australia, where they have a circum-Australian distribution. One species, *Neotrigonia uniophora*, occurs in tropical Australia; four species, *N. strangei*, *N. lamarcki*, *N. gemma* and *N. margaritacea*, are present on the south-east and east coasts and only one, *N. bednalli*, on the south-west and west coasts.

The family had a cosmopolitan distribution during the Mesozoic and was represented by many genera (Fleming 1987). The earliest Australian record is of *Trigonia* from the Middle Jurassic of Western Australia (Skwarko 1963). About 10 genera are known in the Cretaceous of Australia. All genera became extinct at the end of the Cretaceous except for a single representative, *Eotrigonia*, which survived into the Tertiary. *Eotrigonia*, thought to have derived from *Trigonia* in the Late Cretaceous or Early Palaeocene, ranges into the late Miocene of south-eastern Australia. *Neotrigonia* evolved from *Eotrigonia* in the Oligocene or early Miocene. The oldest known representative of *Neotrigonia* occurs in the middle Miocene (Darragh 1986).

Order UNIONOIDA

The Unionoida is nearly cosmopolitan in distribution and comprises nearly 1200 species, among them the pearly freshwater mussels or naiades. The features of the order are in summary: the shell elongate, often with dorsal keel; the umbonal area frequently eroded and directed forwards; the periostracum well developed, usually brown to black, nacre often coloured; the ctenidium eulamellibranch and modified at least partially as a marsupium; and all in freshwater. The order consists of two superfamilies (after Parodiz & Bonetto 1963; modified by Boss 1982), the Unionoidea, with four families, distributed throughout North, Central and South America, Europe, Africa, South-East Asia and Australasia; and the Muteloidea, with three families, from Africa, India, and Central and South America.

The shell is equivalved, variable in shape from circular to narrowly elongate, and may attain up to 300 mm in length. Some unionoids are circular and subglobular while others are soleniform; members of the Amblemidae are heavy and subtrigonal, whereas the Etheriidae in the Muteloidea are called freshwater oysters because of their shape. The periostracum is well developed, and the shell is aragonitic and nacreous, the interior often richly tinted. The hinge is basically schizodont with many unionoideans having well-developed to heavy cardinal teeth. Most muteloideans are more or less edentulous, sometimes with faint tubercles or taxodont teeth (Haas 1969; Boss 1982).

Unionoids are dimyarian. The mantle opens ventrally and is sometimes fused between the inhalant and exhalant apertures; it is rarely drawn out into siphons except in some unionoideans. The ctenidia are synaptorhabdic (that is, the inner and outer demibranchs have interlamellar septa). In the females one or both demibranchs function as a incubatory marsupium. Unionoids are mainly gonochoristic and ovoviviparous, unionoideans producing a glochidium larva with a calcareous bivalved shell and muteloideans producing a lasidium larva with a non-calcareous univalve shell (Parodiz & Bonetto 1963; Marshall & Williams 1972). Many of these larvae are parasitic, chiefly on fish or freshwater crustaceans. All inhabit either lotic or lentic freshwater.

All Australian members of the order belong to the unionoidean family Hyriidae. The earliest fossil members of the order are recorded from the Triassic of North America.

Superfamily UNIONOIDEA

The Unionoidea contains the entire pearly freshwater mussel fauna of Australasia, North America and Europe, and has some species in Central and South America, Africa and South-East Asia. It comprises four families, the Unionidae, Amblemidae, Margaritiferidae and Hyriidae, and about 1000 species (Parodiz & Bonetto 1963; Haas 1969; Boss 1982). Only the Hyriidae are represented in Australia.

All freshwater mussels were assigned to the genus *Unio* until, in 1900, Simpson subdivided this genus. Parodiz & Bonetto (1963) and later Heard & Guckert (1970) developed the presently accepted classification of the superfamily.

The shell varies in shape from nearly circular to elongate-soleniform to subtrigonal, and in size from 25–300 mm. In the Amblemidae, the shells are heavy and solid whereas some hyriids have very thin, light shells. In some groups the umbones bear V- or W-shaped folds. The shell may be smooth, but sculpture is present in some species and varies from mere growth lines to wrinkles or ribs, to rows of tubercules. The periostracum is well developed and in some groups is thick. The hinge is schizodont, often well developed to heavy, but some unionids have an edentulous hinge. The pallial line is entire and the adductor muscles subequal.

The mantle is broadly open ventrally, but is often fused posteriorly into separate inhalant and exhalant apertures. The ctenidia are synaptorhabdic. In the Amblemidae and Hyriidae, the ctenidia form complete or incomplete water tubes running parallel with the filaments. In the female a marsupium for brooding of developing eggs is formed by one or both demibranchs. Both demibranchs form the marsupium in the Amblemidae and Margaritiferidae, but only the outer demibranch in the Unionidae, and only the inner one in the Hyriidae. Most species are gonochoristic and unionids and amblemids may show shell sexual dimorphism. All are ovoviviparous and produce glochidia with calcareous bivalved shells. The larvae are either parasitic or non-parasitic; the life cycles of most species are unknown. Some glochidia in the Unionidae and Hyriidae bear hooks, the remainder are hookless. Most species in the Amblemidae and Margaritiferidae are tachytictic (fast, short-term breeders).

Several unionid and margaritiferid species have been used commercially (especially in North America) for the manufacture of pearl buttons and similar products, and several species in all four families have been recorded to produce pearls.

Family Hyriidae

This is a family of medium-sized to large (35–150 mm), exclusively freshwater bivalves (Fig. 7.9), commonly called freshwater mussels, with a coloured nacreous interior, a conspicuous periostracum and an elongate-oval shape. The larva is a glochidium with a bivalved calcareous shell that nearly always bears hooks. Hyriids are found in all parts of mainland Australia, northern Tasmania, New Guinea, New Zealand and western and southern South America (Boss 1982). The Australasian fauna was reviewed by McMichael & Hiscock (1958) who gave descriptions of all Australian species. The family placement was clarified by Parodiz & Bonetto (1963). Early works on the Australian fauna include those of E.A. Smith (1882), Cotton & Gabriel (1932) and Iredale (1934, 1943).

The shell is equivalve and varies from roundly ovoid to narrowly elongate, usually has a thick periostracum, and has an inner nacreous layer which is often coloured in browns and purples. Shell thickness varies from genus to genus and between species, and also with the habitat, some shells being almost transparent with very little calcareous material except around the umbones and hinge, others having solid shells up to several millimetres thick. Details of shell variation in a few species are described by Walker (1981b) who also showed that the 'winged' and 'non-winged' shell forms in *Alathyria jacksoni* are distinct growth forms related to current velocity. Most forms have some radial or V-shaped ribbing on the umbones, but many populations show extensive pitting or erosion due to reaction with acidic waters, particularly in the umbonal region. The hinge is schizodont with the central teeth tending to become fissured radially. Periostracum colour varies from pale brown to jet black, again with some correlation with habitat type.

The mantle is broadly open ventrally and fused posteriorly to form separate inhalant and exhalant apertures. The mantle may be fused completely or incompletely below the siphonal apertures forming the posterior portion of the septum. The foot is roundly elongate and used for slow and shallow burrowing in some species. All species use the foot to reposition themselves in the soft substratum in which they live, but some species leave furrows in the substratum indicating active surface movement. The ctenidia are synaptorhabdic, the inner and outer demibranchs have inter-lamellar septa forming incomplete, discontinuous water tubes which run parallel to the filaments. The inner parts of the ctenidia are united with the visceral mass and the demibranchs are in contact with the labial palps anteriorly.

The animal lies partially buried in the substratum at an angle of approximately 45° with the umbones and the posterior part of the shell up to the siphonal apertures clear of the sediment. It is not clear whether food particles filtered from the inhalant stream originate as material suspended in the water or come from the surface of the mud. Complex ciliary tracts on the ctenidia and labial palps entrap the food particles and propel them to the mouth. Small particles or irritation between the mantle and shell can readily cause abnormal deposition of extra nacreous material; small, free, ovoid, coloured pearls occasionally occur, with good examples being known from several of the larger species such as *Velesunio ambiguus* and *Alathyria jacksoni* (B.J. Smith personal observation).

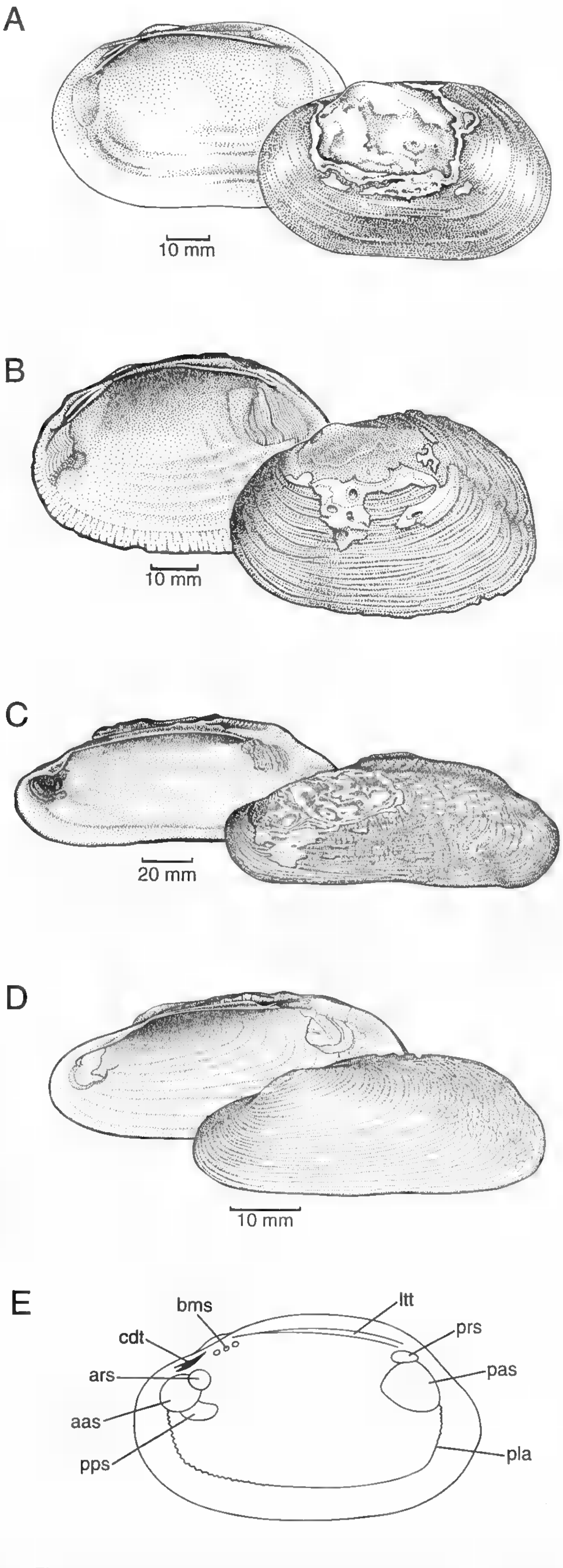

Figure 7.9 Family Hyriidae. **A–D**, shell valves: **A**, *Velesunio ambiguus*; **B**, *Hyridella australis*; **C**, *Cucumerunio novaehollandiae*; **D**, *Lortiella rugata*. **E**, internal shell characters of a freshwater mussel. **aas**, anterior adductor muscle scar; **ars**, anterior retractor muscle scar; **bms**, beak muscle scars; **cdt**, cardinal tooth; **ltt**, lateral tooth; **pas**, posterior adductor muscle scar; **pla**, pallial line; **pps**, pedal protractor muscle scar; **prs**, posterior retractor muscle scar. (E, after McMichael & Hiscock 1958)
[A, R. Plant; B–D, C. Eadie; E, I. Hallam]

Hyriids are gonochoristic, but the shells are not sexually dimorphic (McMichael & Hiscock 1958). In females the inner demibranch is modified as a marsupium to accommodate the developing embryos and glochidia. Fertilised eggs are held in the marsupium until they develop into glochidia. The few glochidia that are known from Australian species are all remarkably uniform in appearance (see Fig. 7.6) (Walker 1981b). The mature glochidium has two subtriangular valves (basal length 0.2–0.3 mm) closed by a single adductor muscle. At the apex of each valve is a small flexible tooth which folds inwards as the shell is closed. The larva trails long sensory and sticky filaments which probably assist in host sensing and attachment. Details of the morphology of the glochidium of an Australian *Hyridella* species are given by Atkins (1979). Enormous numbers of glochidia are released by a female, either all at once or in small clutches, and can survive free in the water for up to two weeks. To develop further the glochidium must then pass through a brief parasitic stage on a fish, tadpole or possibly an aquatic invertebrate, depending on the species. The glochidium attaches to the external surface or gills of the host using the filament and valve teeth and in some way derives nutrients from the host. The host may have an immunity to glochidial attack and absorb the larva. If not the glochidium becomes encysted in the epidermis of the host and remains there for about three weeks undergoing metamorphosis into a juvenile mussel. It then excysts and drops to the bottom to develop. Known details of this process, and a list of the native fish present in the Murray–Darling catchment known to act as hosts to glochidia larvae are given by Walker (1981b).

Studies by Walker (1981b) on *Velesunio ambiguus* have shown that although glochidia may be released at any time of the year, there are two peak release periods, one in spring and another in late summer. The smallest individuals to show marsupium development and contain glochidia were 54–60 mm long and were about 3.5 to 4.5 years old. This species is thought to live for about 11 to 12 years (Walker 1981b). Details of the habitat preferences of species inhabiting the Murray River are given by Walker (1981b) who also showed that the flow regime of the river is the main factor determining species distribution. He described growth and environmental tolerance parameters for those species. Methods of culture and study of several species of freshwater mussels are given by Walker (1981b).

Several species of Australian mussels have been reported as having considerable drought tolerance. Ch'ng-Tan (1968) showed that under conditions of prolonged drought, dissolved substances in the body fluids (blood, pericardial fluid and urine) increase substantially in concentration, with a twofold increase in sodium and potassium, more than a twofold increase in calcium and a fourfold increase in chlorinity. She also reported very large numbers of minute granules concentrated in the tissues of the gills, labial palps and mantle. These were mainly metal phosphates and were probably stored excretory products.

The value of these freshwater mussels for pollution monitoring is equivocal. Millington & Walker (1983) showed that although *Velesunio ambiguus* can take up zinc, iron and manganese from the environment, it would not be a suitable biological monitor as the measured values do not accurately reflect the environmental fluctuations of these metals.

The family contains, worldwide, about 15 genera in six subfamilies (Boss 1982). The Australian fauna consists of 17 species in six genera found throughout mainland Australia and northern Tasmania in most river systems (Walker 1981a; Smith, B.J. 1992). These are placed in four subfamilies. The Velesunioninae include the genera *Alathyria* (*condola*, *jacksoni*, *pertexta*, *profuga*) ranging through eastern mainland Australia and New Guinea, *Velesunio* (*ambiguus*, *angasi*, *moretonicus*, *wilsonii*) distributed throughout Australia, northern Tasmania and north-eastern New Guinea and *Westralunio* (*carteri*) confined to south-western Western Australia and southern New Guinea. The Lortiellinae comprise the genus *Lortiella* (*froggatti*, *rugata*), restricted to north-western Australia. The Hyridellinae include *Hyridella* (*australis*, *depressa*, *drapeta*, *narracanensis*, *glenelgensis*), found in coastal south-eastern Australia and northern Tasmania, New Zealand and south-western New Guinea. The subfamily Cucumerunioninae, with the genus *Cucumerunio* (*novaehollandiae*), occurs in coastal Queensland and New South Wales, and on the North Island of New Zealand.

McMichael (1957) reported on the few records of fossil hyriids in Australia. The earliest records are from the Triassic, but most are from the Upper Cretaceous and Tertiary.

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SUBCLASS HETERODONTA

CHAPTER 8

DEFINITION AND GENERAL DESCRIPTION

The Heterodonta is the largest, most widely distributed and most diverse of the bivalve subclasses (Pls 13.4–16.3). As such it is difficult to define narrowly. Although most heterodonts are marine, many, such as the Corbiculoidea, generally inhabit fresh water. Typically siphonate and dimyarian, heterodonts are mostly filter-feeders with large eulamellibranch ctenidia and correspondingly small palps. Diversity is expressed in the wide array of shell morphologies and sizes, including some of the smallest and the largest clams. They have correspondingly diverse habits, and include free-living, boring and commensal species. Most members of the subclass are united by a 'heterodont' dentition of relatively few, but complicated interlocking hinge teeth, the cardinals and laterals. Shells have some combination of crossed-lamellar, complex crossed-lamellar and/or homogeneous microstructures. The structure of the periostracum is quite variable. The ligament is typically opisthodetic, but some shells have an internal ligament. The mantle margins are often fused, leaving only pedal, exhalant and inhalant apertures. Part of the great success of heterodont bivalves rests with the development of muscular posterior siphons in many taxa, allowing penetration of infaunal habitats. Heterodonts have a Type IV or V stomach (Purchon 1960a) and a rectum that pierces the cardiac ventricle. Most are dioecious and produce planktonic veliger larvae. The heterodonts have a strong fossil record in the Mesozoic, but clearly predate that and extend back into the Palaeozoic.

HISTORY OF DISCOVERY

Although the Heterodonta is the most common and diverse of the bivalve subclasses, there has been surprisingly little published on Australian heterodonts other than field and identification guides. Tate (1889) published a checklist of molluscan genera of Australia, including some 134 genera comprising over 850 bivalve species, most of which are heterodonts. In a plea for a Queensland Biological Station (1910) based on the rich diversity of the region, Charles Hedley included an appendix of the marine Mollusca of Queensland and listed over 350 heterodonts. Additional early lists or notes on Australian heterodonts can be found in Hedley (1914a, 1916, 1917) and Iredale (1929a, 1930a, 1931). Cotton (1934) produced an early list of heterodonts from the Flindersian marine province of southern Australia, and Iredale & McMichael (1962) listed heterodonts from New South Wales. Among the more recent guides outlining the distribution and shell morphology of Australian heterodonts are works by Cotton (1961), Rippingale & McMichael (1961), Macpherson & Gabriel (1962), Wells (1984) and Lamprell & Whitehead (1992). Some basic ecological surveys in which heterodonts play a prominent role include those of Stephenson, Williams & Cook (1974) on southern Moreton Bay; Roberts & Wells (1980) on the Albany area, Wells & Threlfall (1980) on Cockburn Sound, and Slack-Smith (1990) on Shark Bay, Western Australia; and Coleman & Cuff (1980) and Coleman, Cuff, Drummond & Kudenov (1978) on Western Port, Victoria.

Tate (1886) was among the first to examine the fossil bivalves, including heterodonts, of Australia. Chapman & Singleton (1927) examined some Tertiary heterodonts from Fyansford (Victoria) and other Australian sites. More recently there have been some extensive palaeontological works that reveal a rich and informative heterodont history from Australia and New Zealand. These include studies by Ludbrook (1978, 1984), Darragh & Kendrick (1980), and Waterhouse (1987), and from New Zealand, Beu & Maxwell (1990).

MORPHOLOGY AND PHYSIOLOGY

External Features and Shells

The shells of the Heterodonta vary in basic form, microstructure, mineralogy and associated structures. Inequivalve (Chamoidea) (Fig. 8.1) and equivalve (Galeommatoidea, Veneroidea) forms both occur. Shells range from the very small and thin (Galeommatoidea) to extremely large and thick (Tridacnoidea) (Figs 8.19, 8.20). Solenoidea usually have elongate shells whereas some members of the Glossoidea have globose shells. Deeply convex shells are present in free living forms of the Chamoidea but attached members have one valve flattened. Some heterodonts live nestled in crevices where their shell essentially deforms to fit the tight quarters and develops an irregular form (for example, Trapeziidae, Hiatellidae). Shells can be covered with a very thin periostracum (as in the Lucinoidea) or a very thick periostracum (as in the Crassatellidae and Vesicomyidae). Heterodont shells are often prosogyrous (the umbones directed anteriorly). Most are not strongly ornamented although commarginal and radial ribs are not unusual. Some members of the Veneridae have spines and in the genera *Samarangia* and *Granicorium* the shell is coated with a thick and hard layer of sand. *Cardita crassicosta* has a series of radially arranged fluted and arched scales whereas the microscopic *Propecuna subovata* has a shell ornamented by deep commarginal and radial grooves. *Placamen flindersi* has few but prominent commarginal lamellae.

The shell hinge typically has variably developed heterodont dentition, including interlocking cardinal teeth (located beneath the umbones) and peripherally arranged lateral teeth (anterior and/or posterior to the cardinals). A detailed system of terminology to define various hinge dentitions has proven quite useful in understanding the evolution and taxonomy of the bivalves in general. These are reviewed in this volume in the introductory sections on the Bivalvia, and also by Cox (1969a). Heterodont dentition varies in detail. The Veneroida in general have well-developed cardinals and laterals although some representatives have only vague remnants of lateral teeth. The Macomoninae (Tellinidae), Psammobiidae, Solenidae and Hiatellidae lack lateral teeth altogether. Hinge dentition is less well developed in the Myoida, which typically have reduced or desmodont dentition lacking lateral teeth, and may have only reduced cardinals. Myoids often have a well-developed central chondrophore. The extinct hippuritoids are unique in having pachydont dentition, with large, irregular, and heavy teeth. While most authors recognise a number of different and distinct hinge dentitions, F. Bernard (1895, 1896, 1897) very early distinguished two primary types of dentition in the Heterodonta: the lucinoid and cyrenoid types – the latter name was changed by Cox (1969a) to corbiculoid in keeping with taxonomic changes. Lucinoid dentition, found in the Astartidae, Carditidae, Cardiidae, Crassatellidae and Lucinidae, has two cardinal teeth in each valve. Corbiculoid dentition, found in the Corbiculidae and Veneridae, has three cardinal teeth in each valve. Casey (1952) added arcticoid dentition, intermediate between corbiculoid and lucinoid, to the array of 'basic' dentition.

There is some variability in the typically opisthodetic ligament in the Heterodonta. Ligament 'types' include the large, parivincular ligament of the Chamoidea, which is often sunken or internal and situated on nymphs. The ligament of the Crassatelloidea can be external or internal as is that of the Cyamioidea. The Mactroidea typically have a large internal ligament though in some members it is external and sits on nymphs (Yonge 1982a). The ligament of the Galeommatoidea is small. In some heterodonts (for example, Myoidea) the internal ligament sits in an expansive, cup-shaped chondrophore. Yonge (1978) and Waller (1990) have discussed the trends and significance of the ligament in bivalve evolution.

The shell microstructure of the Heterodonta has been examined by Taylor, Kennedy & Hall (1973). Heterodont shells are multilayered and composed of at least two major microstructural components. Most heterodonts have an aragonitic crossed-lamellar/complex crossed-lamellar microstructure. The Chamoidea have a crossed lamellar and complex crossed-lamellar shell composed of calcite (Taylor *et al.* 1973). A derived homogeneous layer is present in some groups such as the Veneroidea. A prismatic-like myostracum, composed of aragonite, underlies areas of pallial, adductor and retractor muscle attachment. This shell layer shows up as muscle scars on the internal shell surface.

The mantle of heterodonts is extensively or only partially fused. Fusion of mantle edges, in part, has played an important role in the success of the Heterodonta through the production of siphons and thus the ability to invade infaunal habitats. Most heterodonts have a thin mantle edge but in the Tridacnoidea the mantle edge is hypertrophied and acts as a home to symbiotic zooxanthellae and associated hyaline bodies that transmit light to deeper tissue layers. The mantle edges of the Chamoidea are fused and form posterior exhalant and inhalant apertures as well as an antero-ventral pedal gape. This is common to many heterodonts, including the Cyamioidea, Arcticoidea and Glossoidea. Additionally, fusion and hypertrophy of the posterior mantle region to form variably produced siphons are common. The latter, found in the Mactroidea, Myoidea and Tellinoidea, has allowed deeper penetration of the substratum and a successful infaunal existence. The Tellinoidea have developed long probing siphons which are used to search the sediment surface for food. Elongate siphons are typically reflected in the interior of the shell by the presence of a deep pallial sinus (Figs 8.28–8.32).

Musculature & Locomotion

Heterodonts typically have two adductor muscles that bring their valves together. This dimyarian condition can be either isomyarian (with equal-sized anterior and posterior adductors as in the Crassatelloidea) or heteromyarian (with unequal-sized adductors as in the Galeommatoidea and Cyamioidea). Rarely a monomyarian or single adductor muscle condition can appear, as in adult Tridacnoidea, through loss of the anterior adductor. Both anterior and posterior pedal retractors are typically well developed. The associated foot varies slightly. That of the Solenidae, perhaps, is the most highly developed, with a piston-like action that allows the animal to rapidly reburrow when cast out from an infaunal niche. Only a few heterodonts retain their byssus and byssus-producing organs as adults. Some of the small heterodonts (for example, Galeommatidae) actively crawl on a flattened foot. Other members of the Galeommatidae use a byssus to 'yo yo' up and down in their burrow (Mikkelsen & Bieler 1989). Many infaunal heterodonts are only capable of sluggish movement or reburial. At least some members of the Corbiculoidea are able to drift downstream on mucoid strands produced by their ctenidia and thus exploit new habitats (Prezant & Chalermwat 1984). Some Solenidae are capable of short bursts of adduction that results in a type of swimming or flight behaviour. Members of the genus *Donax* are found intertidally where they continually emerge and rebury in the intertidal sands to take advantage of the ready supply of food, the high oxygen content of the water and the relative lack of predators.

Feeding and Digestion

The vast majority of heterodonts are suspension-feeders, bringing water and plankton in through an inhalant aperture or siphon and using large ctenidia to trap and filter food particles. In the Tridacnidae a hypertrophied mantle contains zooxanthellae that can be digested by amoebocytes and transferred directly to the digestive diverticula (see Fankboner & Reid 1990; Belda, Lucas & Yellowlees 1993; Klumpp & Griffiths 1994; Klumpp & Lucas 1994). Giant clams have varied means of obtaining nutrition, including the aforementioned zooxanthellae photosynthates, as well as filter-feeding and direct uptake of dissolved organic material (Fankboner & Reid 1990). Lucinids and thyasirids have sulphide-oxidising bacteria associated with their ctenidia (Reid 1990). Most members of the Teredinidae, including the numerous species of Australian shipworms (Turner, this Chapter), find their nutrients in wood particles, obtained from boring into wood with their rasping shell. Wood chips are stored in an accessory caecum and digestion of cellulose is achieved with the help of symbiotic bacteria (see review of feeding and digestion in Morton, B. 1978a).

Variably sized palps transfer food anteriorly to the mouth. Many members of the deposit-feeding Tellinoidea have large palps that are probably used for initial sorting (Yonge 1949). J.G. Wilson (1990) reviews some aspects of feeding and palp morphology in some Tellinoidea.

In most heterodonts, the oesophagus leads to a large, often separate style sac, as in the Solenoidea, Galeommatidae and Mactroidea. Purchon's (1958, 1960a) stomach Types IV (with a large number of primary ducts exiting the stomach and the intestinal groove and major typhlosole entering into the stomach proper) and V (with the major typhlosole and intestinal groove forming a circular ridge that enters the right caecum and another groove entering the left caecum) are most common among heterodonts (Purchon 1990). These stomachs are often complex with various ridges and furrows that further sort 'desired' and 'unwanted' particles prior to their entry into primary digestive ducts that lead eventually to the digestive tubules, the site of final digestion. A crystalline style and associated gastric shield are commonly present (Owen 1955). Purchon (1990) has reviewed the types and evolution of the bivalve stomach.

The heterodont intestine is usually quite simple, functioning to compact and mould faecal material for expulsion. The anus consistently opens over the posterior adductor muscle, usually into the exhalant water flow.

Details on bivalve digestion and metabolism, primarily based on heterodonts, can be found in reviews by de Zwaan (1983; on carbohydrate metabolism), Bishop, Ellis & Burcham (1983; on amino acid metabolism) and Voogt (1983; on lipid metabolism).

Circulation

Most heterodonts have the typical bivalve cardiac system with a single ventricle fed by a pair of lateral auricles, situated in a pericardial chamber that could represent the remnant coelom. In most, the intestine/rectum penetrates the ventricle. Paired cerebro-visceral connectives innervate the heart (Jones 1983). The open circulatory system of some heterodonts contains haemoglobin and it has been assumed that in most heterodonts the blood plays a major role in the transport of respiratory gases. However, in some, it has been discovered that the blood may play only a trivial respiratory role (see Famme 1981). A basic review of the bivalve circulatory system is given by Booth & Mangum (1978).

Apart from studies on the venerid genus *Mercenaria* in North America, there has been little research on the heterodont circulatory system, most being done on palaeoheterodonts and Pteriomorphia (see review in Jones 1983). No work has been done on the circulatory and cardiac system of Australian bivalves.

Excretion

In bivalves, kidneys can serve various functions, including resorption of blood filtrates, ionic regulation, and osmoregulation (Riegel 1972). Aside from studies by Reid, Fankboner & Brand (1984a, 1984b) on the kidneys of *Tridacna gigas*, and Fankboner & Reid (1990), and by Reid & Brand (1989) on the kidneys of *Pinna bicolor* and *Atrina vexillium*, no detailed information is available on the kidneys of Australian bivalves. The bivalve excretory system is reviewed in Andrews (1988). Separate pericardial glands, which aid in filtration processes during excretion, are present in some heterodonts (Andrews 1988). Podocytes have been found in the pericardial gland tissue of heterodonts (Meyhofer, Morse & Robinson 1985). Podocytes are able to concentrate inorganic (that is, heavy metal) and organic constituents from the blood (Pirie & George 1979). Ammonia is the most common nitrogenous waste produced by bivalves. Variations in the cell ultrastructure of the kidneys of osmotically stressed bivalves, including one heterodont, are discussed by Khan & Saleuddin (1990). It is very likely that many tissues exposed within the pallial cavity release excretory compounds by simple diffusion (Jones 1983).

Yonge (1980) and Reid *et al.* (1984a, 1984b) found that the kidneys of *Tridacna gigas* are exceptionally large and contain dense concentrations of small nephroliths. These 'kidney stones' consist of an organic base with high concentrations of calcium phosphate, calcium sulphate, and calcium oxalate. In *T. gigas* the kidneys have a strong proteolytic component and are involved in sequestering oxalate and sulphate ions produced by the symbiotic zooxanthellae, giving the tridacnid kidneys a digestive function as well (Reid *et al.* 1984a). In *Pinna bicolor*, the relatively large nephroliths sequester a variety of toxic metals (Reid & Brand 1989).

Respiration

Within the Bivalvia, the largest and most complex ctenidia occur in the 'eulamellibranch' heterodonts. In this form of ctenidium, the lamellae are joined by interfilament and interlamellar tissue. The fusion of the posterior ctenidial axis with the mantle secures separate infrabranchial and suprabranchial chambers. The large ctenidia, aside from a respiratory function, are involved in filtering out food particles, sorting them, and carrying them to the palps. Additionally the ciliated ctenidia create the water currents that flow through the pallial cavity. Because many tissues within the pallial cavity are directly exposed to water flow, it is likely that they play some respiratory role (Jones 1983). There is variability in the number and comparative size of demibranchs within the Heterodonta. Atkins (1937a) examined about 90 species of 'lamellibranch' bivalves and concluded that they could be categorised into any one of seven groups based on orientation and extent of demibranchs and path of water currents. Refinement of her classification can be found in Owen (1978). Many 'eulamellibranchs' have Atkins' Type C ctenidia, the complete inner and outer demibranchs, with either both or just the inner demibranch having a ventral, ciliated food groove. The Chamoidea have unequal, plicate demibranchs. Members of the Crassatelloidea also have unequal demibranchs, with the external demibranchs reduced, but their large gills are nonplicate. The outer demibranch may be absent in some Cyamioidea. Synaptorhabdic (that is with a reticulate appearance as a result of interlamellar connections), plicate (folded) ctenidia are common in the Mactroidea and Veneroidea. Homorhabdic and synaptorhabdic, smooth or plicate, ctenidia occur in the Hiatellidae (Brunckhorst, this Chapter). The elongate ctenidia of the Teredinidae are composed of inner demibranchs only (Turner, this Chapter). J.G. Wilson (1990) recently detailed the ctenidial and palp morphology of some tellinoideans. The basic bivalve respiratory system is described in Chapter 1.

Sense Organs and Nervous System

The anatomy of the heterodont nervous system is of the standard bivalve form, with connectives between paired (sometimes fused) cerebral, visceral and pedal ganglia. A pair of statocysts is typically associated with the pedal ganglia although they are innervated by the cerebral ganglia (Charles 1966). For many heterodonts, the tentaculate, posterior siphons provide the primary sensory input. The mantle edge itself can also be tentaculate as in the Chamoidea, some Crassatelloidea, and Galeommatoidea.

Reproduction

The Heterodonta exhibits a wide array of reproductive biologies. Most taxa are dioecious (for example, Chamoidea, Cyamioidea, Mactroidea) but several groups are hermaphroditic (for example, some Galeommatoidea, Tridacnoidea). Among Australian bivalves, reproductive biologies are well known only for some commercially important species (for example, Tridacnoidea, Teredinidae). Tridacnid reproductive biology was reviewed by Rosewater (1965), Pearson (1977), Yonge (1980) and Heslinga & Fitt (1987). Turner (1971a) reviewed reproduction in Australian shipworms and noted three patterns in teredinid life histories. Among the dioecious or gonochoristic heterodonts, sexual dimorphism is rare. Some astartids have larger females than males and those galeommatids that are dioecious can have dwarf males that are retained in the larger female's mantle cavity (O'Foighil 1985a). These bivalves produce large eggs that adhere to the substratum near the parent (Saleuddin 1964).

In dioecious heterodonts, the gonads are often intermingled among the intestinal loops embedded in the foot. Some Lucinoidea have the gonad secured onto lateral dendritic pouches of the digestive gland (Mackie 1984). Heterodonts typically have separate gonopores for release of gametes, situated in the suprabranchial chamber. Gametes are released and fertilisation and development are usually external.

Simultaneous hermaphroditic heterodonts show varying degrees of association between the male and female systems. Species of *Cardium* have male and female gonads interfused into a meshwork of male and female acini. Gametes of both types exit by a shared gonoduct located on a papilla that is essentially cloacal since it also acts as a nephridiopore (Coe 1945). Most other heterodonts have male and female gonad regions separated. Separate male and female gonads in *Teredo* open into a common duct that also opens into the base of the kidney and exits through a common duct with the kidney (Mackie 1984). Some heterodonts undergo consecutive or sequential hermaphroditism (for example, some venerids, teredinids). Australian sphaeriids that have been examined are protandric hermaphrodites that brood their young in a modified marsupium composed of the inner gill (Mackie 1979; Kuiper 1983). Surprisingly little information is available on the reproductive biology of Australian bivalves.

Self-fertilisation has been suggested for some Australian Sphaeriidae (Kuiper 1983) but most heterodonts have external fertilisation following a mass spawning event. Spawning can be cued by temperature (some venerids and myoids), lunar cyclicity (some tellinids), nutrient levels (some tellinids, corbiculoideans), and several other factors that are reviewed by Mackie (1984).

Embryology and Development

There are few studies of the embryological or developmental patterns of Australian bivalves. Heterodonts, in general, have indirect or direct development leading to either a planktonic larval form or a 'crawl-away' stage. Most are larviparous producing, in some taxa, trochophore larvae followed by veligers. Most, however, produce only a veliger stage followed by shelled prodissoconch stages I and II. All Galeommatoidea develop at least through a veliger stage, which is retained in the mantle cavity, but some develop well beyond this while in brood (Galeommatoidea, this Chapter; Ponder 1967 on New Zealand

Mysella). Members of the Cyamiidae also produce 'crawl-away' young from a few large eggs (Cyamioidea, this Chapter). Tridacnoideans, which produce millions of eggs in a single reproductive season, develop planktonic veligers (Yonge 1980; Braley 1984; Heslinga & Fitt 1987). Mactroidea are both dioecious and larviparous (Boss 1982; Jones, Murray & Skilleter 1988). Larval development of the Tellinoidea is described by Frenkiel & Mouëza 1979). Some tellinoideans use 'byssal drifting' as a pediveliger dispersal mechanism (Frenkiel & Mouëza 1979). Postlarval development of some non-Australian tellinoideans is described by Webb (1986).

NATURAL HISTORY

Life History

The life history of relatively few Australian heterodonts is fully known. Turner (1971a) examined the life history of Australian Teredinidae, Roberts (1984a) that of the venerid *Katelysia* from Western Australia, Coleman (1982) that of *Tellina mariae* from Victoria, and Jones *et al.* (1988) that of the mactroidean *Notospisula trigonella*. The life histories of a few commercially important tridacnoideans are also well known (Yonge 1980; Heslinga, Perron & Orak 1984; Heslinga & Fitt 1987).

Ecology

Few studies have targeted Australian bivalve ecology directly although more general studies have concentrated on habitats occupied by bivalves. Several reports detail the distribution, population dynamics, and diversity of Australian malacofauna (Coleman & Cuff 1980; Roberts & Wells 1980; Wells 1984), but most take a broader view and include molluscs among the many organisms examined (Stephenson *et al.* 1974; Coleman *et al.* 1978; Poore 1982; Marchant, Lake & Doeg 1991; Peterson 1991). Maxwell (1968) reviewed the ecology and malacofauna of the Great Barrier Reef and Rippingale & McMichael (1961) similarly reviewed the 'reef shells'. Roberts & Wells (1980) documented the molluscan fauna of the Albany area of Western Australia, including numerous heterodonts; in this area alone, close to 60 heterodonts are found. Poore (1982) examined the fauna of the estuarine Gippsland Lakes, Victoria, and found it similar to most south-eastern Australian estuaries, but containing a 'depauperate bivalve fauna'.

Marine heterodonts are probably most abundant in sublittoral zones, although they are found intertidally as well as in the abyss. While most are common in shallow and shelf waters, there are two families that have significant representation in the deep sea: the Thyasiridae and Xylophagidae (Allen 1983). The general stability and lack of competition within the deep-sea realm is in good part responsible for the success of these two families (Allen 1983). The difficulties encountered in obtaining living abyssal specimens, however, causes knowledge of the deep-sea malacofauna to remain elusive. Sphaeriids are very common in various freshwater biomes including bogs, creeks, rivers, farm pools and even road side ditches (Kuiper 1983).

Heterodonts inhabit a wide range of habitats, ranging from wood to freshwater sediments to coral rock. Coleman & Cuff (1980) demonstrated that the distribution of bivalves in Western Port, Victoria, is related to the sediment type. For example, *Venericardia bimaculata* is a suspension-feeding heterodont and is among the dominant species found in medium to coarse sands of deeper channels of Western Port. Wells & Threlfall (1980) found that bivalves dominated the softbottom communities of Cockburn Sound, Western Australia. In their study, bivalves comprised over 85% of the biomass and over 72% of total individuals collected. The venerid *Dosinia incisa* accounted for 57% of the molluscan biomass and 32% of the total molluscs collected (surpassed in numbers only by *Musculista glaberrima* with 43.5% of the total individuals but less than 13% of molluscan biomass). Several Australian galeommatids are variously associated with heart urchins, burrowing anemones, mantis shrimps and sea cucumbers (Boss 1965; Ponder 1967, 1968). Tridacnids living on tropical reefs, have significant morphological adaptations including hypertrophied mantle edge, reflecting an association with symbiotic zooxanthellae. As adults, tridacnids have few predators; as juveniles they are preyed upon by various fish, turtles and cephalopods (see Chapter 11). A few tridacnids, such as *Tridacna crocea*, bore into hard substrata but most, although byssate as juveniles, rely on their great weight as adults to remain in place on the reef. Detailed studies on Australian mactrids have not yet been presented but it appears that they are most common within shifting sediments of the littoral zone (this Chapter). The Veneroida is the largest group of Australian bivalves and is diverse in habitat requirements. The range in siphonal length reflects different depths of burial and those bivalves with elongate siphons, living deeper within the sediment, have a correspondingly lower predation risk (Zwarts & Wanink 1989). Members of the Veneridae are present in coral reefs, mangroves, intertidal mud flats, and offshore silts and sands. Some species nestle in coarse sediments and others bore into clay and coral. Commonly present in shallow, oligotrophic waters, the lucinids are infaunal bivalves that often construct mucus-lined tubes to the surface (Reid & Slack-Smith, this Chapter). Corresponding to the possession of symbiotic sulphide-oxidising bacterial symbionts in the ctenidia (Reid 1990), lucinids often live in regions with high sulphide content (Allen 1958).

Solenoideans are common in fine sands and muds, often among seagrasses. They can burrow very rapidly to avoid predators but still occasionally fall prey to shore birds and crabs. The tellinoideans are a diverse group of heterodonts that are usually deeply buried. Their highly flexible siphons are used for feeding on organic deposits (Gilbert 1977). The siphons are a renewable resource; siphon-nipping is a common ploy of many shore fish (Brewer & Willan 1985) and birds. Several bivalve species can regenerate their siphons after their excision. Wells & Threlfall (1980) found populations of *Tellina cockburnensis*, a member of a group with very long siphons, in concentrations exceeding 153 m^{-2}, making them a dominant member of some habitats and an important resource for siphon-nipping fish. Most psammobiids occur in sediments with low organic content but Pohlo (1972) suggested that at least *Sanguinolaria nuttallii* is a nonselective deposit-feeder. Members of the Trapeziidae are primarily inhabitants of coral reefs of northern Australia although some live in coastal lagoons of eastern Victoria northward and in protected embayments of south-western Western Australia (Slack-Smith, this Chapter). Predators include various fish and octopuses.

The relatively sluggish glossids are found in shallow waters to depths of up to 400 m (this Chapter). Here they assume a shallow infaunal position in fine sediments (Owen 1953a). Corbiculoideans are either infaunal in freshwater sands (Corbiculidae) or attached to plants (Sphaeriidae). Populations of sphaeriids from ephemeral North American ponds have been examined by Heard (1977) and Hornbach, Wissing & Burky (1982). The latter authors suggest that sphaeriids from these ponds show a 'bet-hedging' strategy designed to succeed in these temporary habitats.

J.G. Carter (1978) and B. Morton (1983a) noted that, although the ability of gastrochaenids to bore into various substrata is partly mechanical, it is mainly a chemical process that involves secretions from the juvenile mantle. Boring takes place throughout adulthood (Savazzi 1982) and some of these embedded bivalves deposit a calcareous 'igloo' around the siphons (Yonge 1982b; Morton, B. 1982a, 1983a). The Hiatelloidea is another group of nestling or boring marine bivalves. The Pholadoidea, however, represent the apex of specialisation for boring bivalves. These often worm-like bivalves bore into clay, peat, soft rocks, cement, shells and wood. Turner (this Chapter) records at least 15 Australian species of Pholadidae and another 32 species of Teredinidae. The latter family includes the shipworms, notorious for damaging ships and pilings. Many of these species line their burrows with calcium carbonate and most use wood or other plant

PLATE 7: APLACOPHORA & POLYPLACOPHORA

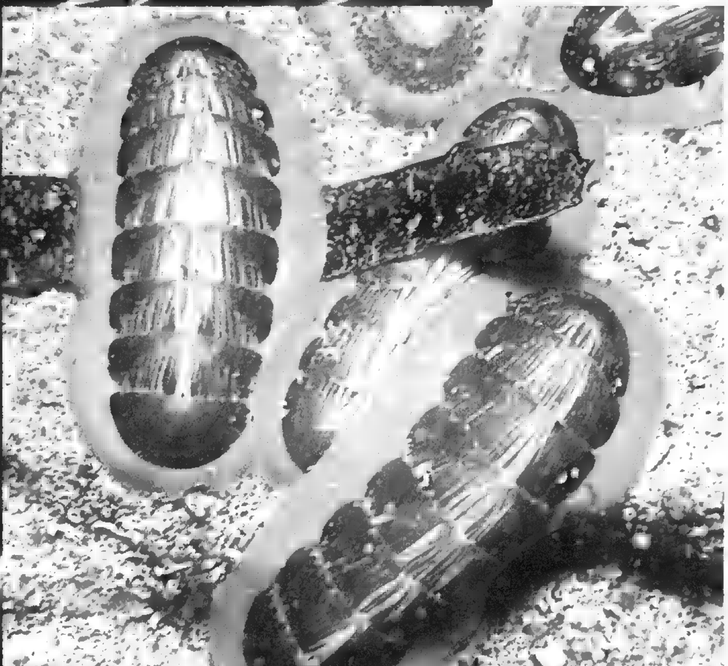
1 The aplacophoran *Epimenia australis* (Epimeniidae) lives amongst coral slabs and rubble, associated with its soft coral prey, *Scleronephthya* species.

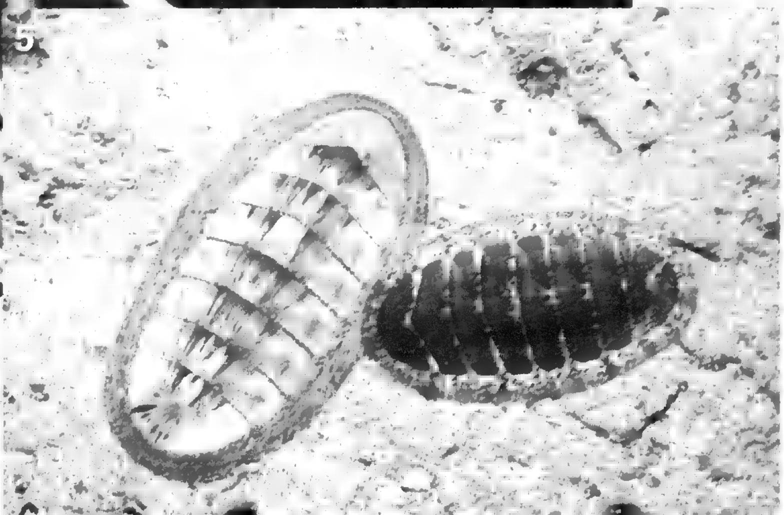
2 *Stenochiton longicymba* (Ischnochitonidae), endemic to southern Australia, lives on old sheaths of *Posidonia australis*.

3 *Eudoxochiton inornatus*, a large Tasmanian ischnochitonid, lives subtidally on moderately exposed shores.

4 *Ischnochiton torri* (Ischnochitonidae), a specialist feeder on drift seagrass, inhabits the edges of shallow reefs.

5 In southern Australia, *Ischnochiton contractus* (Ischnochitonidae) frequently aggregates on stones and shells in sand.





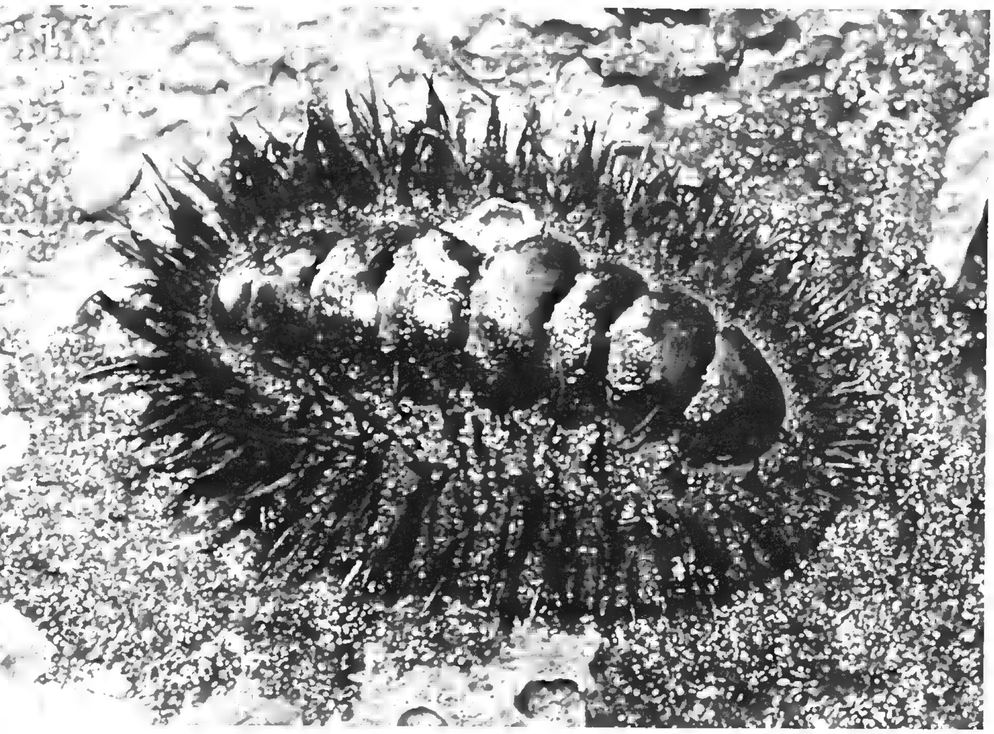


PLATE 8: POLYPLACOPHORA

1 The tropical chitonid *Acanthopleura spinosa* grazes at night on intertidal crustose algae.

2 Common along the southern coast, *Rhyssoplax exoptanda* (Chitonidae) lives under a thin layer of silty sand on smooth sedimentary rocks.

3 *Rhyssoplax diaphora* (Chitonidae) lives on medium to high energy rocky shores, feeding largely on crustose coraline algae.

4 *Rhyssoplax calliozona* (Chitonidae) shelters under rocks in sandy habitats, emerging at night to feed on sponges, bryozoans and algae.

5 Valve and girdle colouration may vary widely in chiton species as shown by *Rhyssoplax tricostalis* (Chitonidae) from southern Australia.

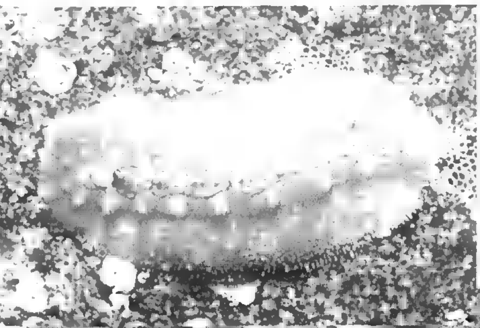


PLATE 9: POLYPLACOPHORA

1 *Bassethullia matthewsi* (Acanthochitonidae) clings to stones and shells in sand pockets on southern Australian subtidal reefs. The genus *Bassethullia* is endemic.

2,3 The last four valves of juvenile *Cryptoplax striata* (Cryptoplacidae) articulate (2), becoming separated in adults (3).These chitons graze on drift seagrass, encrusting algae and sponges in the sublittoral zone.

4 *Leptochiton liratus* (Lepidopleuridae) feeds on sand-dwelling diatoms and detritus in temperate waters.

5 The schizochitonid *Lorica volvox* feeds on bryozoans and annelids on shallow reefs along the southern coast.

6 Encrusting growth usually covers the distinctive colour pattern of southern Australian *Plaxiphora matthewsi* (Mopaliidae).

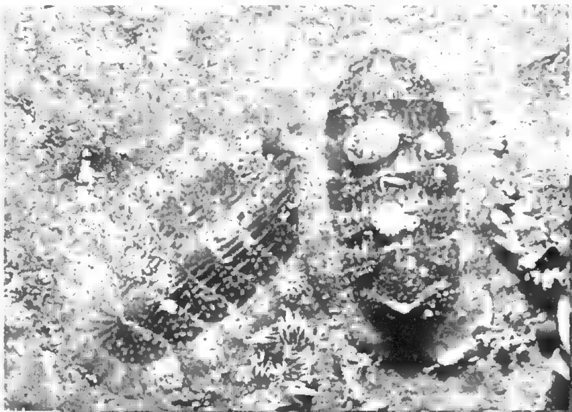


PLATE 10: BIVALVIA

1 An inhabitant of benthic silts and muds, this *Solemya* species (Solemyidae) utilises carbohydrates synthesised by symbiotic sulphide-oxidising bacteria.

2 The mussel *Brachidontes rostratus* (Mytilidae) may be extremely abundant at mid-tide level on ocean rock platforms of the southern and south-eastern coasts.

3 The blue mussel, *Mytilus edulis planulatus* (Mytilidae), is harvested commercially by divers and grown in mariculture in southern and south-eastern Australian waters.

4 *Vulsella spongiarum* (Pteriidae), a sponge finger, is found fully embedded in host sponges, often in high numbers.

5 The southern Australian wing shell, *Electroma georgiana* (Pteriidae), commonly attaches to benthic plants, such as algae and seagrasses.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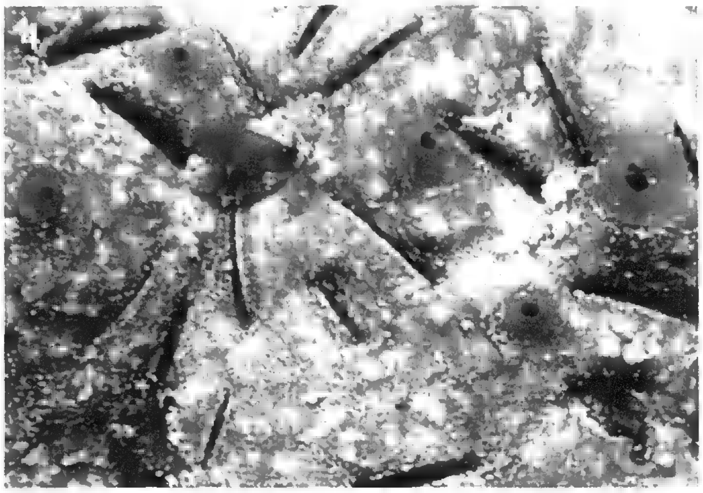
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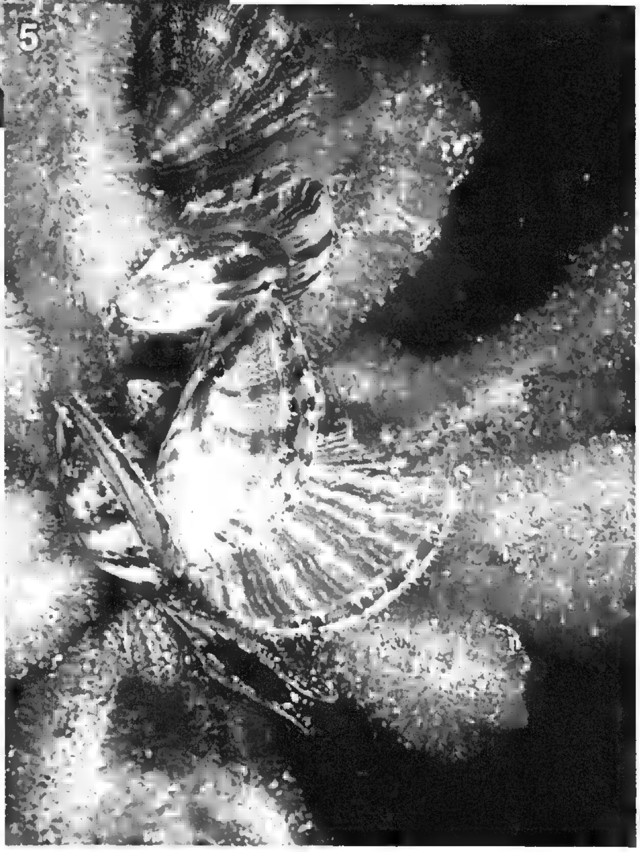
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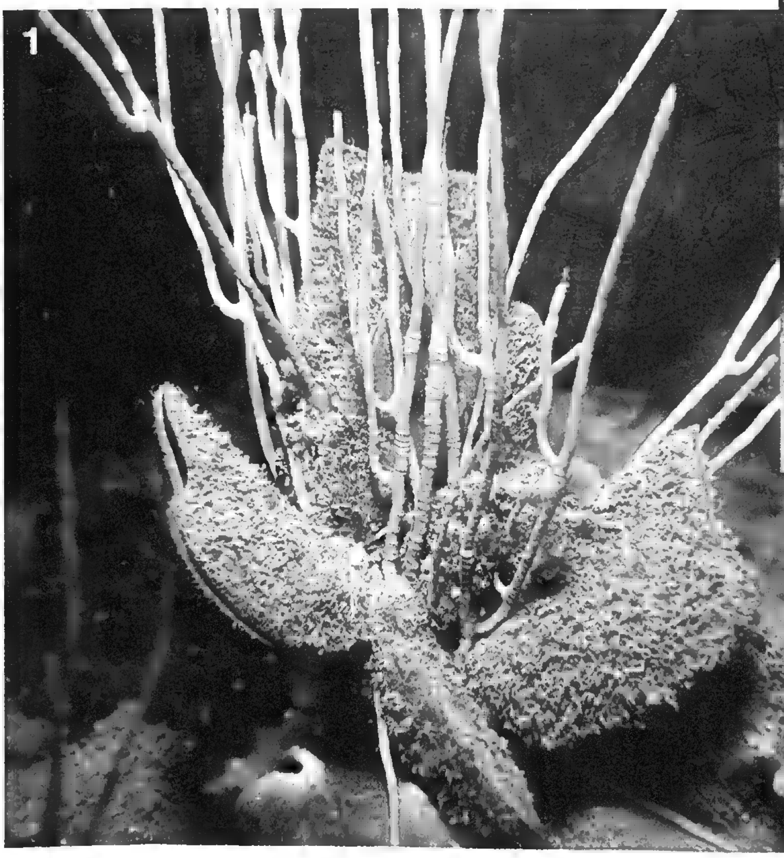


PLATE 11: BIVALVIA

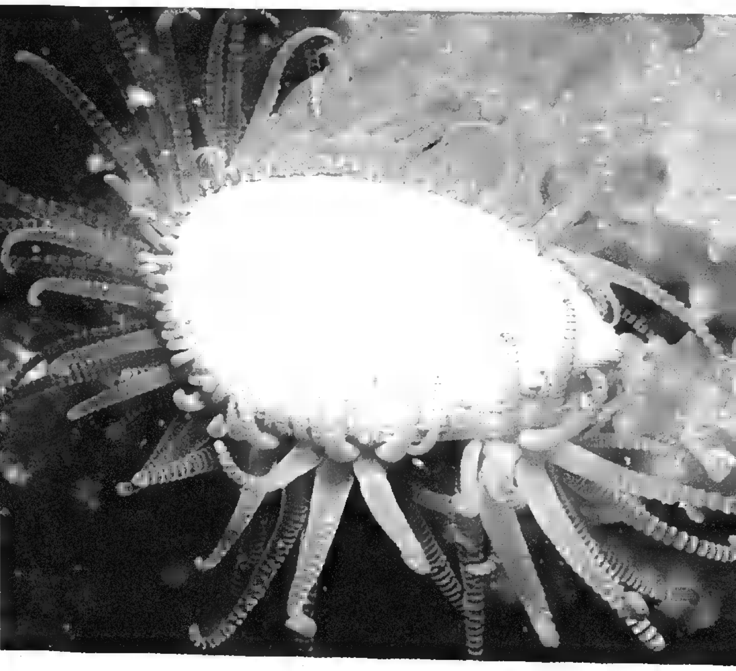
1 The red-winged pearl shell, *Pteria saltata* (Pteriidae), settles and grows on sea whips and gorgonians on shallow northern Australian reefs.

2 *Pinna bicolor* (Pinnidae), widely distributed in tropical and temperate Australian waters, may live for some 10 years and reach 400 mm in length.

3 When swimming, the file shell, *Limatula strangei* (Limidae), opens and closes its valve rapidly, and rows with its tentacles.

4 The widely distributed file shell *Lima lima* (Limidae) lives in rock or coral crevices, attached by a byssus.

5,6 The widespread, gregarious Sydney rock oyster, *Saccostrea commercialis* (Ostreidae), is the basis of a long-standing fishery in south-eastern Australia.



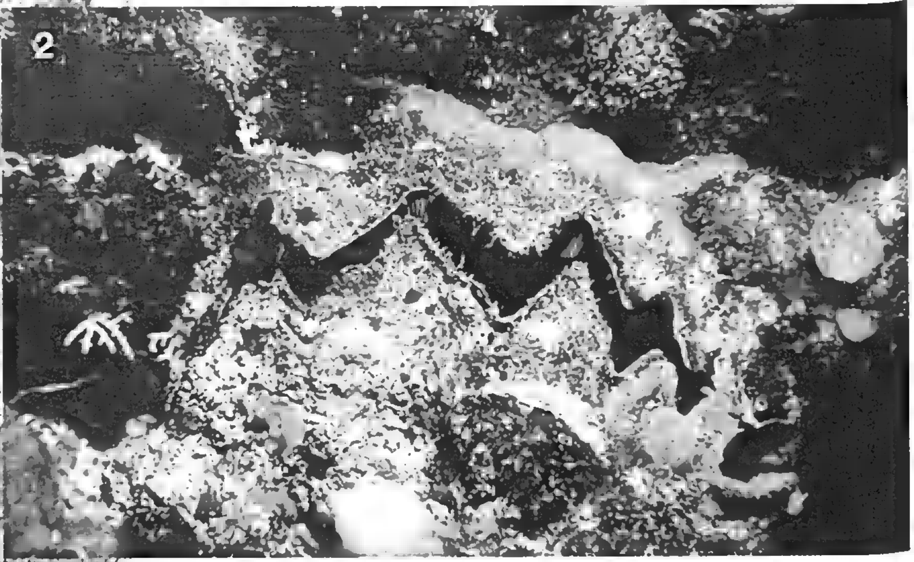


PLATE 12: BIVALVIA

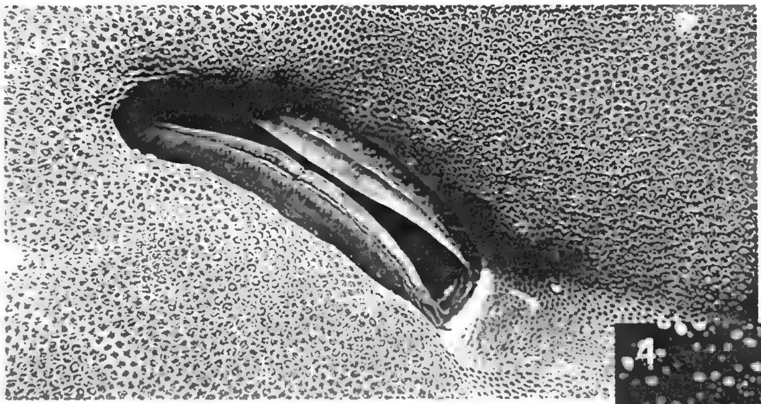
1 Cockscomb oysters, *Lopha cristagalli* (Ostreidae), are usually more concealed by sponges than this specimen.

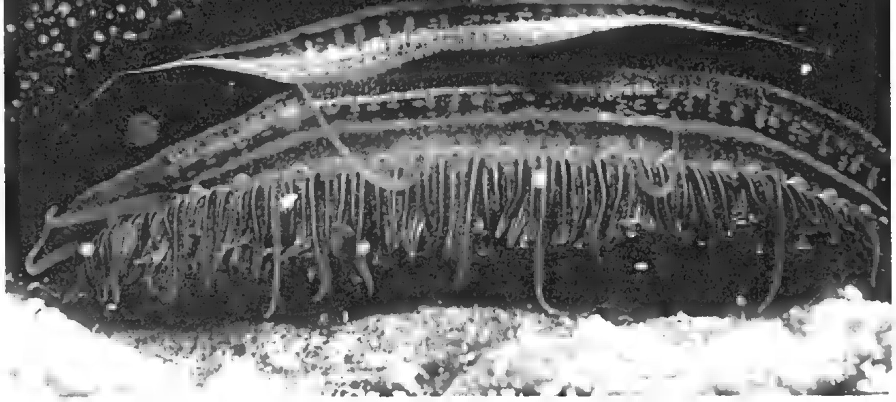
2 Found attached to reef walls, *Hyotissa hyotis* (Gryphaeidae) is widespread throughout the Indo-West Pacific.

3,4 The rows of tentacles and eyes along the mantle margins are important sensory organs in *Pedum spondyloideum*, a pectinid inhabiting crevices in live corals.

5 *Spondylus varius* (Spondylidae) is found throughout the western Pacific, cemented to reef walls.

6 Encrusted with growth, *Spondylus tenellus* (Spondylidae) attaches to rock and other hard substrata on the southern Australian coast.





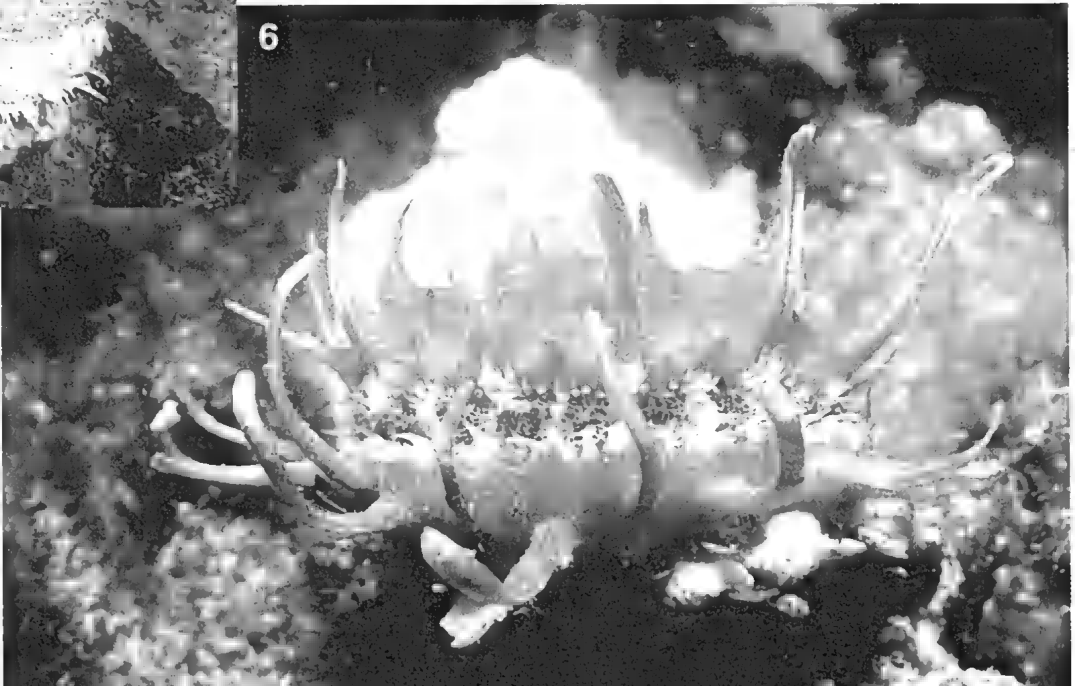


PLATE 13: BIVALVIA

1 The southern scallop, *Pecten fumatus* (Pectinidae), is the subject of a significant fishery in Bass Strait and south-eastern Australian waters.

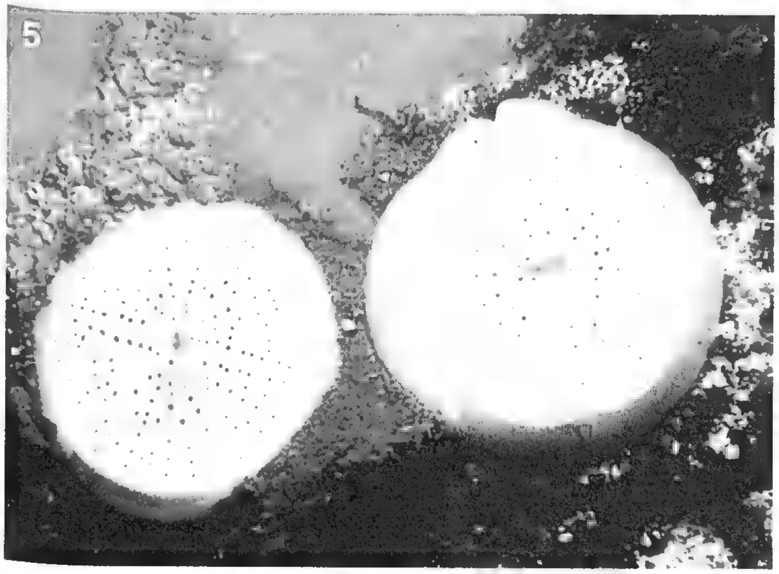
2 The queen scallop, *Equichlamys bifrons* (Pectinidae), is fished commercially by divers in South Australia.

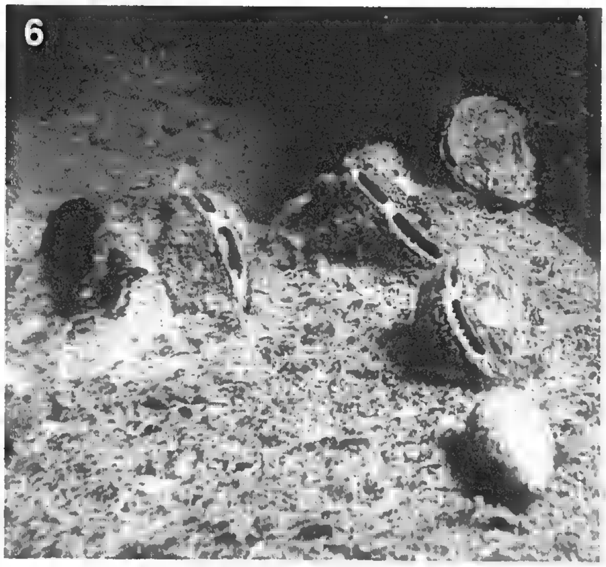
3 The doughboy scallop, *Mimachlamys asperrima* (Pectinidae), is fished by recreational divers in Tasmania.

4 The smooth, elongate shell of *Solen vaginoides* (Solenidae) permits rapid burrowing.

5 *Ephippodonta macdougalli* (Galeommatidae) has permanently open valves, and is attached to the substratum by its mantle.

6 After settlement, some chamids, such as *Chama* species, become cemented to rocks or other hard substrata; they may be common in sublittoral areas of open coasts.



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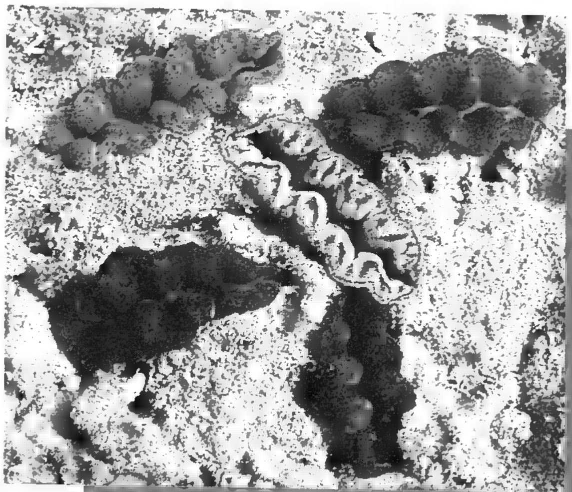
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PLATE 14: BIVALVIA

1,4 The giant clam, *Tridacna maxima* (Tridacnidae), showing the massive shell with its ventrally orientated hinge, and the brightly coloured mantle tissue in which zooxanthellae live.

2 *Tridacna crocea* (Tridacnidae) is the only giant clam that becomes totally embedded in the coral.

3 Release of spawn by the giant clam, *Tridacna gigas* (Tridacnidae).

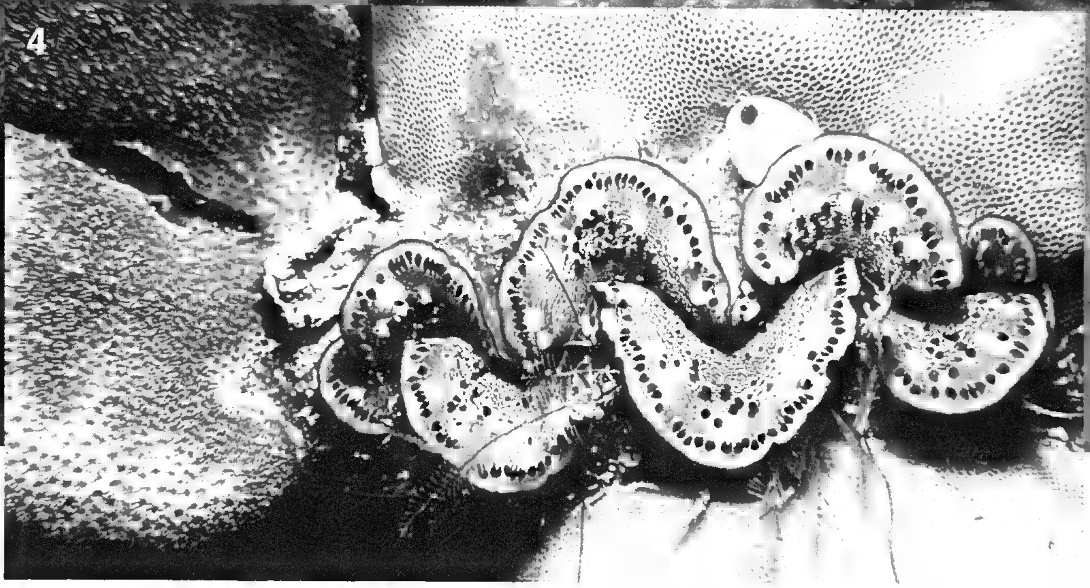
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PLATE 15: BIVALVIA

1 A pipi, *Donax (Plebidonax) deltoides*, showing the powerful foot used for rapid reburial in the zone, and short, stout siphons tipped with branched lobes, typical of the Donacidae.

2,3 *Tellina pharaonis* (Tellinidae), showing two stages in burrowing; the foot is visible anteriorly, and the siphons posteriorly in (2).

4,5 *Lutraria rhynchaena*, a large mactrid of southern and south-eastern Australian sandy shores.

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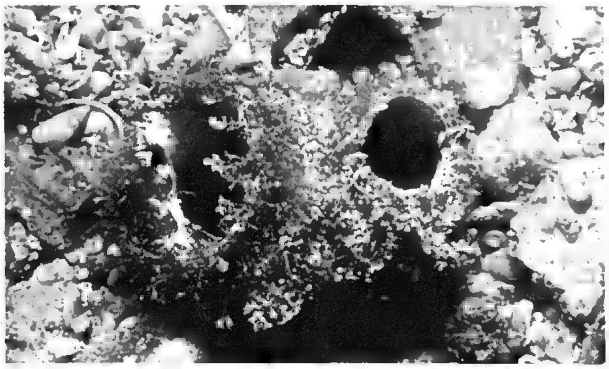


PLATE 16: BIVALVIA & SCAPHOPODA

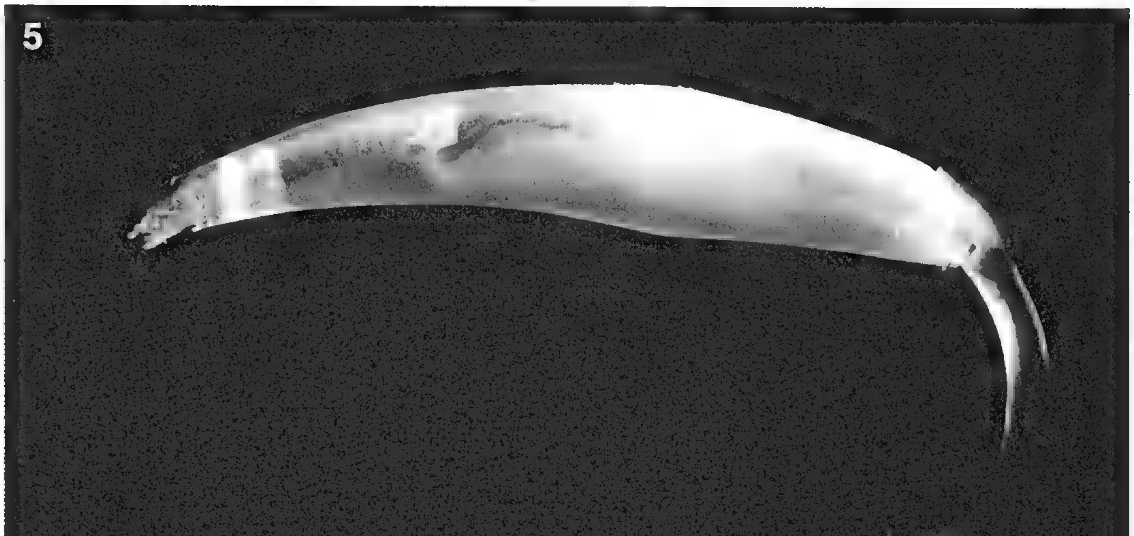
1 *Gastrochaena gigantea* (Gastrochaenidae) *in situ* in a sectioned burrow, showing the massive, fused siphons and the lining applied to the burrow wall.

2 Shipworms (Teredinidae) secrete a calcareous lining to their burrows, which may protrude in highly eroded timber.

3 The protruding siphons of two buried *Barnea obturamentum* (Pholadidae) are visible behind a dead shell of this species.

4 *Cleidothaerus albidus,* sole member of the endemic Australasian Cleidothaeridae, has a thick, inequivalve shell and lives cemented to rock on exposed shores.

5 *Cadulus* species (Gadilidae), showing the protruding foot, smooth glossy shell, indented apex and posterior mantle.



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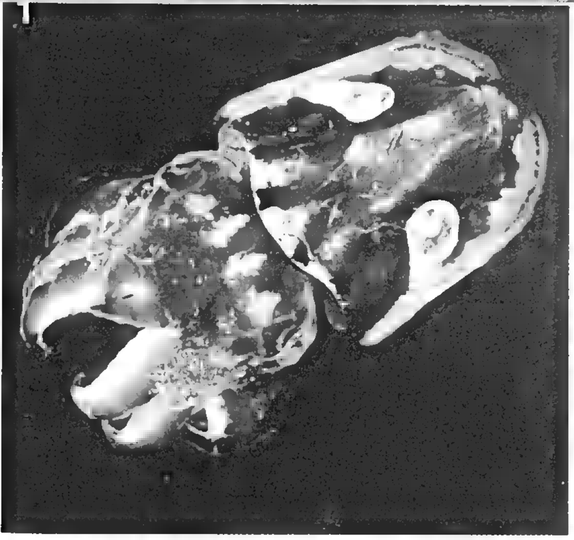

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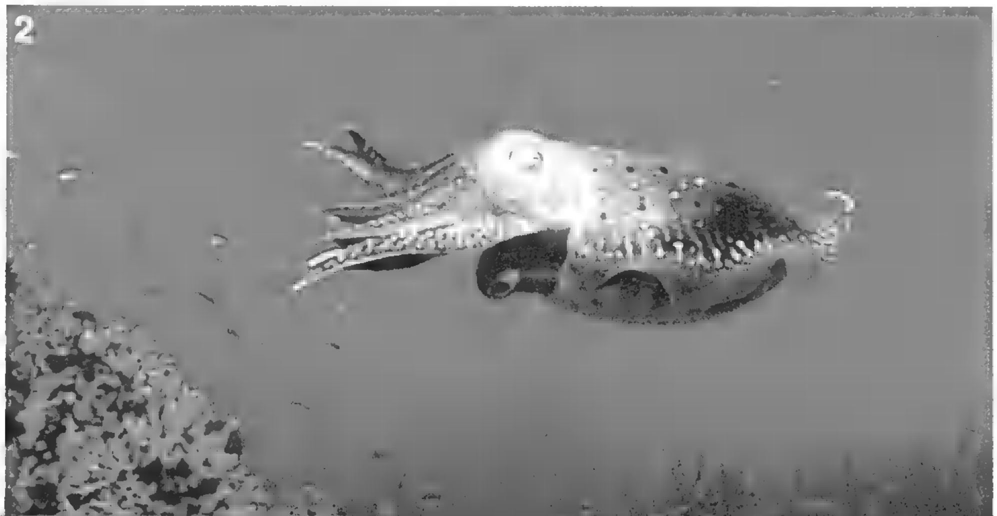

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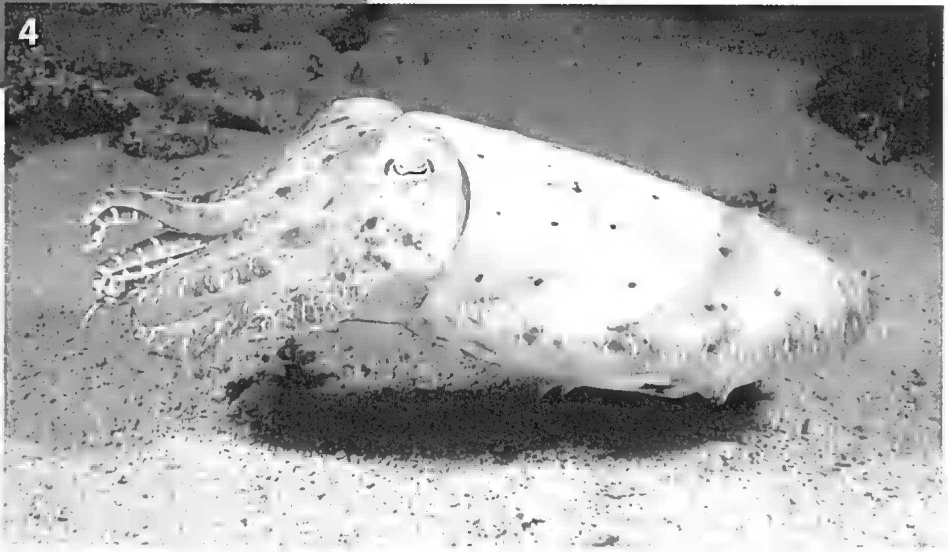

PLATE 17: CEPHALOPODA

1 The colourful *Metasepia pfefferi* (Sepiidae) is widespread on shallow reefs from northern Australia to the Philippines.

2,3,4 *Sepia latimanus* (Sepiidae), a common Indo-West Pacific coral reef cuttlefish, shows changes in colour pattern.

5 Changing skin texture and colour camouflages the giant cuttlefish, *Sepia apama* (Sepiidae), amongst the kelp.

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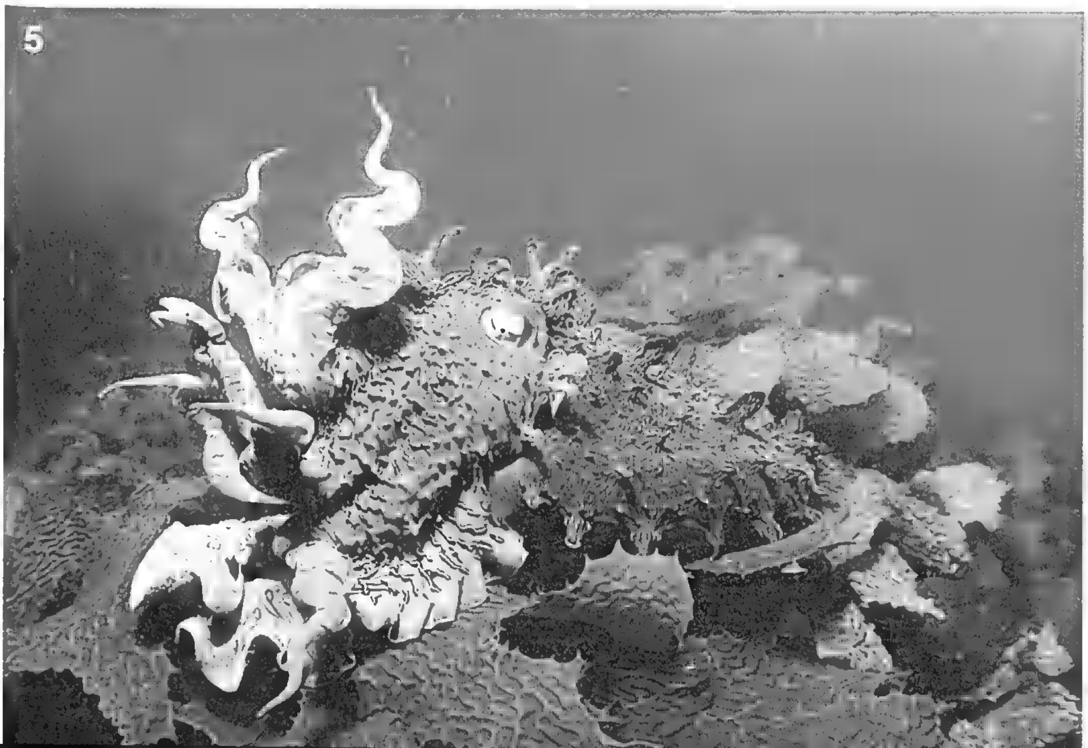

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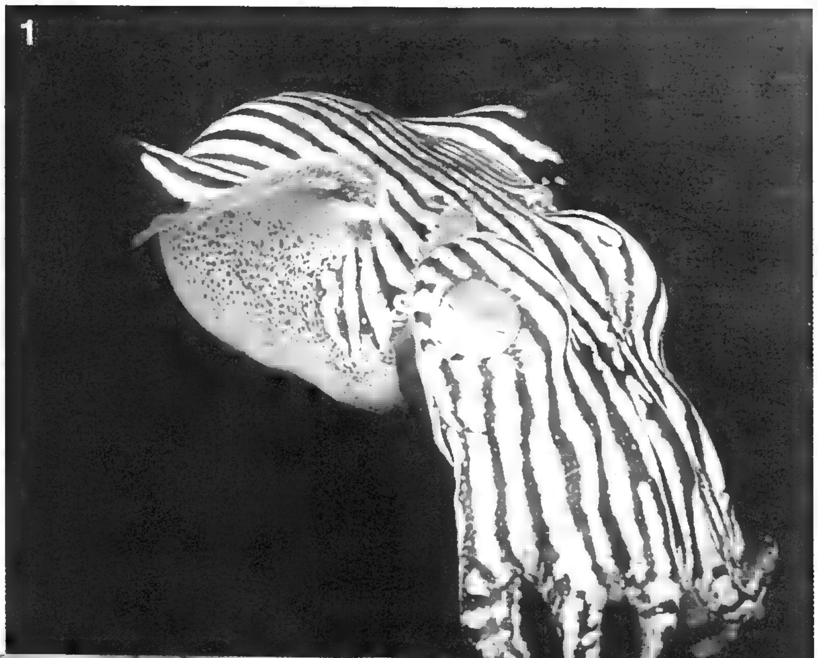

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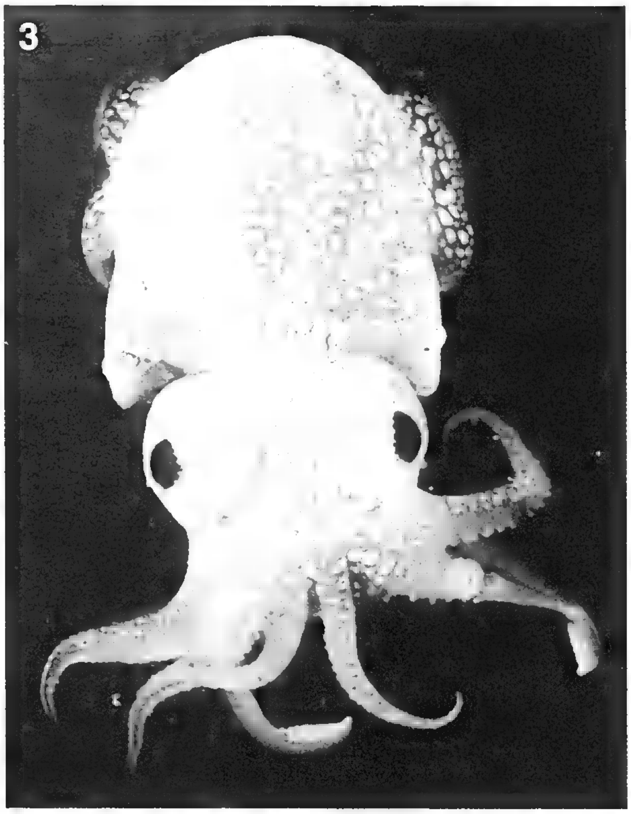

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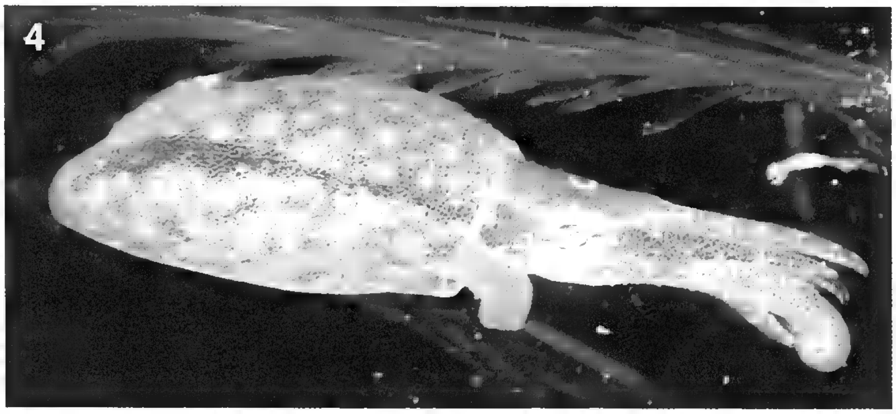

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PLATE 18: CEPHALOPODA

1,2 Swimming adult and newly hatched young amongst eggs, of *Sepioloidea lineolata* (Sepiadariidae); this benthic species occurs in most Australian coastal waters.

3 *Sepiadarium kochi* (Sepiadariidae) is an Indo-West Pacific species found in northern Australian waters.

4 At 22 mm or less in length, idiosepiids are the smallest known cephalopods. *Idiosepius notoides* lives in seagrass beds along southern Australian shores.

5 Mating behaviour in a dumpling squid, *Euprymna tasmanica* (Sepiolidae), from southern Australian waters.

6,7,8,9 *Sepioteuthis lessoniana* (Loliginidae), showing (6) laying of eggs in seagrass, (7) freshly laid egg capsules attached to seagrass, (8) an egg capsule ready to hatch and one hatchling, and (9) a school of adults.

10 *Cranchia scabra* (Cranchiidae), an oceanic squid with numerous cartilaginous tubercles on the body.

11 The arrow squid, *Nototodarus gouldi* (Ommastrephidae) is abundant in southern Australian and New Zealand waters, and forms the basis of important squid fisheries.

12 *Enoploteuthis galaxias* (Enoploteuthidae) occurs over the continental slope off eastern Australia and New Zealand.

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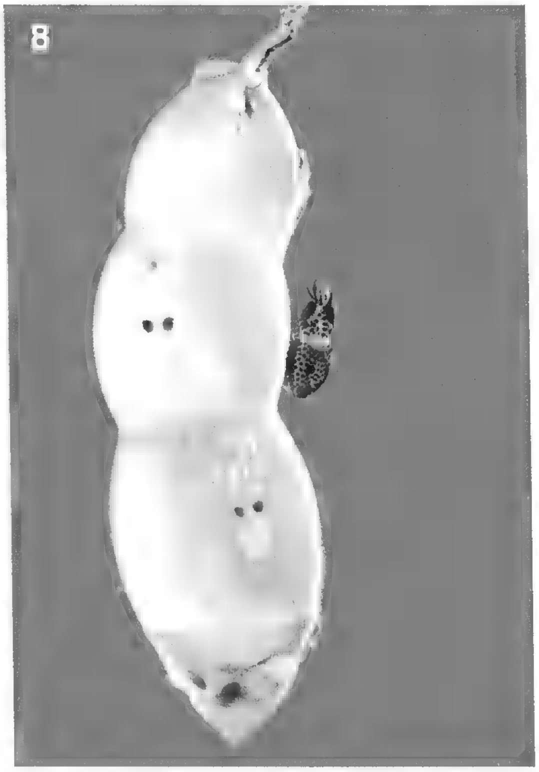

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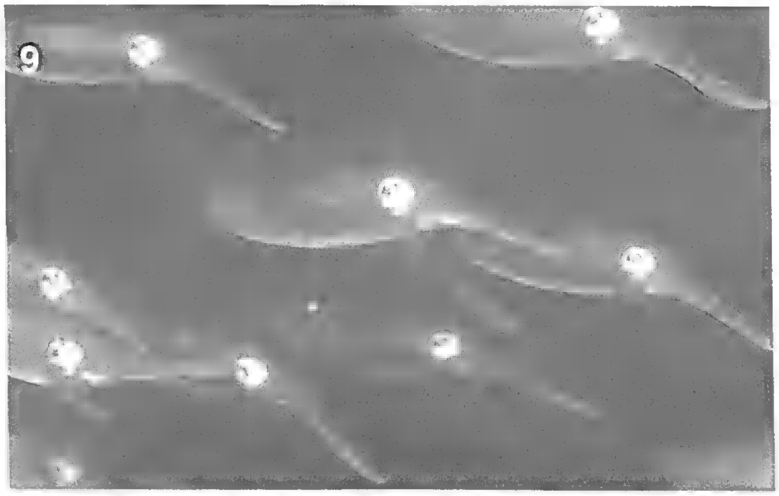

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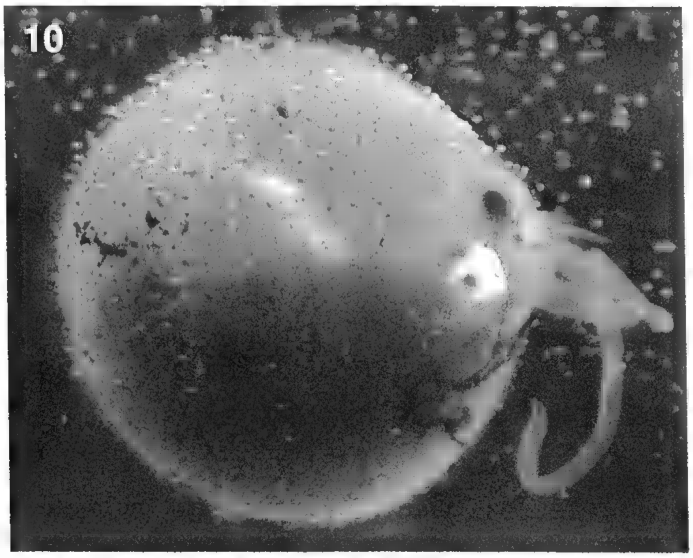

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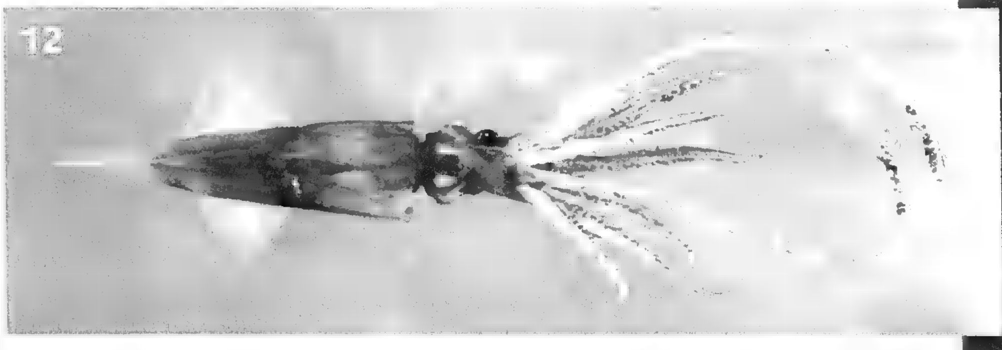


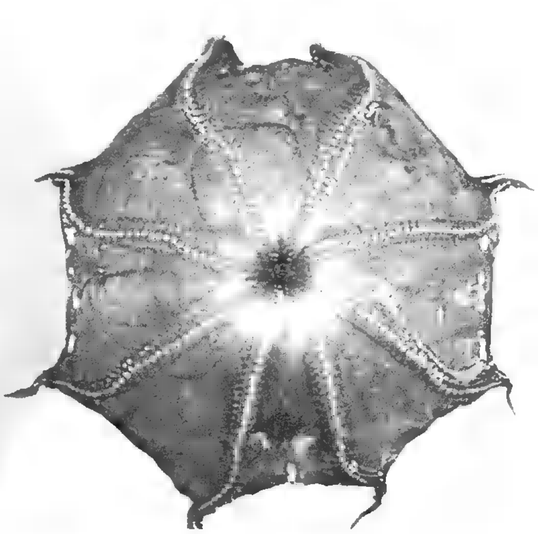


PLATE 19: CEPHALOPODA

1 Ventral view of the gelatinous pancake octopus, *Opisthoteuthis persephone* (Opisthoteuthidae), from the southern and eastern Australian continental slope.

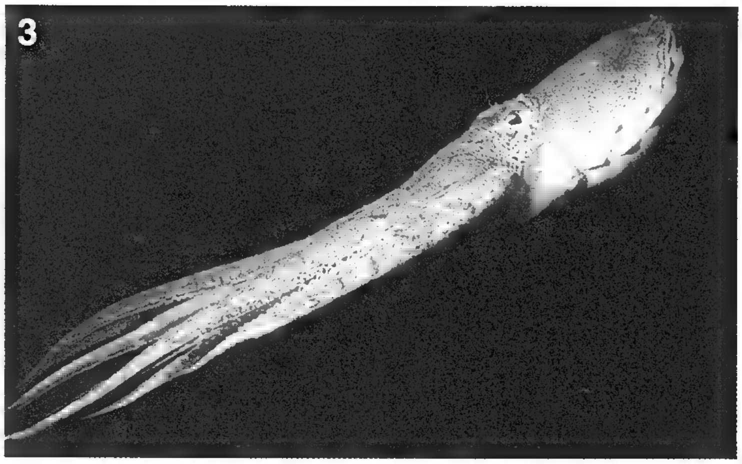
2 A female *Hapalochlaena maculosa* (Octopodidae) pulls her eggs beneath her before moving following disturbance. Although venomous, these inhabitants of intertidal or subtidal reefs are not aggressive.

3 *Octopus berrima* (Octopodidae), shown swimming, is common in southern Australia.

4 *Ameloctopus litoralis* (Octopodidae), discovered recently in northern Australian waters, is able to autotomise its arms at the level of the fifth sucker pair.

5 *Octopus tetricus* (Octopodidae) is common in estuaries and on rocky shores.

6 An unnamed species of *Octopus* (Octopodidae), one of the *Octopus horridus* group of Papua New Guinea.



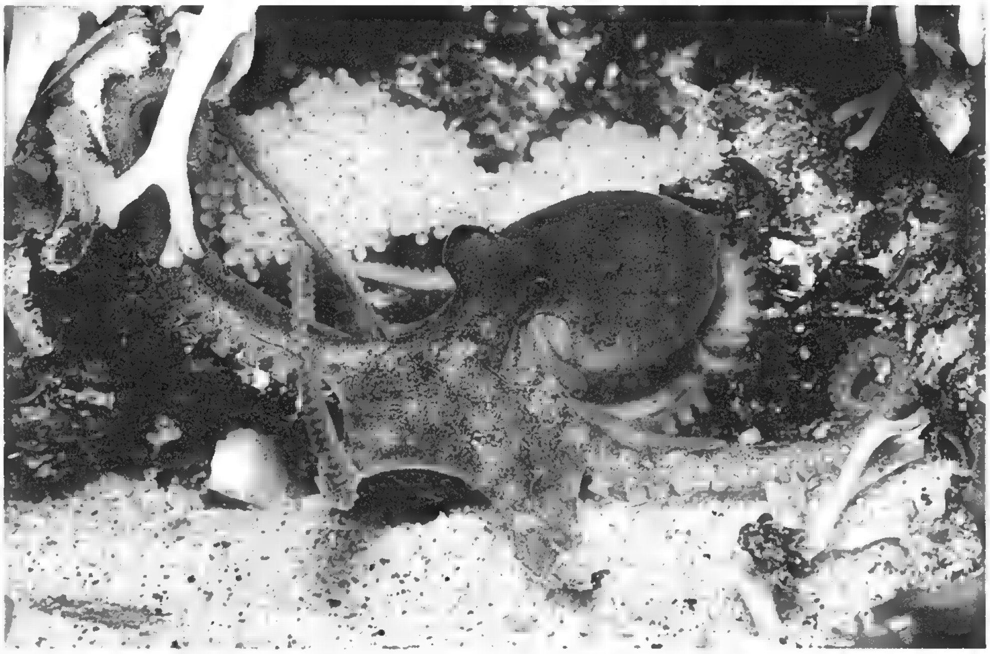


PLATE 20: CEPHALOPODA

1,2 Fighting *Octopus berrima* (Octopodidae), showing (1) pre-fight posture, as they move closer together, and (2) the deflated loser blending with its surroundings, signalling defeat.

3 Hatchlings and eggs of *Octopus berrima* (Octopodidae).

4 Female *Octopus* species (Octopodidae) guarding eggs laid among kelp holdfasts.

5,6 Burrowing behaviour in *Octopus kaurna* (Octopodidae) from southern Australia.

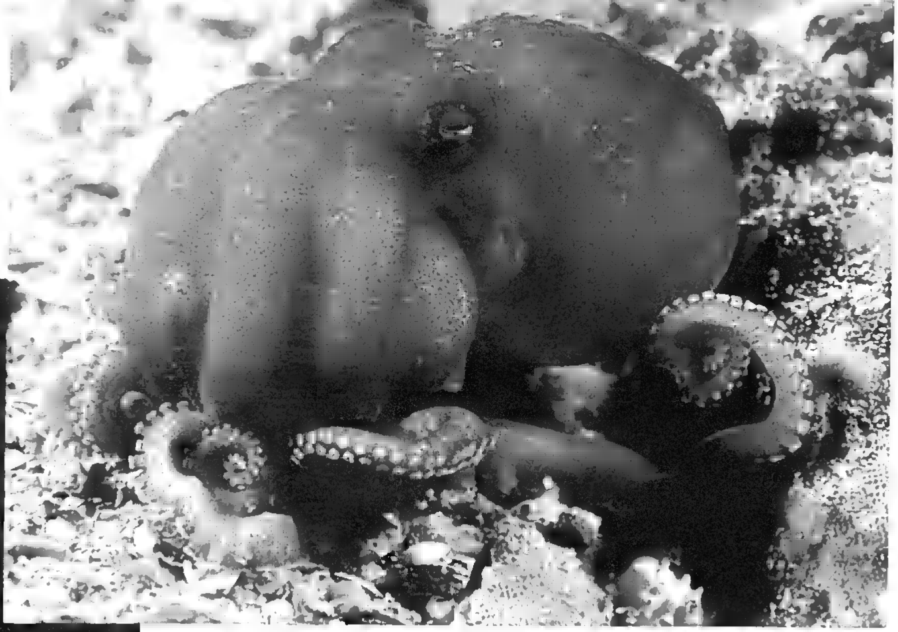


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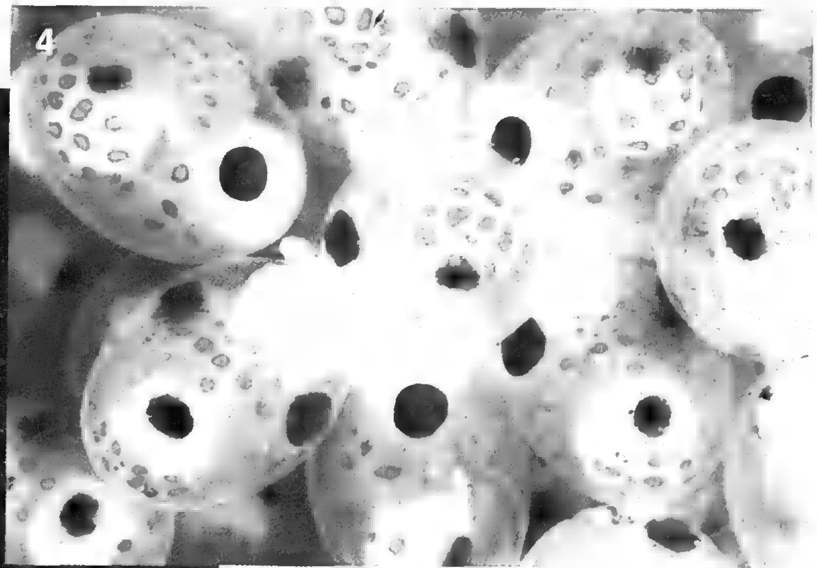
PLATE 21: CEPHALOPODA

1 The endemic *Grimpella thaumastocheir* (Octopodidae) lives in sand, rubble or seagrass habitat off southern and south-eastern Australia.

2 Living *Nautilus stenomphalus* (Nautilidae) is known only from around Lizard Island, Great Barrier Reef, Australia.

3,4,5 Paper nautilus, *Argonauta nodosa* (Argonautidae), from southern Australia, showing (3) a cloud of hatchlings in water on the right of adult female, (4) an egg mass nearly ready to hatch, (5) young hatchlings in front of the female's shell.

4



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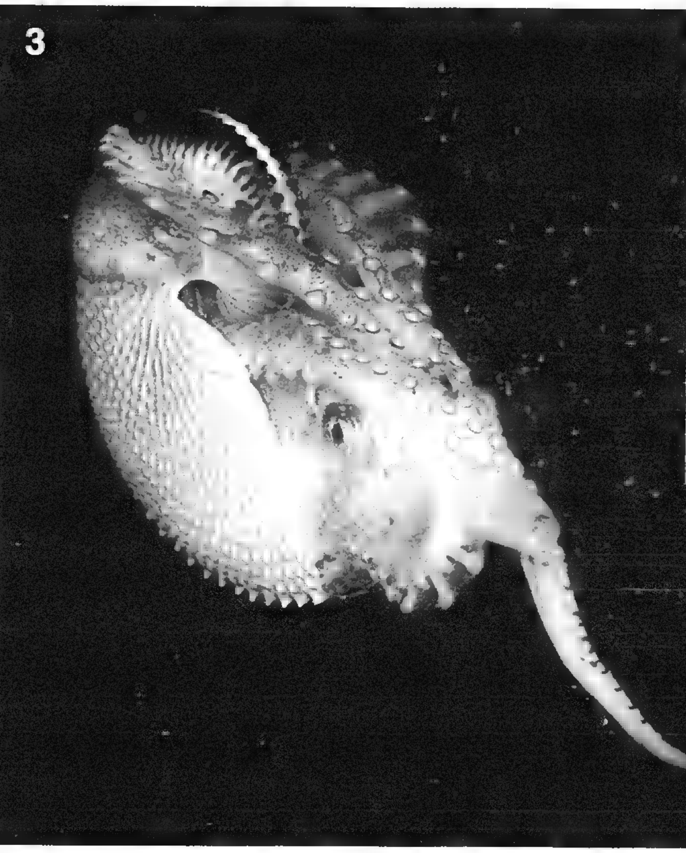


5

material, in which they have bored, as a food resource. The ecology of *Jouannetia cumingii* and *Martesia striata* are reviewed by Moore (1947) and B. Morton (1986a), respectively.

Little published information is available on factors limiting the distribution and abundance of Australian bivalves. To a large extent, these variables reflect physiological limitations. A review of some of these (for example, oxygen concentrations, temperature, suspended particles) can be found in Bayne & Newell (1983). Temperature is probably one of the primary environmental variables limiting the latitudinal and depth distributions, and dispersal patterns of many bivalves. The constraining features of temperature and thermal regime on the physiology, ecology, distribution and behaviour of marine bivalves has recently been summarised by Dame (1996). The impact of temperature on actual survival, physiology and behaviour has also been widely examined (see Newell 1979; Newell & Branch 1980; Buxton, Newell & Field 1981).

Behaviour

Heterodonts are behaviourally diverse, reflecting their habitats and general lifestyles. Burrowing and filter-feeding are associated with the elaboration of a muscular foot and siphons, the byssus being lost in most species. Some adult heterodonts, such as members of the Astartidae and Tridacnidae, are quite sedentary; only juvenile tridacnids have a functional foot. Others, such as the Corbiculidae, are active burrowers and additionally have evolved a means of dispersal that involves extension of the foot, protrusion of the siphons, and wide abduction of the valves in conjunction with active production of a mucoid drogue line to induce drift in the water column (Prezant & Chalermwat 1984). Some sphaeriids disperse via attachment to birds and insects (McMichael 1967; Smith, B.J. & Kershaw 1979). Galeommatids retain an active foot and the ability to produce a byssus for temporary attachment (Ponder, this Chapter). Members of the Mactroidea and Tellinoidea usually retain an active foot involved with rapid burrowing behaviour, although the Solenoidea probably are the fastest of the infaunal burrowing bivalves. Solenoideans can also jet about the surface, using rapid expulsion of water from the mantle cavity for thrust, to escape predators. Some tellinids can rapidly burrow to depths of about 400 mm (Gilbert 1977).

Antipredatory responses of heterodonts, which are often fed upon by crabs, birds, fish and seastars, usually involve rapid burial or leaping escape behaviours. Ansell (1967) described the leaping escape behaviour of some British psammobiids. Similar responses are seen in *Glycydonta* species among the venerids. These, as well as some tellinids and other siphonate heterodonts, can undergo siphonal autotomy as part of a predator escape mechanism. In these shallow-water or intertidal heterodonts, the siphons are utilised as a 'renewable resource' by predators. Cotton (1961) also described several Australian sphaeriids as being active burrowers that used their agile foot for burial.

Gale (1976) and McKee & Mackie (1980) have described a form of 'aestivation' during times of drought for some North American sphaeriids that live in ephemeral ponds. Burrowing into moist sediments is one form of physical protection.

Economic Significance

Heterodonts have been used for various economic and commercial purposes through time. Aboriginal hunter-gatherers frequently included heterodonts in their foray (Allan 1959; on mactrids). *Mactra rufescens* is a common item in Aboriginal kitchen middens in Victoria and is considered to be a worthy fishing bait (Macpherson & Gabriel 1962). Cotton (1961) shows a figure (fig. 172) of *Eucrassatella verconis* being used as a hand-axe by the Tangane people of the Coorong and the Ramindjeri people of Encounter Bay, South Australia.

At least two commercial clam hatcheries for tridacnids have been developed recently near Cairns on the Great Barrier Reef (Heslinga & Fitt 1987). In some early mariculture efforts, giant clam mass cultivation has been very successful, producing up to 22 tonnes/ha/year of meat with 140 tonnes of shell as an additional product (Heslinga & Watson 1985). Production of giant clams by mariculture will not only produce an important food and shell resource, but will help stop destruction of reef habitats and save natural populations, already taxed by other biotic stresses through over collection (see for example, Alder & Braley 1989 on histopathological deaths of *Tridacna gigas* and *T. derasa* from Lizard Island). The incidental impact humans have on reefs of New South Wales has been documented by Kingsford, Underwood & Kennelly (1991).

Heterodonts also are a major food resource for many fish, snails, octopuses, ducks and seabirds, and other predatory organisms including some which have economic importance. Many larger Solenoidea, Veneroidea and Mactroidea are important human food resources. *Donax (Plebidonax) deltoides* is fished commercially in New South Wales (Macpherson & Gabriel 1962; Kailola, Williams, Stewart, Reichelt, McNee & Grieve 1993; see Chapter 1). Also in Australia, local fisheries exist for the venerids *Katelysia scalarina* and *K. rhytophora* (see Chapter 1).

Shipworms have historically caused extensive damage to wooden ships, piers, pilings and other wooden structures in the sea (Turner 1971b). *Martesia striata* still costs millions of dollars each year in protective measures. B. Morton (1983b) reviews the destruction of mangrove timbers by various teredinids, including those of Australia.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Heterodonta have a worldwide distribution, and are present from shallow freshwater systems to the marine abyssal zones. Australia, based on climatic partitioning, can be divided into two principal biogeographical zones: the tropical Indo-West Pacific Region (including northern Australia) and the southern Australia Region (Poutiers 1992). Within these regions, smaller regions and provinces have been defined, through the identification of endemic taxa (Briggs 1974; Pielou 1979).

In Australia, heterodonts are among the most common molluscs in shallow and intertidal marine and estuarine systems and also make up a major component of lentic freshwater systems. The general distribution of described heterodonts in Australian marine, estuarine and freshwater systems can be found in Tate (1887b, 1889), Hedley (1910, 1914b, 1916, 1917), Iredale (1929a, 1930a, 1931, 1939), Cotton (1953, 1961), Rippingale & McMichael (1961), Macpherson & Gabriel (1962), Maxwell (1968), Stephenson *et al.* (1974), Coleman *et al.* (1978), Roberts & Wells (1980), Wells & Threlfall (1980), Wells (1984) and Lamprell & Whitehead (1992).

Endemism at the species level characterises the heterodonts of Australia, especially southern Australia. The distributions of individual groups are left to the subsections that follow (for example see Ponder on the Galeommatoidea, Smith on the Veneroidea, *etc.*). Several cardiids are endemic to temperate Australasia (Poutiers 1992); at the subgenus level *Pratulum* is endemic to Australasia. In fact, Poutiers (1992) suggested that the isolated occurrence of some Protocardiinae could identify the bathyal zone of the south-western Pacific around New Caledonia as a refugium that represents the eastern border of Gondwanaland. Several heterodont groups are presently unknown from Australian waters. These include the Vesicomyidae, Dreissenoidea, Cardiniidae, Bernadinidae, Cooperellidae and Turtoniidae.

Affinities with Other Groups

The evolution of the Heterodonta is summarised by Allen (1985). Scarlato & Starobogatov (1978) summarised views on the early history of the bivalves in general. The taxonomic categorisation used by Allen (1985) is not that accepted in this volume, nevertheless, he offers important insights into the Heterodonta, which is the largest group in the 'subclass' Lamellibranchia. Allen suggests that the tremendous diversity of this group is a primary reason why it is difficult to resolve clearly the evolutionary relationships of the 'lamellibranchs'.

The ancestral stocks for all major bivalve groups were already in existence by the Middle Ordovician (Pojeta 1975, 1978). Runnegar & Bentley (1982) suggested that the microscopic Australian Middle Cambrian bivalve, *Pojetaia runnegari*, was the stock for all higher bivalve taxa. This genus, with specimens measuring no more than 1 mm long, resembles Ordovician palaeotaxodonts, supporting the notion of the protobranchiate bivalves as ancestral to the heterodonts. Waller (1990), however, does not believe that *Pojetaia* was a palaeotaxodont (= protobranch) since the shell microstructure and the ligament differ from those of extant members of this subclass. Nevertheless, he does agree that the heterodonts and all other higher bivalve taxa stem from a protobranch stock.

Significant adaptive radiation took place in the Ordovician, when several heterodont superfamilies appeared. Among these were shallow-burrowing and asiphonate Veneroida; only the Lucinoidea were at that time adapted to a deep burrowing habit (Clarkson 1986). Epifaunal heterodonts did not appear until later in the Ordovician. It appears that mantle fusion and the concomitant development of siphons in the Heterodonta took place in the late Palaeozoic (Clarkson 1986). The development of siphons allowed rapid expansion to diverse habitats. Major radiation of burrowing and siphonate heterodonts, such as Tellinoidea and Myoidea, occurred in the early Mesozoic (Stanley 1968). An excellent discussion of the adaptive radiation of bivalves, including many heterodonts, based on functional morphology, is given by Clarkson (1986). Most phylogenetic links within the Heterodonta are based on shell structure and microstructure, characters that for the most part hold true after long periods of fossilisation. Yonge (1978) suggested that the bivalve ligament is an excellent character for analysis of bivalve phylogenies. A review of the evolution of the bivalve ligament system is given by Waller (1990).

Affinities within the Taxon

There is limited direct information concerning evolution within many groups of Australian heterodonts. Gill & Darragh (1963) have examined the evolution of and relationships within the Zenatiinae, a group of mactrid heterodonts. Present in Australia from the Oligocene to Pleistocene, and New Zealand from Oligocene to present, the subfamily is composed of three genera confined to Australasia. Unlike most mactrids, the zenatiines live in muddy sediments of relatively low energy marine habitats (for example, bays and inlets). *Zenatiopsis* is an extinct genus present in fossil beds from South Australia and Tasmania (Gill 1961). Accounts of other familial relationships are given in the individual sections on heterodont families.

Fossil Record

The fossil record of bivalves in general, including many heterodonts, is very well documented in Australia. A detailed study of Late Palaeozoic molluscs from eastern Australia, including many heterodonts, is given by Waterhouse (1987). In early studies, Tate (1886, 1887a), reviewed the Tertiary heterodonts. Subsequently, Chapman & Singleton (1927) gave cursory coverage to Australian Tertiary bivalves. Various lucinids and carditids have been described by Darragh & Kendrick (1980) from the Eocene Pallinup Siltstone in Western Australia. The age and palaeoecology of Tertiary molluscs from Red Bluff, Victoria, were examined by Gill (1963). A revision of large Tertiary crassatellids from Victoria and Tasmania was presented by Darragh (1965a). Excellent reviews of the Quaternary heterodonts of the western portion of the Eucla Basin and from South Australia were given by Ludbrook (1978, 1984, respectively). The fossil record of the oldest group within the Cardiidae, the Protocardiinae, from Australasia has been described by Poutiers (1992). A review of the fossil record and proposed evolutionary history of the bivalves and the placement of the heterodonts within the proposed history can be found in Cox (1969a).

Classification

Classification of the Heterodonta is not completely resolved, even at the ordinal level. Cotton (1961) divided the bivalves into three orders: Prionodesmacea, Anomalodesmacea and Teleodesmacea. Most Heterodonta, as accepted by most recent authors, would fall into his Teleodesmacea. B.J. Smith (1992), in his work on non-marine molluscs of Australia, utilised a classification that divides the Bivalvia into the order Eulamellibranchia within which is the suborder Heterodonta. The Heterodonta (as accepted by Vokes 1968; Cox 1969a; Abbott 1974; Seed 1983) consists of three orders: the extinct Hippuritoida and the extant Veneroida and Myoida. The Hippuritoida is composed of the extinct, cemented rudist bivalves. The large order Veneroida comprises about 18 superfamilies; the smaller order Myoida comprises four superfamilies. The classification adopted in this volume is outlined in Table 8.1.

Order VENEROIDA

The order Veneroida comprises over a third of all the Recent bivalve species in the world and consists of about 18 diverse and speciose superfamilies worldwide; 15 occur in Australia. Members mainly have a more or less equivalved shell, are dimyarian and are generally active burrowers or nestlers, rarely sessile. They are mainly marine though the order does contain a few important freshwater families. The Australian fauna contains members of all these superfamilies and the order accounts for 50% of the bivalves found in Australia.

The main reasons for the success of the Veneroida, and its great radiation into niches previously not open to bivalves, are considered to be the loss of the byssus in the adult and restriction of the inhalant flow to the posterior mantle margins through an aperture distinct from the pedal gape. These adaptations allowed development of siphons thus enabling these bivalves to exploit soft sediments, many becoming infaunal burrowers, some penetrating well into the sediment (Allen 1985). The radiation of the Veneroida, predominantly in shallow seas in the Triassic and Jurassic, produced a large number of taxa with new body forms and life styles that were ancestral to the diverse lineages within this most successful and diverse of bivalve orders.

Some superfamilies still show primitive bivalve features such as an antero-ventral inhalant current flow (in the Lucinoidea, Crassatelloidea and Cardioidea), some with byssal attachment to hard surfaces, and absence of siphons. Members of the Galeommatoidea include very many microscopic species that are undoubtedly neotenous, showing simple larval features. These include an antero-ventral inhalant flow, lack of posterior mantle fusion, a functional byssus, a simple stomach and a simple gill (Allen 1985). However, many are specialised commensals, frequently host-specific (Boss 1965; Ponder 1967) and many crawl on the flattened sole of the foot like a gastropod.

The primitive form of the shell is round or ovate-triangular in outline and laterally compressed with little ornamentation, and this is seen in the Crassatelloidea, Tellinoidea and Veneroidea. In some groups an increase in ornamentation of the shell assists both in penetration of the sediments and in the maintenance of position once established (Stanley 1969). Shell shape in the Solenoidea has diverged considerably, becoming greatly elongated, and the foot is adapted for fast burrowing through sand by a piston action (Allen 1985). The giant clams, Tridacnoidea, are highly specialised; they are immobile and are modified for living within coral reefs. During their development they have undergone a 180 degree rotation of mantle and shell so that the umbones and hinge are now situated at the anterior end of the large byssal gap (Young 1980). The mantle margins have hypertrophied and the tissue

Table 8.1 Taxonomic summary of heterodont bivalves treated in this volume. Families not yet recorded from the Australian region, either by fossil or living representatives, are indicated with an asterisk.

Subclass HETERODONTA

- Order VENEROIDA
    - Superfamily CHAMOIDEA
        - Family Chamidae
    - Superfamily LUCINOIDEA
        - Family Lucinidae
        - Family Fimbriidae
        - Family Thyasiridae
        - Family Ungulinidae
        - Family Mactromyidae
    - Superfamily GALEOMMATOIDEA
        - Family Galeommatidae
    - Superfamily CYAMIOIDEA
        - Family Cyamiidae
        - Family Neoleptonidae
        - Family Sportellidae
    - Superfamily CARDITOIDEA
        - Family Carditidae
        - Family Condylocardiidae
    - Superfamily CRASSATELLOIDEA
        - Family Crassatellidae
        - Family Astartidae*
    - Superfamily CARDIOIDEA
        - Family Cardiidae
        - Family Hemidonacidae
    - Superfamily TRIDACNOIDEA
        - Family Tridacnidae
    - Superfamily MACTROIDEA
        - Family Mactridae
        - Family Mesodesmatidae
        - Family Cardiliidae
    - Superfamily SOLENOIDEA
        - Family Solenidae
        - Family Pharidae
    - Superfamily TELLINOIDEA
        - Family Tellinidae
        - Family Semelidae
        - Family Psammobiidae
        - Family Solecurtidae
        - Family Donacidae
    - Superfamily ARCTICOIDEA
        - Family Trapeziidae
        - Family Kelliellidae
        - Family Vesicomyidae*
    - Superfamily GLOSSOIDEA
        - Family Glossidae
    - Superfamily CORBICULOIDEA
        - Family Corbiculidae
        - Family Sphaeriidae
    - Superfamily VENEROIDEA
        - Family Veneridae
        - Family Petricolidae
        - Family Glauconomidae
- Order MYOIDA
    - Superfamily MYOIDEA
        - Family Myidae
        - Family Corbulidae
    - Superfamily GASTROCHAENOIDEA
        - Family Gastrochaenidae
    - Superfamily HIATELLOIDEA
        - Family Hiatellidae
    - Superfamily PHOLADOIDEA
        - Family Pholadidae
        - Family Teredinidae

contains symbiont zooxanthellae which provide most of the energy required by the clam. Members of the Chamoidea, the jewel box shells, are mostly sessile in habit, being cemented by one valve to a hard substratum. However, typical heterodont hinge and valve characteristics, obscured in the adults, are seen readily in juveniles.

During the great radiation of the Veneroida in the Mesozoic, in which they came to dominate the soft sediments of the shelf seas, three major evolutionary trends in the form and function of the posterior siphons emerged. First, was the development of short separate siphons as in the Veneroidea and Cardioidea, members of which are shallow-burrowing suspension-feeders. Second, was the development of long, separate, slender siphons allowing burrowing to considerable depth, as in the Tellinoidea; these show great development of particle-sorting mechanisms and of specialised burrowing techniques. Third, in some taxa, such as the Mactroidea, the siphons have combined; many are very long, and these groups are deep-burrowing suspension-feeders.

Superfamily CHAMOIDEA

This superfamily consists of only one family, the Chamidae, commonly known as jewel box shells. The family comprises species which are, at some time in their development, cemented by one shell valve to a hard substratum. This character is shared with a few pteriomorph families within the order Ostreoida, notably the Ostreidae, Gryphaeidae, Spondylidae, Plicatulidae, Dimyidae and some of the Pectinidae. The cemented habit is also shared with a few extant anomalodesmatan groups such as the Cleidothaeridae and some of the Myochamidae. From these taxa, a chamid may be distinguished by the strong elongate amorphous ridges occupying its hinge plate.

Chamid fossil history is generally accepted as extending back to the Palaeocene, though apparently confidently identified fossils have been found in Upper Cretaceous deposits in Europe and Baluchistan (Kennedy, Morris & Taylor 1970).

The origins of this superfamily seem to be among the early veneroids (Allen 1985). Although the group shows no close relationship to any other veneroid family, recent work by Taylor, Kennedy & Hall (1973) on shell characters indicates that, on balance, chamids most closely resemble the Carditoidea from which they might have arisen in the Cretaceous (Kennedy *et al.* 1970). This similarity is further illustrated by the work of Stasek (1963a) on the labial palps, of Purchon (1958, 1960a) on the stomach structure and of Atkins (1937a) on the gill structure and ciliation of these and related groups. There seems not to be any close relationship with the extinct rudists and other hippuritoids (Newell 1969; Vokes 1980), which chamids resemble superficially (Yonge 1967).

Extant and extinct groups are distributed through warmer seas, most being coral reef or rocky shore dwellers in relatively shallow waters. From the fossil record their distribution during the Tertiary appears to have been wider than at present.

Family Chamidae

The members of this family are characterised by being permanently or temporarily cemented to hard substrata (Pl. 13.6). Species of the genus *Arcinella*, which are attached as juveniles, are free-living and epifaunal as adults, whereas *Chama* and *Pseudochama* species are attached throughout life. The attached habit of these species renders their shell morphology vulnerable to the effects of ecological factors, and has resulted in much intraspecific variation and consequent taxonomic confusion. Healy, Lamprell & Stanisic (1993) discuss the phenomenon of left versus right valve attachment in chamids, particularly in relation to valve attachment being used as a reliable feature for distinguishing *Pseudochama* from *Chama*; a key to the Australian species is also given.

Chamid shells (Fig. 8.1A–E) are generally inequivalve, this characteristic being least developed in unattached species, more definitely developed in deeper-water species attached over only a small area and best developed in shallow-water species extensively cemented to exposed, littoral rocks. In general, shell ornamentation follows this same trend. Unattached and deeper-water species exhibit the greatest development of spines and scales, whereas littoral species, particularly gerontic specimens, show reduced sculpture.

The shell is, in general, expanded laterally. Both valves are almost equally convex in unattached forms, but in attached forms the lower attached valve is more convex than the upper. Deeper-water forms show a marked discrepancy in the convexity of the valves, the upper (or unattached) valve often being almost flat and fitting like an operculum over the aperture of the deeply cupped lower valve. This difference in convexity is enhanced by the development in the lower valve of a deep umbonal recess, formed by growth and the migration of the hinge ventrally. The beaks of both valves are strongly prosogyrous, though that of the upper valve may be obscured by the progressive growth of the shell margin dorsal to the hinge line.

The hinge of the dissoconch stage, which is equivalve, regular and unattached, is of the typically heterodont form present in other veneroid groups. However, this tooth structure is later overlain by thick ridges. Two ridges on the attached valve form a socket between them, into which the single ridge on the unattached valve fits. These ridges become more elongate due to the coiling of the shell during growth. They are not considered to be formed from the basic tooth structure, but as a result of the commonly experienced stresses of movement and growth, in a pattern which is similar whether the chamid is attached by the left or the right valve.

The shell is porcellaneous with two crossed-lamellar layers of calcite laid down internal to the periostracal outer layer. The innermost of these layers is of a complex crossed-lamellar structure. Sites of muscle attachment, such as those of the usually almost-equal, elongate adductor muscles and of the entire line of pallial muscles are formed of aragonite. An extra aragonitic layer is also present exterior to the calcitic layer in a few species (Kennedy *et al.* 1970).

The ligament is large, parivincular and sometimes deeply sunken between the slopes of a poorly defined indented escutcheon. This ligament is supported on nymphs, grows at its posterior end and splits anteriorly due to the growth of the dorsal margins of the valves, which progressively separates the two umbones (Owen 1953b).

The opposing lips of the shell valves may be wide and set off at an angle from the slope of the shell interior, forming flat commissures which may be smooth, crenulated or pustulose. They fit together without a gape and are circular or elongate-oval in outline, reflecting (and determining) the shape of the shell. These lips or commissures are elevated, at least posteriorly, above the substratum and the sediment and pseudofaeces which may settle on it. Thinner-shelled deeper-water species are cup-shaped with well elevated lips. In general, shallow-water species with thicker shells are elevated only posteriorly with the upper valve inclined at an angle to the substratum, and with the anterior and antero-ventral margins of the lower valve remaining in contact with the substratum to allow for continuing attachment during growth.

Aspects of chamid internal anatomy are illustrated in Figure 8.1F. The pallial lobes are fused, leaving only a posterior exhalant aperture, a postero-ventral inhalant aperture and an antero-ventral pedal aperture. Except at the dorsal hinge area, only the inner

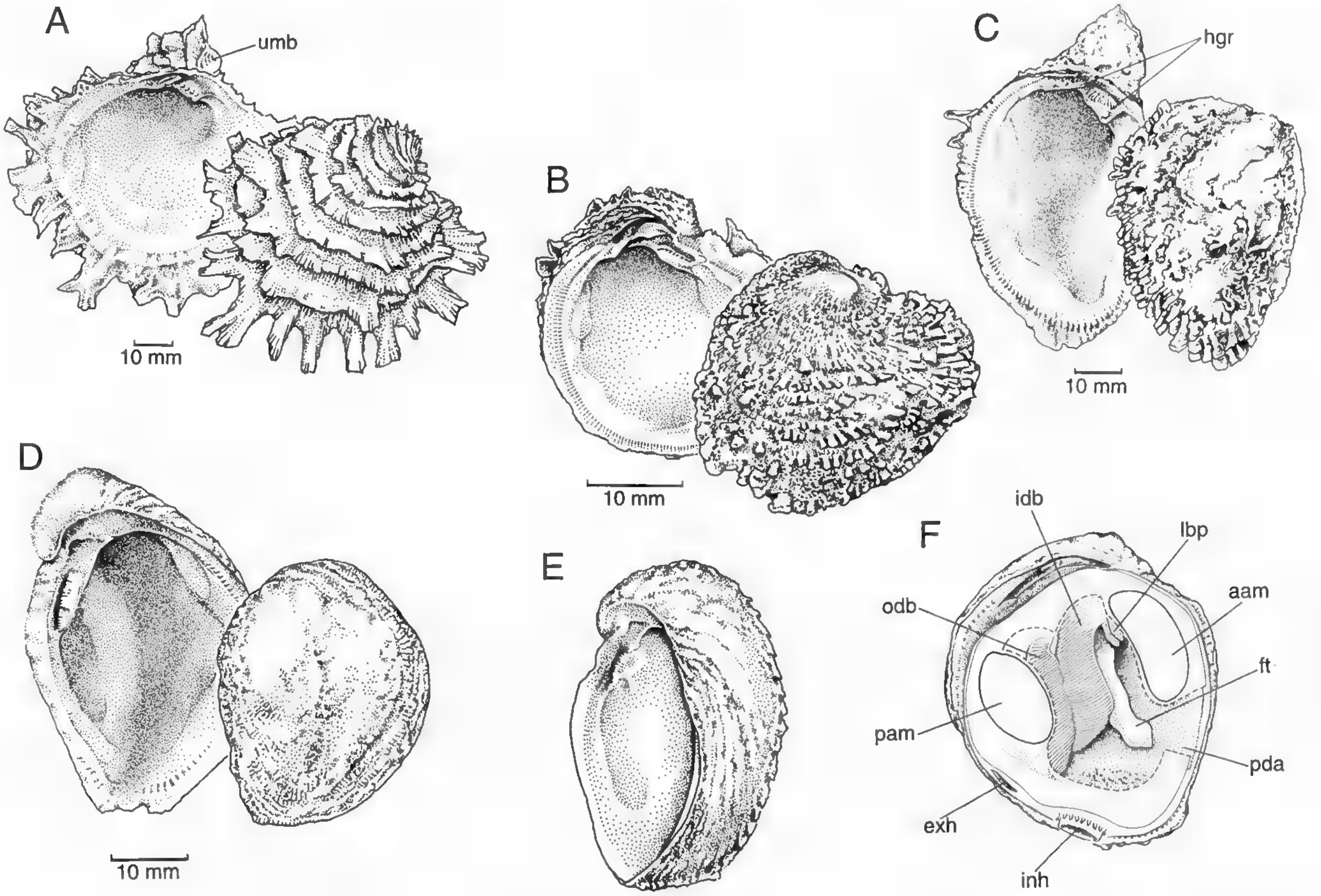


Figure 8.1 Family Chamidae. A–C, shell valves, left valve in internal view, right valve in external view: **A**, *Chama lazarus*; **B**, *Chama ruderalis*; **C**, *Chama pacifica*. **D**, **E**, *Pseudochama* sp.: **D**, right valve, in internal view, left valve in external view; **E**, right valve, lateral view showing the depth of the valve. **F**, *Chama ruderalis*, internal organs, from right, right pallial lobe partly removed. **aam**, anterior adductor muscle; **exh**, exhalant aperture; **ft**, foot; **hgr**, hinge ridges; **idb**, inner right demibranch; **inh**, inhalant aperture; **lbp**, labial palps; **odb**, outer right demibranch; **pam**, posterior adductor muscle; **pda**, pedal aperture; **umb**, umbo. [R. Plant]

folds of the pallial edge participate in this fusion. This fold is papillose in most forms and bears small tentacles in some (best developed in unattached species). It may be expanded to form short, invaginable siphons, and may be glandular, especially around the pedal aperture.

The foot is fairly small and without a byssus or byssal groove in the adult, though some species are known to be temporarily and delicately byssate in the dissoconch stage (La Barbera & Chanley 1971). The foot is laterally flattened, very extensible and appears to function in cleaning the surfaces of the gills and other organs in the inhalant section of the mantle cavity.

The gills are attached to the mantle lobes laterally, and to the visceral mass and to each other medially, so separating inhalant and exhalant chambers. Each consists of two unequal demibranchs which are plicate, eulamellibranchiate and with the filaments ciliated as in Atkins' (1937a) category I. The ventral edge of the inner demibranch and its anterior end, which is joined to the distal oral groove as in Stasek's (1963a) category II, are non-plicate.

The plicate labial palps of chamids are of moderate size. The stomach is of Dinamani's (1967) Section III Group A and of Purchon's (1958, 1960a) Type IV and V (though Allen (1976) doubts the validity of the distinction between these two types). The rectum, after passing through the ventricle of the posteriorly situated heart, opens at the anus on the face of the posterior adductor muscle dorsal to the exhalant siphon. The kidneys lie lateral to the comparatively large pericardium; they are sac-shaped and connect with one another (White 1942).

The sexes are separate, though alternation of sex may occur, at least in some species (Allen 1976), and the gonads develop laterally in the visceral mass. Associated storage of glycogen within the mantle lobes was often mistaken in the past for the extension of the gonads into those organs (Dall 1895; White 1942). The breeding cycle and larval development of chamid species is very poorly known but possibly all species exhibit external fertilisation, with the small fertilised eggs developing into larvae with a long planktonic phase as La Barbera & Chanley (1971) found in a Western Atlantic species.

Chamids are suspension-feeders and most are intolerant of highly turbid conditions. Intertidal species can withstand prolonged emersion in very hot situations. Some species have been collected at depths of up to 200 m but deeper water records are thought to be based on transported material. Chamid species are stenohaline and so are not inhabitants of brackish estuaries (Bernard, F.R. 1976). They are most abundant in the shallow sublittoral zone of open coasts and of rock and coral reefs.

Though chamids were once eaten in Hawaii (Kay 1979) they are reported as being non-edible in Queensland (Allan 1959) and the Aboriginal communities of the Kimberley area do not eat them (S. Smith personal communication).

There are about 70 extant chamid species living in temperate to tropical waters, most in the Indo-West Pacific region (Bernard, F.R. 1976). The Chamidae are a highly successful, but conservative group in which only two genera other than the genus *Chama* are recognised, and these also date from the Palaeogene (Keen 1969a). Most workers consider that this family consists of three extant genera: *Chama* and *Pseudochama*, which are recorded from Australia, and *Arcinella*. The genus *Arcinella* (= *Echinochama*) is restricted to a few temporarily attached species along the Pacific and Atlantic coasts of the Americas where the genus first appeared in the early Miocene (Nicol 1952a, 1952b). Adults usually become detached from the small areas of hard substratum to which they are cemented, to lie with either side uppermost.

Permanently attached chamid species date from the late Cretaceous and are widespread in tropical and temperate seas, though with a geographic distribution restricted to warmer waters than in the past (Odhner 1919). These attached species are regarded as belonging to the diverse genus *Chama* if attached by the left valve, whereas the genus *Pseudochama* comprises far fewer species attached by the right valve (Keen 1969a). However, intraspecific variation in orientation, whether determined by genetic and/or ecological factors or by chance, is still suspected by some workers in some of the many species of the Indo-West Pacific and in at least one of the two southern Australian species.

In Australia, the distributions of tropical Indo-West Pacific species of *Chama* and *Pseudochama* extend from northern waters southwards along both eastern and western coasts. The geographic ranges of some half-dozen wide-ranging tropical species such as *C. lazarus*, *C. iostoma* and *C. pacifica*, overlap those of temperate-water, endemic species *C. fibula* in the south-east and *C. ruderalis* in the south-west. The distributional range of some small deep-water forms of the northern continental shelf and their relationship to similar tropical forms is currently undetermined. The paucity of information on this poorly collected group is illustrated by the doubt concerning the endemicity of a species of *Pseudochama* which is relatively abundant at one of the few well-surveyed areas on the Pilbara coast of Western Australia.

Southern Australian fossils of *Chama* species are recorded from the Miocene of Tasmania and Victoria (T. Darragh personal communication) and from Miocene or Pliocene deposits in South Australia (Ludbrook 1955) and southern Western Australia (G.W. Kendrick personal communication). The oldest record of a chamid from Australia is from the Late Eocene deposits in the Kennedy Range, Carnarvon Basin, Western Australia (G.W. Kendrick personal communication). The paucity of marine fossil deposits in the north of the continent undoubtedly contributes to the rarity of such records.

Other publications which contribute to an understanding of the Australian chamid fauna are those of Hedley (1917) and Thiele (1929–1935). The Australian Chamidae are described and shells illustrated in Lamprell & Whitehead (1992) and Healy *et al.* (1993). Studies that contain information of relevance to the Indo-West Pacific chamid fauna are those by Lamarck (1815–1822), Broderip (1835a, 1835b), Deshayes & Milne-Edwards (1835), Reeve (1846–1847), Tryon (1872), Clessin (1889), Hidalgo (1903), Lamy (1928), Kira (1962), Habe (1964), Kilburn & Rippey (1982), Qiqian (1984) and Delsaerdt (1986). Important studies on chamid anatomy and/or shell morphology include those of Pelseneer (1911), Grieser (1913), Odhner (1919), Owen (1953b, 1955) and Taylor & Kennedy (1969).

Superfamily LUCINOIDEA

The Lucinoidea is a highly distinctive bivalve superfamily, traditionally assigned to the heterodont order Veneroida (Adams & Adams 1854–1858). The shells of this group are usually equivalve and have two muscle scars, the anterior one often narrow and vertically elongate. In shape they are subcircular, oval or subtrigonal, and the outer surface, which usually has a weak periostracum, is often smooth, although radial and commarginal sculpture may occur (Figs 8.3A–D, 8.4A). Lucinoideans are infaunal, usually inhabiting soft or sandy silts. They generally lack a posterior inhalant siphon and have an anterior opening for feeding and respiration, through which they communicate with the water column by way of an inhalant tube constructed by the foot. The Fimbriidae are exceptional in having a definite posterior inhalant opening. A distinct exhalant siphon is present only in the Lucinidae and Fimbriidae. The foot is highly extensible, with the tip in the form of a pointed bulb, capable of secreting mucus that lines the inhalant tube (Fig. 8.3E, F).

The major families are Lucinidae, Thyasiridae and Ungulinidae. Chavan (1969a) added Cyrenoididae, Mactromyidae and accepted the familial status of the Fimbriidae that has been challenged by Allen & Turner (1970) and questioned by B. Morton (1979a). All the families are represented in the Recent Australian fauna except for Cyrenoididae which comprises one genus, *Cyrenoida*, found mainly in the Americas and western Africa (Boss 1969a). Features of the genus *Fimbria* certainly require special consideration, but, although showing affinity with the Lucinidae, it is here treated in a separate family.

All Lucinidae and some Thyasiridae have bacteria in their gills, and engage with these micro-organisms in a sulphide-oxidising symbiosis (Reid 1990). This symbiosis may be the clue to the origin and evolution of the Lucinoidea and it can be argued that the features of the group, and especially the features of the Lucinidae and Thyasiridae are correlated with the symbiosis. Many Lucinoidea inhabit relatively barren, anoxic environments with high levels of free or sediment-bound sulphide that represents an energy source for organisms that possess sulphide-oxidising bacteria or sulphide-oxidising mitochondria. (See Chapter 5, Protobranchia, for a more complete account of sulphide-oxidising symbiosis.) Kauffman (1969) considered the absence of an inhalant siphon to be an adaptation that allows mobility in a deep-burrowing animal, in contrast to the siphonate condition that obstructs locomotion and commits the organism to the liability of energetic investment in sometimes massive siphons. He also considered that the postero-dorsal location of the gills, and the resulting large space between the gills and the inhalant opening are adapted for indiscriminate uptake of particulate matter, allowing physical removal of dense particles before they are filtered by the gills. This arrangement also accommodates the coils of the foot. Reid & Brand (1986) argued that the anterior inhalant opening, the absence of an inhalant siphon, gut-simplification, labial palp reduction, and, in some taxa, gill modification, are all paedomorphic features in a group that has evolved the capability of deriving energy from inorganic sources. Although often a feature of minute bivalves with short life spans, such as certain Veneroidea and Galeommatoidea, in many Lucinoidea paedomorphosis can be correlated with the accommodation of symbionts and the nutritive consequences of the symbiosis. General reviews pertaining to shell morphology of the Lucinoidea are by Dall (1901a), Lamy (1920), and Chavan (1937–1938, 1969a). Atkins (1937a) investigated the gill ciliation; Allen (1953, 1958) reviewed functional morphology; Purchon (1960a) studied gastric morphology; and Kauffman (1969) considered fossil and living Thyasiridae in a general review of bivalve form, ecology and evolution. Various authors have investigated sulphide-oxidising symbioses (reviewed by Reid 1990).

The origins and affinities of Lucinoidea are uncertain. In a radical hypothesis, McAlester (1965) postulated that the Middle Ordovician bivalve genus *Babinka* was ancestral to the Lucinoidea. As several authors have suggested, *Babinka*, with its multiple pairs of muscle scars, could have been one of a line of bivalves newly evolved from a gastropod or monoplacophoran ancestor (Vokes 1954; Cox 1959, 1960; Horny 1960; Ruzicka & Prantl 1960). However, the derivation of an early, undoubted lucinoidean such as *Iliona* from *Babinka* requires the interpolation of a hypothetical intermediate that would have both multiple muscle scars and a vertically elongate anterior adductor muscle scar (which, together with the absence of the inhalant siphon, is taken to be a definitive feature of lucinoideans). Because such a link is missing and the conchological evidence is weak, the ancestral role of *Babinka* remains in doubt (Boss 1969a). Pojeta (1978) provided a recent review of the arguments.

On the basis of shell morphology, the Lucinidae are considered the most primitive family, appearing in the Silurian. The radiation of the Lucinoidea did not occur until the late Mesozoic (McAlester 1966), with the family Thyasiridae appearing in the Cretaceous and the Ungulinidae arising later in the same era. If the Lucinoidea constitute a natural, monophyletic taxon of the order Veneroida, the fossil sequence is puzzling. The youngest family (Ungulinidae) has the Type V stomach (Purchon 1960a) and the double-demibranched, eulamellibranchiate gills characteristic of the Veneroida. The oldest family (Lucinidae) is the most highly derived, so the sequence as it presently stands, seems to be upside down. The stomach structure especially, and the W-shaped gill filaments are unlikely to have arisen by convergent evolution from the simpler structures of the Lucinidae and Thyasiridae, therefore the simplicity of the latter must have been derived by regression (or paedomorphosis). This line of argument is followed by Allen (1958) on the grounds that macrophagy (that is, consumption of relatively large food particles) required specialisation of nutrition and digestion, and by Reid & Brand (1986), who further argued that the nutritional driving force was the possession of a sulphide-oxidising symbiosis by the ancestral lucinoideans. Boss (1969a) contended that the double demibranchs of the Ungulinidae were secondarily derived, and B. Morton (1979a) supported Boss's contention that 'the geological record itself provides a better clue to phylogeny than do inferences based on supposed anatomical features of fossil lineages' (Boss 1970). However, shell morphology is not dictated by the soft morphology in question and it may be argued that the shells of early putative lucinids in fact enclosed ungulinid soft parts, which then became modified regressively to the thyasirid and then the 'true' lucinid conditions. A conservative line, exhibiting the original functional morphology, acquired the superficially ungulinid characters after the Thyasiridae and Lucinidae had diverged. The verified existence of sulphide-oxidising symbiosis in two lucinoidean families requires the re-examination of the whole issue of the putative soft morphology of primitive Lucinoidea, and need not be entirely inferential. Fossil Lucinoidea might be examined for mineralogical data such as the presence of high sulphur levels in the gill regions which would confirm the idea that symbiosis is a primitive condition for the superfamily.

The Galeommatoidea is sometimes aligned with the Lucinoidea, but similarities between the two superfamilies probably result from simplification through paedomorphosis rather than reflecting a close relationship.

There is relatively little published information on Australian lucinoideans. The expedition by Angas, reported by him in 1865, 1867 and 1877, yielded only four lucinid species and one ungulinid species. The *Challenger* produced little more: from the Port Jackson (Sydney) station E.A. Smith (1885) reported two new lucinids and an unidentified *Diplodonta* species (Ungulinidae). Collections at Station 185B offshore from Cape York included two new *Lucina* species collected from coral sand at 155 fathoms, and the inshore Cape York station yielded another new lucinid. Four new species of *Diplodonta* were collected from Torres Strait in water of six fathoms, and three lucinids and two *Diplodonta* species were collected at Station 188, off southern New Guinea, in mud at a depth of 28 fathoms. This station would have been challenging indeed to modern malacologists who are concerned with niche partitioning and the environmental physiology of sulphide-oxidising bivalves. Hedley (1904, 1907, 1909, 1911, 1913, 1917) laid the taxonomic foundations of the Australian-based study of Lucinoidea. Iredale (1924, 1930a, 1936, 1939) made significant contributions, including the erection of several, supposedly endemic genera. Cotton & Godfrey (1938) named six new Australian species. Subsequently, Cotton (1961) listed and described 24 species in Lucinidae, three in Thyasiridae, and five in Ungulinidae, from South Australia. Iredale & McMichael (1962) recorded 24 lucinoidean species from New South Wales. Wells (1984) listed six Lucinidae in his survey of common estuarine molluscs of the south-western area of Western Australia and Slack-Smith (1990) detailed the distribution of 12 lucinid and two ungulinid species from Shark Bay, Western Australia.

Family Lucinidae

Lucinid shells are usually small to medium-sized, thick, suborbicular, ovate or trapezoidal in shape, and occasionally have crenate margins. Strong commarginal sculpture is common, and radial sculpture may combine with this to produce a cancellate pattern, especially posteriorly. Some species have prominent divaricate sculpture. The marked adductor scars are conjoined by a marked pallial scar which indicates the position of the mantle attachment in the living animal. Cardinal hinge teeth vary from a pair in each valve to an obsolete or absent condition. Elongate lateral teeth may be present in the right valve and also in the left valve in some species.

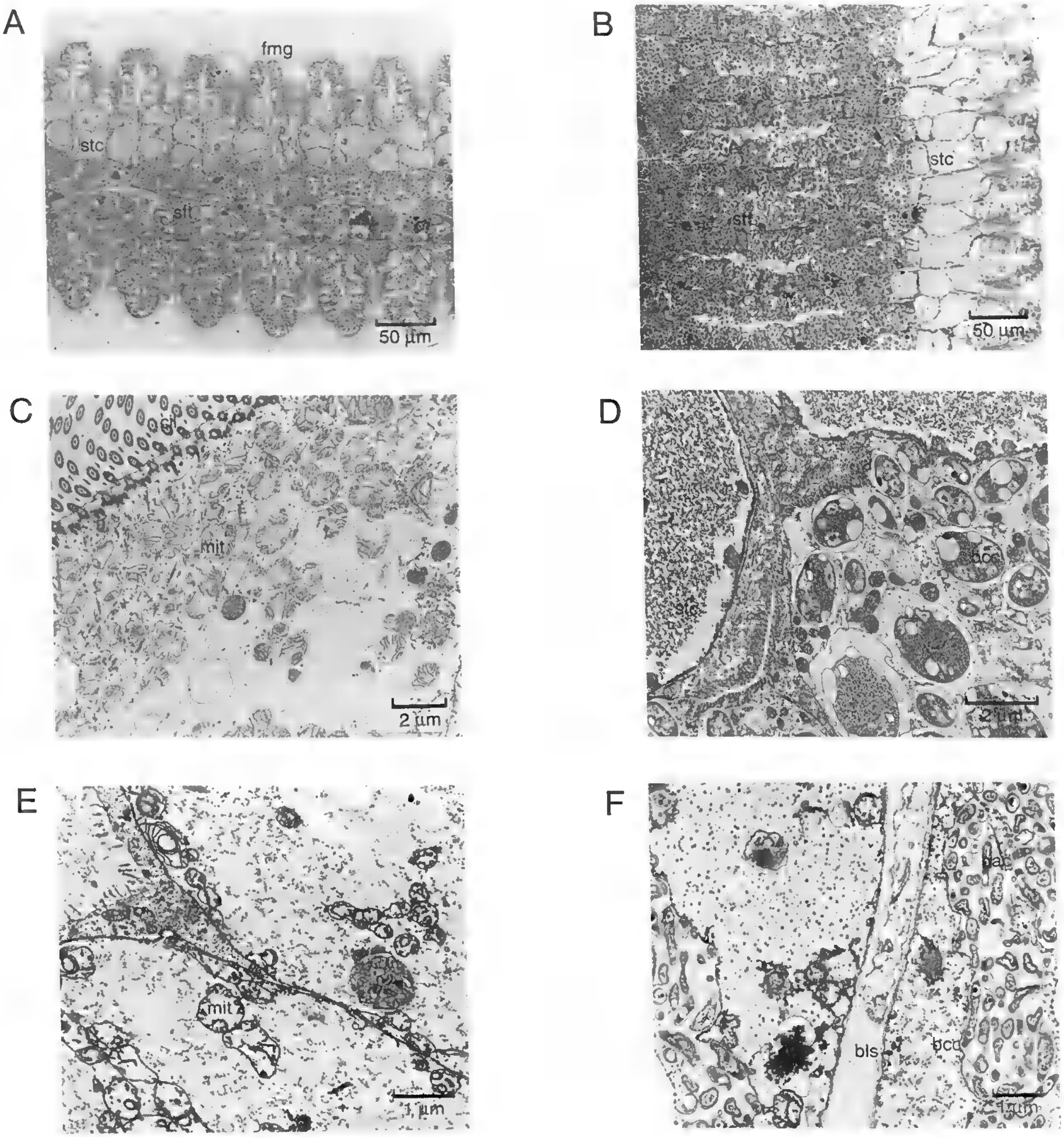


Figure 8.2 Superfamily Lucinoidea. **A–D**, family Lucinidae, *Parvilucina tenuisculpta*. **A**, **B**, light photomicrographs of sections across gill filaments: **A**, near ventral margin; **B**, near centre of gill, black granules are metallic or sulphurous deposits. **C**, **D**, ultrastructure of frontal ciliated margin of gill filaments: **C**, showing cilia and mitochondria; **D**, bacteriocyte and adjacent storage cell in gill, note bacteria in individual vacuoles. **E**, **F**, family Thyasiridae, *Axinopsida serricata*: **E**, subfilamental cells showing mitochondria, storage products and microvilli; **F**, bacteriocytes in the gills, note many bacteria in large bacteriosome at cell margin. **bac**, bacteria; **bcc**, bacteriocyte; **bls**, blood sinus; **cil**, cilia; **fmg**, frontal margin of filament; **mit**, mitochondria; **sft**, subfilamental tissue; **stc**, storage cell. (After Reid & Brand 1986)

Fourteen Recent genera and about 50 species are recorded from tropical and temperate waters of Australia. Among the genera are three first proposed for Australian species by Iredale (1930a, 1936): *Monitilora*, *Nevenulora* and *Divalucina* (Chavan 1969a). *Epicodakia* and *Wallucina* were also accepted as genera by Chavan (1969a).

The lucinid mantle cavity is depicted in Figure 8.3E. The foot forms the inhalant tube, and as in other Lucinoidea is highly extensible. In some taxa, the foot is differentiated into the vermiform structure that makes the inhalant tube, and a short, broad 'heel' that is concerned with locomotion (Fig. 8.3F; Allen 1958). The exhalant siphon is of variable length in Lucinidae. Allen (1958) noted that this organ is unique in the Bivalvia in being formed from the inner muscular lobe of the mantle only; he also generalised that it can be extended to the same degree as the foot, and therefore can extend to the water column.

The feeding appendages and alimentary tract of Lucinidae are reduced in size and complexity. The gills consist of single demibranchs, the filaments forming a V rather than the usual W of the typical heterodont filament (Fig. 8.3G). The ascending and descending limbs of the filament are fused towards the distal margin, and subfilamental tissue forms the gills into narrow lamellae (Fig. 8.3H). Adjacent filaments are joined by numerous tissue bridges. Food particles collected by the gills are transferred to a small, marginal food groove, whence they are carried past vestigial labial palps to the mouth. In the Northern Hemisphere *Parvilucina tenuisculpta*, the posterior portions of the gills are fused dorsally with the muscular mantle edge, the contraction of which may cause a bellows action to supplement the inhalant current normally produced by cilia (Reid & Brand 1986). Since, in a number of Lucinidae, the exhalant siphon may invert into the exhalant, suprabranchial chamber (Allen 1958), water may enter

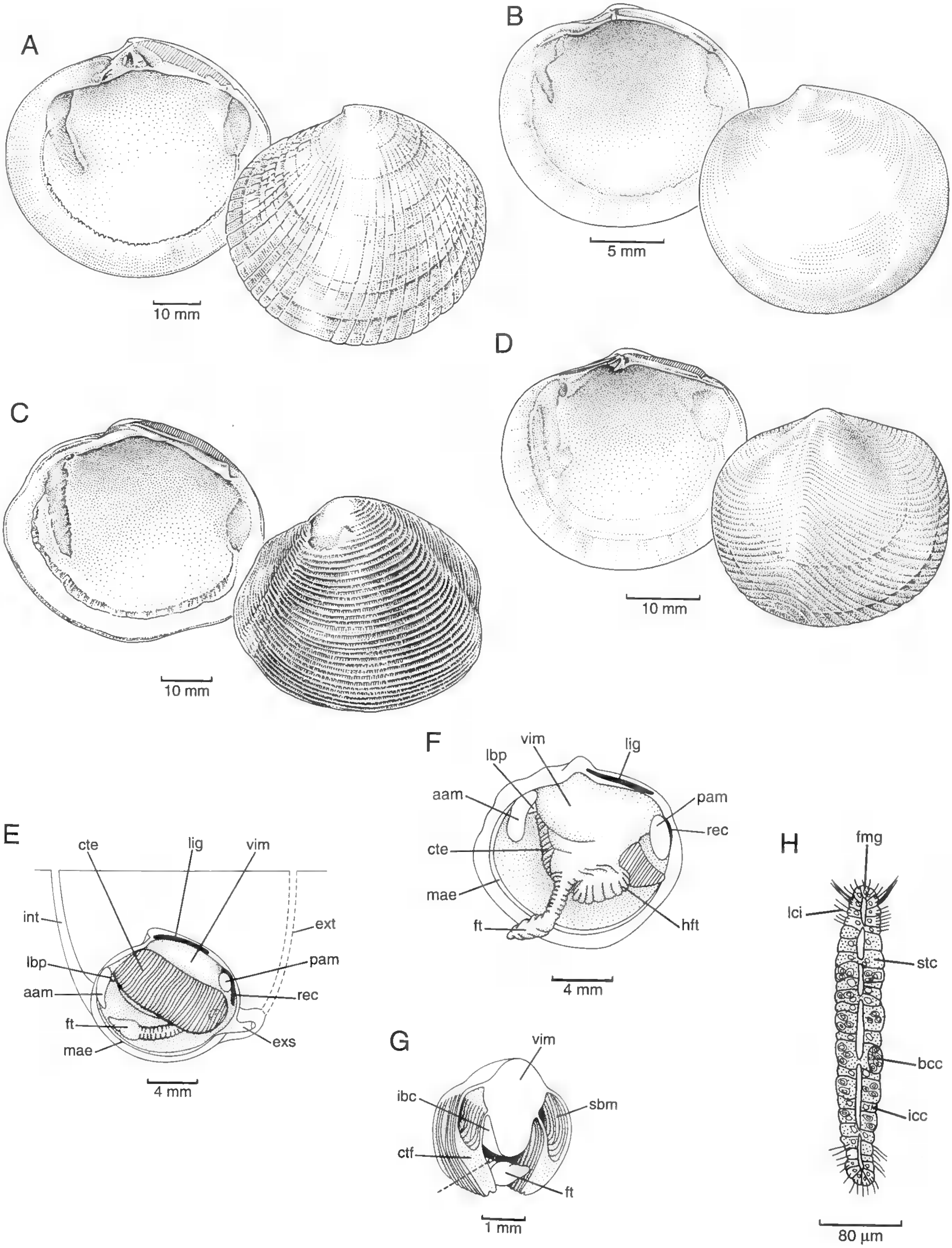


Figure 8.3 Family Lucinidae. **A–D**, shell valves, right valve in internal view, left valve in external view: **A**, *Codakia punctata*; **B**, *Monitilora ramsayi*; **C**, *Austriella sordida*; **D**, *Divalucina cumingi*. **E**, *Parvilucina tenuisculpta, in situ*, showing inhalant feeding tube created by the foot. **F**, *Divaricella quadrisulcata*, with the left ctenidium removed to display the locomotory 'heel' of the foot. **G**, **H**, ctenidia of *Parvilucina tenusiculpta*: **G**, solid section of ctenidial filament, stippled area represents region occupied by bacteriocytes, dashed line shows position of section given in **H**; **H**, cross section of ctenidial filament, stippled area indicates position of bacteriocytes. **aam**, anterior adductor muscle; **bcc**, bacteriocyte; **cte**, ctenidium; **ctf**, ctenidial filament; **exs**, exhalant siphon; **ext**, exhalant tube; **fmg**, frontal margin of gill filament; **ft**, foot; **hft**, heel of foot; **ibc**, infrabranchial chamber; **icc**, intercalary cell; **int**, inhalant tube; **lbp**, labial palp; **lci**, lateral cilia; **lig**, ligament; **mae**, margin of mantle; **pam**, posterior adductor muscle; **rec**, rectum; **sbm**, suprabranchial chamber; **stc**, storage cell; **vim**, visceral mass. (F, after Allen 1958)

[A–D, R. Plant; E–H, C. Eadie]

as well as leave by this route. Allen (1958) interpreted the ciliated surface of the anterior adductor muscle as a supplementary particle-collecting structure that collects additional food and directs it to the mouth. The gut is simplified, the stomach being a comparatively simple ciliated sac with two or three duct openings to the digestive diverticula, whose digestive tubules, which are short, wide and few in number, may be discerned at the surface of the visceral mass, near the base of the foot. A comparative discussion of stomachs in Lucinoidea is given in the section on Ungulinidae below.

In all Lucinidae that have been examined, including 15 species of eight genera, symbiotic bacteria that can fix carbon dioxide and contribute to a sulphide-oxidising symbiosis are present, usually in large vacuoles in bacteriocytes in the subfilamental tissues of the gills (Fig. 8.2A–D). The gill filaments are differentiated into ciliated frontal cells, storage cells containing glycogen and acid mucopolysaccharides, bacteriocytes, and between the latter, intercalary cells with microvillar borders (Fisher & Hand 1984; Dando, Southward, Southward, Terwilliger & Terwilliger 1985; Reid & Brand 1986). Reid (1990) surveyed the current status of information pertaining to this symbiosis in Bivalvia. The subfilamental cells contain a variety of granules, including metallo-phosphoritic and sulphurous components (Reid & Brand 1986). Stored sulphur may constitute an energy store, capable of further oxidation to sulphate (Vetter 1985).

Lucinidae usually occur intertidally or in shallow benthos. Allen (1958) noted that they are commonly found in environments with low nutritive qualities, and often with high sulphide content. The universality of sulphide-oxidising symbiosis in the Lucinidae validates the argument that the morphology of the family has been dictated by the symbiosis, perhaps since its emergence. The first author has found dense populations of *Parvilucina tenuisculpta* in shallow benthic sinks with high organic and sulphide levels and it is common in the vicinity of the main Los Angeles sewage outfall (Stull personal communication). Metal-sequestering granules in the gills of this genus allow it to detoxify metal pollutants. Fisher & Hand (1984) reported *Lucina floridana* in seagrass beds, and Berg, Alatalo, Cavanaugh, Felbeck, Jannasch & Somero (1982) discussed lucinids from anoxic areas of fringing reefs. Read (1962) described the haemoglobin in the lucinid *Phacoides pectinatus* from South American mangroves. This organism has gills that are coloured dark red with the blood pigment which is present also in species of *Myrtea* and *Parvilucina* (Dando *et al.* 1985; Reid & Brand 1986). The function of haemoglobin in animals dwelling in anoxic silts may be in storage of oxygen under respiratory stress, but in view of the ability of some forms of haemoglobin to combine reversibly with oxygen and sulphide (see above in reference to the Solemyidae) it is likely that lucinid haemoglobin is associated with the sulphide-oxidising symbiosis. The ecological distribution of Lucinidae is indubitably correlated with their possession of a sulphide-oxidising symbiosis. Both oxygen and sulphide are required for this symbiosis, and the inhalant tube constructed by the foot is necessary for respiratory ventilation as well as providing a sparse, particulate food supply. Fisher & Hand (1984) reported the curious association of *Lucina floridana* with seagrass, the roots of which appear to supply photosynthetic oxygen.

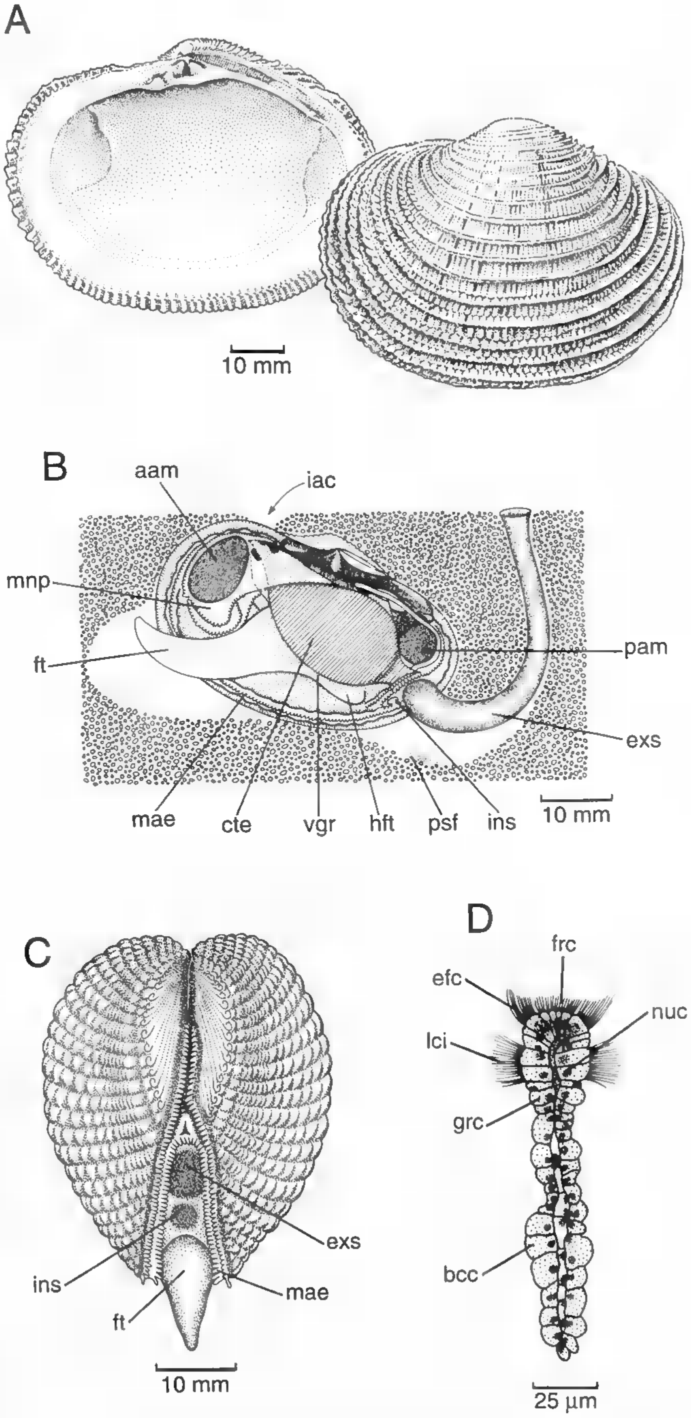


Figure 8.4 Family Fimbriidae. A, *Fimbria sowerbyi*, shell valves, right valve in internal view, left valve in external view. B–D, *Fimbria fimbriata*: B, animal, *in situ*, left valve removed to show pallial morphology; C, animal, posterior view; D, ctenidial filament, transverse section. **aam**, anterior adductor muscle; **bcc**, putative bacteriocyte; **cte**, ctenidium; **efc**, eulatero-frontal cilia; **exs**, exhalant siphon; **frc**, frontal cilia; **ft**, foot; **grc**, granular cell; **hft**, heel of foot; **iac**, inhalant anterior current; **ins**, inhalant siphon; **lci**, lateral cilia; **mae**, margin of mantle; **mnp**, mantle palp; **nuc**, nucleus; **pam**, posterior adductor muscle; **psf**, pseudofaeces; **vgr**, ventral groove. (B–D, after Morton, B. 1979a) [A, R. Plant; B–D, C. Eadie]

Family Fimbriidae

The unique presence of an inhalant siphon, the unusual form and function of the mantle gills (or palps), and the paedomorphic retention of pedal-feeding are distinctive features that may justify the familial status that Nicol (1950) has claimed for the Fimbriidae, although many affinities between the Fimbriidae and the Lucinidae are also apparent.

The shell shape in the Fimbriidae is commonly ovate, with rounded umbones (Fig. 8.4A, C). The hinge is usually massive, with large median cardinals, and laterals are usually present. Adductor scars are small, and there is no vertical elongation of the anterior adductor. The family, which appears in the Carboniferous, includes nine genera, only one of which, *Fimbria*, is Recent. Five species of this rare, but cosmopolitan genus are present in the Australian fauna. *Fimbria fimbriata* is widely distributed in sands in the Tropic of Capricorn, ranging in Australia from Queensland to North West Cape in north-western Australia according to Dr Joyce Allan (cited as a personal communication by Nicol 1950).

Shells of *Fimbria fimbriata* and *F. sowerbyi* are illustrated photographically and a brief description is given of each by Lamprell & Whitehead (1992).

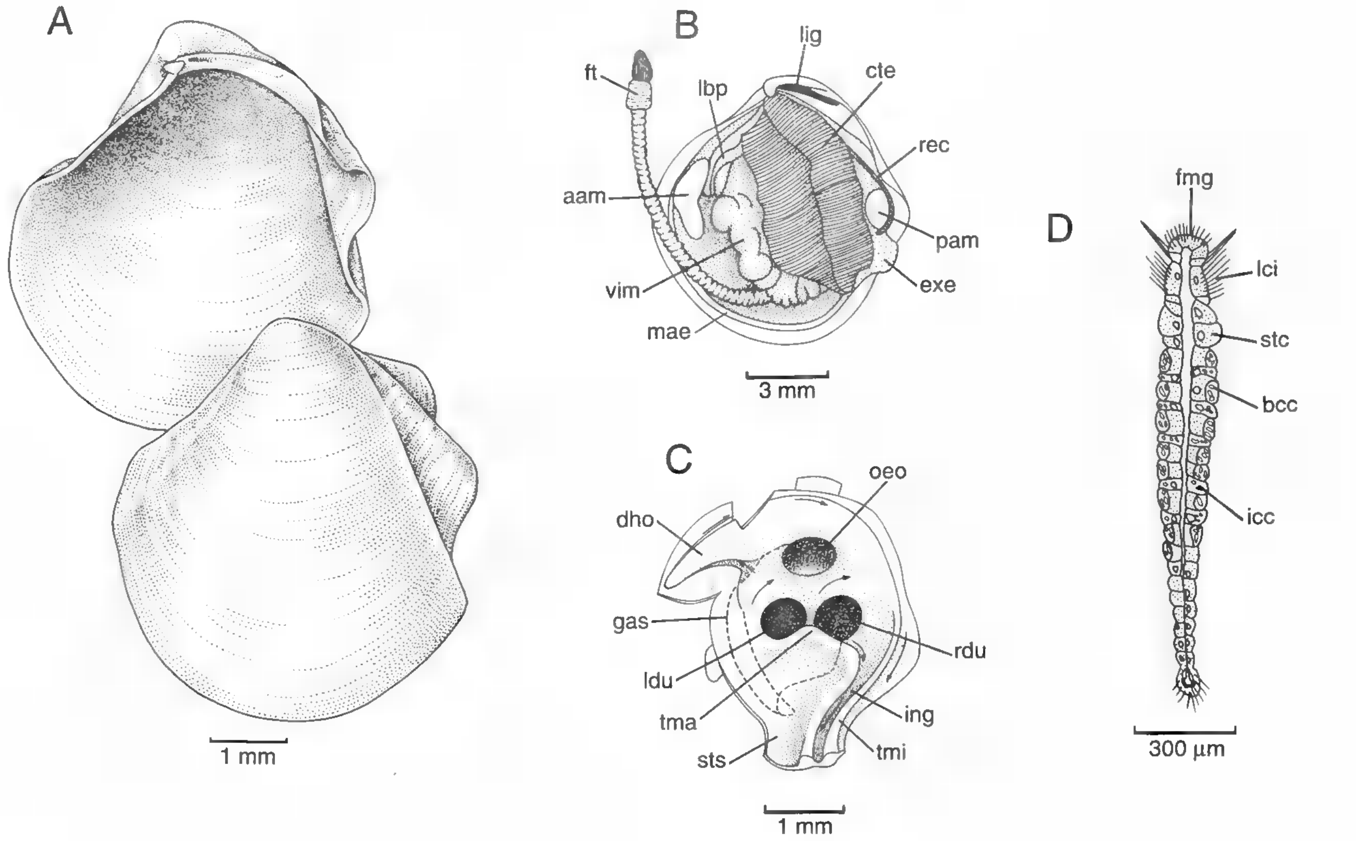


Figure 8.5 Family Thyasiridae. *Thyasira flexuosa*: A, shell valves, right valve in internal view, left valve in external view; **B**, internal anatomy, left view, left shell valve removed; **C**, internal arrangement of stomach, dashed line indicate the position of the gastric shield; **D**, cross section of ctenidial filament. **aam**, anterior adductor muscle; **bcc**, bacteriocyte; **cte**, ctenidium; **dho**, dorsal hood; **exe**, exhalant extension of mantle margin; **fmg**, frontal margin of filament; **ft**, foot; **gas**, gastric shield; **icc**, intercalary cell; **ing**, intestinal groove; **lbp**, labial palp; **lci**, lateral cilia; **ldu**, left duct; **lig**, ligament; **mae**, margin of mantle; **oeo**, oesophageal opening; **pam**, posterior adductor muscle; **rdu**, right duct; **rec**, rectum; **stc**, storage cell; **sts**, style sac; **tma**, major typhlosole; **tmi**, minor typhlosole; **vim**, visceral mass. (B–D, modified after Allen 1958) [A, R. Plant; B–D, C. Eadie]

Fimbriids are reef dwellers in shallow water in coralline sand. They probably burrow shallowly, since the foot is not constructed like that of lucinids for constructing a long anterior mucous inhalant tube. Allen & Turner (1970), who reinstated this genus in the Lucinidae, noted lucinid affinities such as an internal and opisthodetic ligament similar to that of *Codakia*, an invertible exhalant siphon, and simple mantle gills similar to those of the Lucinidae. The thickened gills consist of only the inner demibranchs, the labial palps are small and simple, and the Type IV stomach has three diverticular duct openings. B. Morton (1979a) provided the first detailed description of live *Fimbria* specimens, revealing two important, distinctive features: a short, postero-ventral inhalant siphon, and a pedal-feeding habit. The exhalant siphon can be extended to the water column, and also withdrawn and involuted within the valves. Through the small inhalant siphon pseudofaeces are occasionally extruded (Fig. 8.4B). B. Morton noted that there is a strong inhalant stream created anteriorly by the mantle cilia; the pedal ciliation also contributes to this anterior influx. The foot does not, however, construct an inhalant tube connected with the water column. The ciliary currents of the foot direct particles of potential food towards the ventral gill margins. This is similar to the condition found in the freshwater bivalve *Corbicula fluminea* (Reid, McMahon, O'Foighil & Finnigan 1992). As noted in Chapter 5, a pedal-feeding habit is a universal feature of juvenile bivalves and its retention by *Fimbria* is probably a paedomorphic characteristic. The mantle gills, which B. Morton called 'mantle palps', collect food particles entering anteriorly from the pedal and mantle influx. B. Morton's description of the gill filaments, which have extensive, granular, subfilamental tissue (Fig. 8.4D), is reminiscent of the Lucinidae (Allen 1958; Dando *et al.* 1985; Reid & Brand 1986). The hypobranchial gland is another distinctive character of the genus, presumably related to the formation of copious pseudofaeces.

Although B. Morton described *Fimbria* as a denizen of 'clean' coral sand, we add here that, as Dando *et al.* (1985) noted, some lucinoideans with symbiotic bacteria can utilise the energy of sediment-bound sulphide in aerated sediments. Also the structure of the gills indicates the presence of bacteria and sulphur granules that characterise sulphide-oxidising symbioses.

Family Thyasiridae

The shells of this family are usually thin, somewhat trigonal, and often with a marked postero-dorsal flange or keel (Fig. 8.5A). A translucent periostracum is sometimes present and sculpture is minimal, consisting of fine commarginal striations or folds. Hinge teeth are variable, but usually weak, and both adductor scars tend to be slightly vertically elongate.

Chavan (1969a) listed 11 genera, with five – *Thyasira*, *Leptaxinus*, *Maorithyas*, *Parathyasira* and *Tauraxinus* – occurring in Australia. *Parathyasira* is endemic to Australia, New Zealand and Japan. The composition and biology of the Australian fauna is poorly known; most thyasirids inhabit deeper waters. There may be about eight species in Australia including *Thyasira adelaideana* and *Parathyasira verconis* from southern waters (see Iredale & McMichael 1962; Iredale 1930a). The Northern Hemisphere *Thyasira flexuosa* (Fig. 8.5) is among the better-studied of the thyasirid species.

Kauffman (1967, 1969) provided a detailed reconstruction of the biology of Cretaceous thyasirids, noting that pyrites in the shales containing their fossils indicate an ancient preference for high sulphide, reducing environments like those inhabited by Recent forms. Hickman (1984) made similar inferences concerning the *Thyasira–Lucinoma–Solemya* communities of the Cainozoic.

In their soft morphology, Thyasiridae are similar to Lucinidae, with reduced labial palps and alimentary tracts, but the gills retain a pair of demibranchs, although the outer set are shortened (Fig. 8.5B). *Thyasira flexuosa* has a ctenidial cytology somewhat similar to that of Lucinidae (Figs 8.2F, 8.5D). However, its symbiotic bacteria are in large vacuoles that are arguably not intracellular (Reid & Brand 1986; Southward 1986); see Figure 8.2F. This species inhabits relatively well-aerated sandy silts (Dando *et al.* 1985) and is believed to use sediment-bound sulphides in its symbiotic metabolism (Dando *et al.* 1985; Dando, Southward, Southward & Barrett 1986b; Dando & Southward 1986). Five species of Thyasiridae are known to lack symbiotic bacteria. *Axinopsida serricata* is a case in point: lacking the symbiosis it nevertheless retains the cytological characteristics of the ctenidia of symbiotic Lucinoidea (Fig. 8.2E, F). In the North East Pacific it is, in the first author's experience, the most ubiquitous benthic bivalve of shallow waters, attaining high densities in some areas (Slack-Smith 1994). The clue to its ecology may lie in the discovery by Powell & Somero (1986) that mitochondria in some bivalves (*viz. Solemya reidi*) are independently sulphide-oxidising, so that even in the absence of carbon dioxide fixing bacteria, organisms with such mitochondria may both detoxify environmental sulphide and also derive ATP energy directly from it. The simple thyasirid stomach (Fig. 8.5C) is described in comparison with the ungulinid stomach below.

Family Ungulinidae

Ungulinidae is a senior synonym of the name Diplodontidae, which is descriptive of a diagnostic shell feature for this family: the pair of cardinal teeth, the median being bifid. The shell shape is variable, from round and rotund (Fig. 8.6A) to trigonal or oblong. Sculpture is usually weak or absent. The anterior adductor scar is elongate, but not ventrally separate from the pallial line as in the Lucinidae. The posterior adductor scar is large and sometimes vertically elongate. Chavan (1969a) listed 10 fossil and Recent genera for the Ungulinidae. The genera *Cycladicama* (= *Toralimysia*) (one species), *Felaniella* (three species), *Diplodonta* (three species) and *Numella* (two species) have been recorded from Australia.

Ungulinids retain both demibranchs, the outer set being shortened as in Thyasiridae (Fig. 8.6B). Allen (1958) noted that the gills of Ungulinidae lack the subfilamental fusions that thicken the gills of Lucinidae and Thyasiridae (Fig. 8.6D). The labial palps, although small, retain transverse ridges and grooves that constitute a functional particle-sorting area. The stomach is a typical Type V organ (Fig. 8.6C), characterised by duct caeca into which flaps of the major typhlosole extend, constituting a Type C sorting area (Allen 1958; Purchon 1960a; Reid 1965). A well-developed ridged and grooved posterior sorting area is another character of the Type V stomach. In comparison the stomachs of Lucinidae and Thyasiridae are much simplified, the distinct flaps of the major typhlosole being absent, and the duct caeca being reduced to single duct openings (*cf.* Fig. 8.5C). The posterior sorting area is also much reduced. The Type C sorting mechanism in which the tongues of the major typhlosole deliver gastric juice with suspended food particles to the diverticular duct openings in the caeca is a diagnostic feature. Although Purchon (1958) considered the stomachs of Lucinidae and Thyasiridae to be in the Type IV category, he recognised that their structure may be paedomorphically simplified (Purchon 1978). In gill, labial palp and gastric structure, Ungulinidae are most closely allied to other Veneroid groups, and Allen (1958) and Reid & Brand (1986) contended that the functional morphology of Ungulinidae is primitive and that the condition seen in Thyasiridae and Lucinidae is secondarily simplified. The family has not been surveyed for bacterial symbionts, however Dando, Southward & Southward (1986a) have reported that *Diplodonta rotundata* has no ctenidial bacteria. The absence of subfilamental bacteriocytes in other species indicates that the family is non-symbiotic.

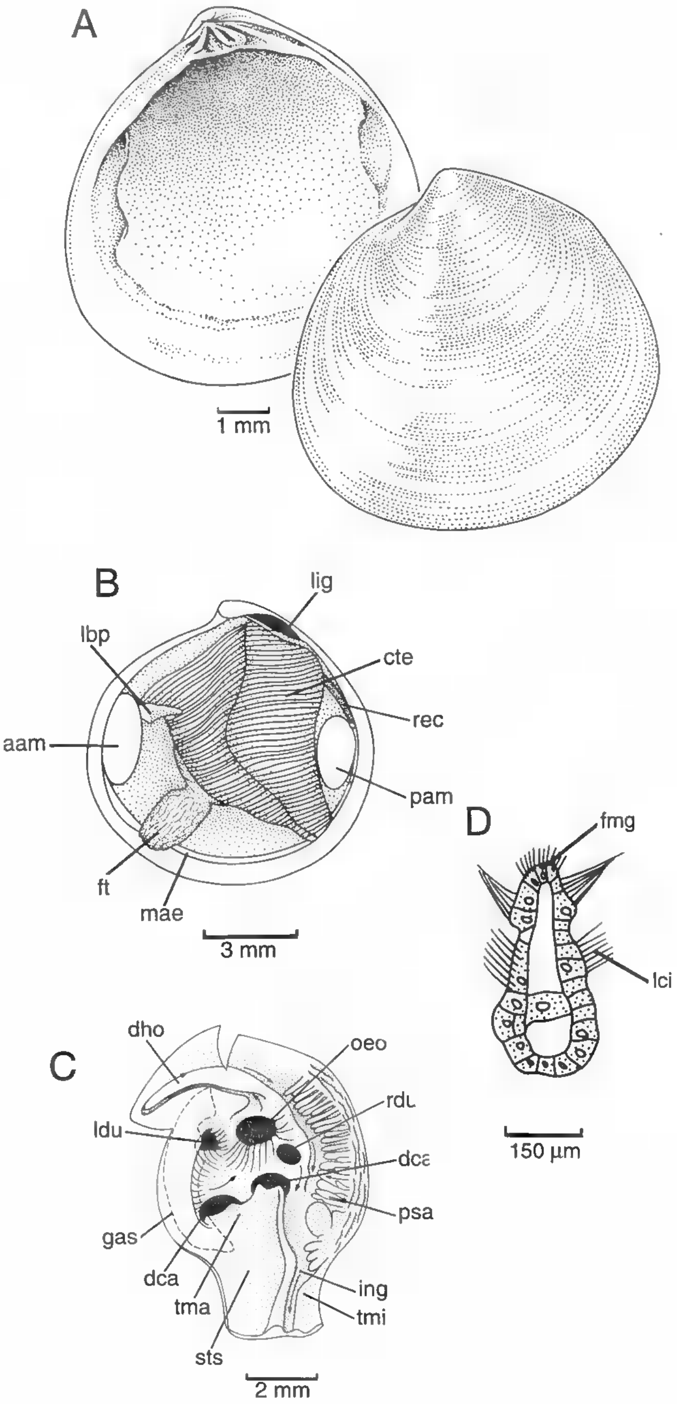


Figure 8.6 Family Ungulinidae. **A,** *Numella adamsi*, shell valves, right valve in internal view, left valve in external view. **B, C,** *Diplodonta semiaspera*: **B,** internal anatomy, left view, left valve removed; **C,** stomach, showing internal arrangement, dashed lines indicate position of gastric shield. **D,** *Diplodonta punctata*, ctenidial filament, transverse section. **aam,** anterior adductor muscle; **cte,** ctenidium; **dca,** duct caecum; **dho,** dorsal hood; **fmg,** frontal margin of filament; **ft,** foot; **gas,** gastric shield; **ing,** intestinal groove; **lbp,** labial palp; **lci,** lateral cilia; **ldu,** left duct; **lig,** ligament; **mae,** margin of mantle; **oeo,** oesophageal opening; **pam,** posterior adductor muscle; **psa,** posterior sorting area; **rdu,** right duct; **rec,** rectum; **sts,** style sac; **tma,** major typhlosole; **tmi,** minor typhlosole. (B–D, modified after Allen 1958) [A, R. Plant; B–D, C. Eadie]

Family Mactromyidae

The shells are globose and often elongated antero-posteriorly, and are commarginally sculptured. The hinge has a simple cyclodont pattern. The anterior adductor scar is not vertically elongated. The family, which appeared first in the Devonian, has 13 genera, of which the Australian genus *Bathycorbis* is the only Recent representative (Fig. 8.7). *Bathycorbis percostata* is recorded from South Australia and *B. despecta* from New South Wales. Little is known of this family.

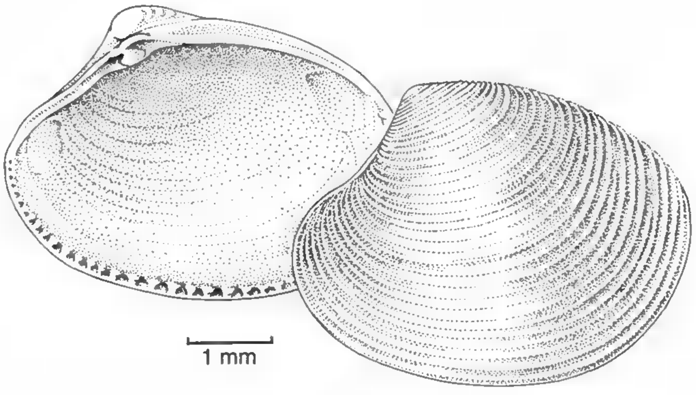


Figure 8.7 Family Mactromyidae. *Bathycorbis percostata*. Shell valves, right valve in internal view, left valve in external view. [R. Plant]

Superfamily GALEOMMATOIDEA

Galeommatoideans are small-sized marine bivalves that often have commensal relationships with other invertebrates. They have equivalve shells and the mantle, which shows varying degrees of reflexion over the shell, is often tentaculate. The inhalant pallial opening is anterior, the exhalant posterior. Siphons, if present, are usually short and composed of the inner mantle lobe. There is a small inner resilium and, rarely, a marginal ligament, and the hinge teeth consist of short cardinal teeth and lateral lamellae. They have an active foot, in many species used for crawling, and a byssus gland and groove are present. The ctenidia have one to two demibranchs, the outer demibranch reduced or lost in many species. The style sac is separated from the stomach and usually from the intestine, and the rectum passes through the ventricle.

Other superfamily names have been used (for example, Leptonoidea, Erycinoidea), but Galeommatidae has precedence over the other family names in the group and, consequently Galeommatoidea is the valid superfamily name. More than one family is often recognised within the superfamily, but these groupings are ill-defined when a range of characters and taxa are considered (Ponder 1971a). For this reason only the family Galeommatidae is used here for the four to five families of the Galeommatoidea (as Leptonacea) recognised by Boss (1982) and Chavan (1969b). Numerous other family names, such as Leptonidae, Mysellidae, Montacutidae and Erycinidae, have also been proposed. There is little doubt, however, that with proper comparative studies based on key taxa, additional family-level groupings will eventually be justified.

Purchon (1987b) has reviewed the anatomical data for this group and placed it in the suborder Unionoida along with the Unionoidea, Crassatelloidea, and Carditoidea, a classification that has yet to gain general acceptance.

Family Galeommatidae

We recognise here only one family, and hence the superfamily diagnosis applies also to the family. Galeommatid shells are small (usually less than 20 mm in length) and typically thin, often fragile, and morphologically diverse (Fig. 8.8A, D, F, I–L). The prodissoconch is small to minute, the umbones small and median to posterior in position. Shells are generally smooth or have a sculpture of radial or, less commonly, commarginal (concentric) or divaricate ribs. The pallial line is simple, and the hinge plate and hinge teeth are strong to very reduced (Fig. 8.8B, C, E, G, H); both the hinge plate and teeth are absent in a few genera. The cardinal teeth are short and there are usually posterior marginal lateral teeth and (sometimes) anterior lateral teeth. A small, variable resilium is usually present in a pit or chondrophore. The less specialised genera have normal shells which close tightly and the animal is contained within the shell. Some genera have the shell gaping widely when the animal is at rest, but can close the shell when disturbed, and in others the shell gapes permanently. In some taxa the shell is enclosed in the mantle and can be reduced, sometimes to a rudiment (Popham 1939; Morton, B. 1981). A few taxa have the shell margin of one or both valves deeply notched (Coney 1990).

Galeommatids have subequal anterior and posterior adductor muscles and both retractor and protractor pedal muscles are present. The foot is well developed (Fig. 8.8I–L) and often modified for crawling on a dorso-ventrally flattened sole and sometimes raised sensory structures are developed on its antero-dorsal surface. There is usually a byssal gland and associated groove and one to a few byssal threads utilised in temporarily anchoring the shell. Some species are highly mobile, and others remain semi-permanently attached. Many galeommatids crawl or creep with their shell held upright, sometimes widely gaping, but, depending on habitat and life-style, burrowing or ploughing are also employed.

The mantle cavity has two openings, the posterior exhalant and anterior inhalant (Fig. 8.8L). The latter is continuous with the large pedal gape. The mantle edge and outer surface often has specialised papillae, tentacles or glands and is reflected over the shell in some taxa, permanently enclosing the shell in a few. The ctenidium is loosely bound with interlamellar septa, smooth and homorhabdic and typically consists of two demibranchs, the outer demibranch often reduced and sometimes lost. Only the inner demibranch has a ventral food groove (Popham 1940; Ponder 1967, 1971a; Morton, B. 1972, 1973a, 1980a).

Despite their often commensal habits (see below), galeommatids are filter-feeders like most other bivalves, only differing from other higher bivalves in the position of the inhalant opening. The oesophagus is usually elongate and the stomach is of Type IV (Purchon 1958, 1987a; Morton, B. 1972, 1973a). The style sac is separated from the intestine and the major typhosole is on the left side of the stomach, near the opening of the digestive diverticula. The gastric shield is well developed and covers a large area of the dorsal and posterior walls of the stomach (Purchon 1987a). Commensal species presumably obtain food from water currents created by their host.

In the heart, the ventricle is traversed by the rectum, the auricles are paired and auricular pericardial glands are present (Morton, B. 1980a). The renal organ lies beneath the heart and encircles the posterior pedal retractor muscles.

Galeommatids either have separate sexes or are protandric or simultaneous hermaphrodites. Dwarf males have been recorded in a few species, sometimes housed in the female's mantle cavity (Morton, B. 1976; O'Foighil 1985a). Dimorphic sperm is known in some species of *Lasaea*, *Montacuta* and *Mysella* (Ockelmann 1965; O'Foighil 1985a, 1985c), these being the only example in the Bivalvia, although it is not known if this condition is common in the family. Sperm transfer by spermatophores has been recorded in a few species (O'Foighil 1985a, 1985b). Larval development is direct or indirect, but all species retain the veliger larvae in the mantle cavity until at least the shelled prodissoconch stage, the larvae being released to develop further in the plankton. The release of larvae, for many species, is usually at its peak during the summer months, but other species release larvae intermittently throughout the year (Booth 1979). Many species, especially of genera from temperate and Subantarctic waters, release their larvae at the crawling stage. Small species with direct development often have very few (less than four) larvae in the mantle cavity. *Lasaea australis* has planktotrophic larvae, a different reproductive strategy from all other species (which have direct development) in this common, intertidal, cosmopolitan genus (O'Foighil 1989).

Galeommatids live in association with many types of invertebrates. Some live beneath stones attached by fine byssal threads, others in tunnels and tubes or on the bodies of some annelids, other bivalves, sea anemones, sea urchins, shrimps and holothurians – see Boss (1965) for a review and B. Morton (1988) and B. Morton & Scott (1989) for details on several associations

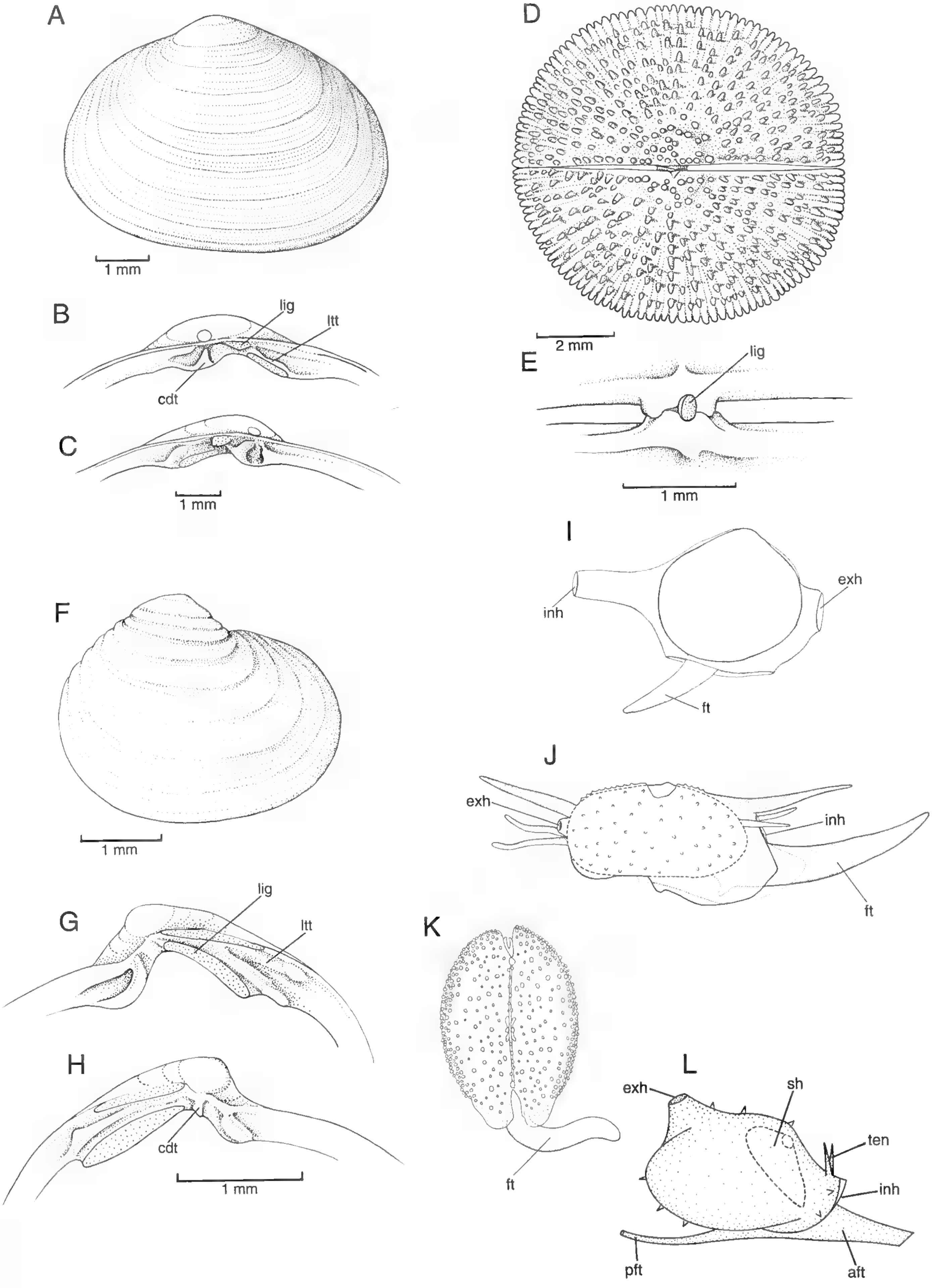


Figure 8.8 Family Galeommatidae. **A–C**, *Marikellia solida*: **A**, left shell valve, external view; **B**, right valve hinge; **C**, left valve hinge. **D**, **E**, *Ephippodonta macdougalli*: **D**, shell, dorsal view; **E**, internal view of hinge. **F–H**, *Lasaea australis*: **F**, right shell valve, external view; **G**, right valve hinge; **H**, left valve hinge. **I–L**, animals, external appearance: **I**, *Kellia* sp., from Sydney; **J**, *Scintilla strangei*, from Sydney; **K**, *Galeomma* sp., from Darwin; **L**, *Phlyctaenachlamys* sp. **aft**, anterior portion of foot; **cdt**, cardinal tooth; **exh**, exhalant aperture; **ft**, foot; **inh**, inhalant aperture; **lig**, ligment; **ltt**, lateral tooth; **pft**, posterior portion of foot; **sh**, shell; **ten**, tentacle. (L, after Popham 1939) [A–K, S. Weidland; L, C. Eadie]

in Hong Kong. Some species of *Entovalva* live in the gut of holothurians, others on the outer surface. No galeommatids are truly endo- or ectoparasitic. Even though they may live in or on the skin of the host, none is known to feed directly on the host's tissues or body fluids. Instead they gain nutrients from the surrounding water. Benefits to the galeommatids include shelter and protection (for example, in a burrow) and the water currents produced by the host. Some galeommatids have been shown to respond to chemical stimuli released by the host, cues for contact with new hosts (see Morton, B. 1973a).

This large family comprises many genera. Some such as *Lasaea* and *Mysella* are cosmopolitan. The European *Lasaea rubra*, like Australasian species of *Lasaea*, lives in the intertidal zone and shows resistance to desiccation when exposed to high temperatures and low humidity (Morton, J.E., Boney & Corner 1957). This species also absorbs and regrows the crystalline style in conjunction with tidal movements (Morton, J.E. 1956). Species of *Mysella* have triangular shells, shortened posteriorly and obliquely elongate in front. Several species occur in Australia, but their taxonomy, like that of the rest of the family, is very poorly resolved. The mantle edge of *Mysella* is not reflected over the shell and the foot is large and modified for burrowing (Popham 1940; Ponder 1967). *Arthritica* (see Ponder 1965; Morton, B. 1973b; Chanley & Chanley 1980; Wells & Threlfall 1982) is represented by at least one free-living species in Australia, which is very common in estuarine lagoons in the temperate half of the continent. They have ovate shells and the mantle edge is not reflected over the shell and is fringed with small tentacles. The cosmopolitan genus *Montacuta*, species of which typically live on heart urchins, is also represented in Australia (Boss 1965; Ponder 1968). A probably related genus, *Montacutona*, lives in the tubes of the burrowing anemone *Cerianthus* (Ponder 1971b; Morton, B. 1980a). *Myllita* species have ovate shells with divaricating sculpture and occur mostly in the south-western Pacific, there being at least seven species in Australia. Species in this group have a tentaculate mantle edge which is not reflected over the shell (Ponder 1967). The genus *Borniola* has oval shells with fine radial sculpture and is represented in Australia by two named species, one common in New South Wales. They live byssally attached beneath stones and have a non-reflected mantle (Ponder 1967). *Isoconcha (= Benthoquetia) integra* and *Mesothuria* is commensal on the deep-water holothurian *Mesothuria* (Ponder 1968) in Australia and New Zealand. *Marikellia* is a genus represented in Australia by a few common species that have oval, solid, inflated shells with a smooth exterior and a reflected, tentaculate mantle (W.F. Ponder personal observation). *Kellia* is a taxonomically problematic genus, with common species in Australia, several of which have been incorrectly included in *Marikellia* from which they differ in having a simple non-reflected mantle (Popham 1940; W.F. Ponder personal observation), and a few species have the mantle extended into a long inhalant siphon (Fig. 8.8I; Yonge 1952). Species of *Lepton* have been named from several parts of the world, five from Australia, although the generic placement of some of the Australian species is questionable. Species of *Lepton* typically have ovate, subquadrangular, flattened valves and a tentaculate mantle. Many species of *Scintilla* occur throughout the Indo-West Pacific including Australia and have thin shell valves, which are largely subelliptical and straightened on the hinge margin, and are covered with a tentaculate (Fig. 8.8J) or papillate mantle (Ponder 1967; Morton, B. & Scott 1989). *Galeomma* occurs worldwide and several species, at least, occur in Australia, some of them undescribed. These species hold the valves wide apart (Fig. 8.8K; Popham 1940; Morton, B. 1973a). This habit is taken to extremes by *Ephippodonta* (Fig. 8.8D; Pl. 13.5) which comprises three Australian species and at least two in South-East Asia. The Australian species of *Ephippodonta* and *Axius plectorhynchus* live in the burrows of the mud shrimp *Axius plectorhynchus*, and they hold the valves permanently spread and have a thickened ventral mantle with a slit through which the foot emerges (Cotton 1938). *Galeomma (Paralepida) takii* lives under stones (in Japan and Hong Kong) and has numerous pallial tentacles which it can autotomise; it is thought to release a noxious substance to deter predators (Arakawa 1960; Morton, B. 1973a). Species of *Phlyctaenachlamys* and, an Australian genus, are commensal in the tubes of the Mantis Shrimp *Lysiosquilla maculata* and has a much reduced shell contained in a mantle sac (Fig. 8.8L; Popham 1939). There are also several similar undescribed species. Other unusual species have been described from stomatopod borrows from Florida (Mikkelsen & Bieler 1989) and New Zealand (Judd 1971).

No comprehensive reviews of Australian species have been published except Laseron's (1956) revision of the New South Wales species of 'Leptonidae', which also included several taxa no longer considered to be galeommatids. A great deal of work remains to be done on this group. Not only are the family and genus level groups much in need of review, but a large proportion of the Australian species are not described, and almost nothing is known of the biology of even the common taxa. The only reasonably well known Indo-west Pacific fauna is that of Hong Kong (Morton, B. & Scott 1989).

The earliest probable galeommatid fossils are from the Cretaceous, with definite fossils from the Palaeocene. Fossil species in this group are so poorly known in Australia that no meaningful statement can be made about their local fossil history.

Superfamily CYAMIOIDEA

The families in this superfamily are united by their simple, short posterior siphons which lack retractor muscles and are surrounded by short tentacles. Pedal protractor muscles are absent. A byssal gland and groove is present or absent, one group (Gaimardiinae) being byssally attached to algae, others free-moving crawlers or shallow-burrowers (for example, Neoleptonidae and some Cyamiinae). The shell is diverse, with cardinal and lateral teeth present, the ligament external or sunken into a resilifer, and a shallow pallial sinus is present.

The grouping of families is somewhat tentative as only very limited data are available on cyamioidean morphology. For this reason also, and because many of their characters may be simplified by heterochrony, the relationships of the superfamily are not clear cut.

The gill is composed of one or two demibranchs, the outer, if present, is typically smaller than the inner and may lack a food groove. Larval development is planktonic or direct; the larvae are often brooded.

Three of the four families recognised in this superfamily by Chavan (1969c) occur in Australia, the Cyamiidae, Neoleptonidae and Sportellidae. Cyamioideans are often confused with galeommatoideans and their shells are sometimes difficult to distinguish. However, galeommatoideans never have a pallial sinus, and the inhalant aperture located anteriorly, not posteriorly as in most other bivalves, including cyamioideans.

Sportellids are known from the Jurassic (Chavan 1969c), but generally there is a poor fossil record of the group, neoleptonids and cyamiids being first recorded from the mid Tertiary.

Family Cyamiidae

These small marine bivalves have equivalve, usually thin shells. They have subequal anterior and posterior adductor muscles and lack pedal protractor muscles (Fig. 8.9H). The hinge plate is weak to broad and sometimes has a well-defined resilifer; cardinal and lateral teeth are present but may be reduced. The outer demibranch, if present, is smaller than the inner, and the foot has a byssal gland and groove. The eggs and larvae are brooded.

This family includes the taxa previously attributed to the Perrierinidae and Gaimardiidae, although the latter is maintained as a subfamily by Ponder (1971a). Previous authors (for example, Fleming 1969; Thiele 1929–1935) have given the Gaimardiinae superfamily status. The Gaimardiinae have been said to be closely related to the Arcticoidea or higher veneroids (for example McCormick & Moore 1969). B. Morton (1979b) regarded Gaimardiidae and Cyamiidae as being separate, closely related families.

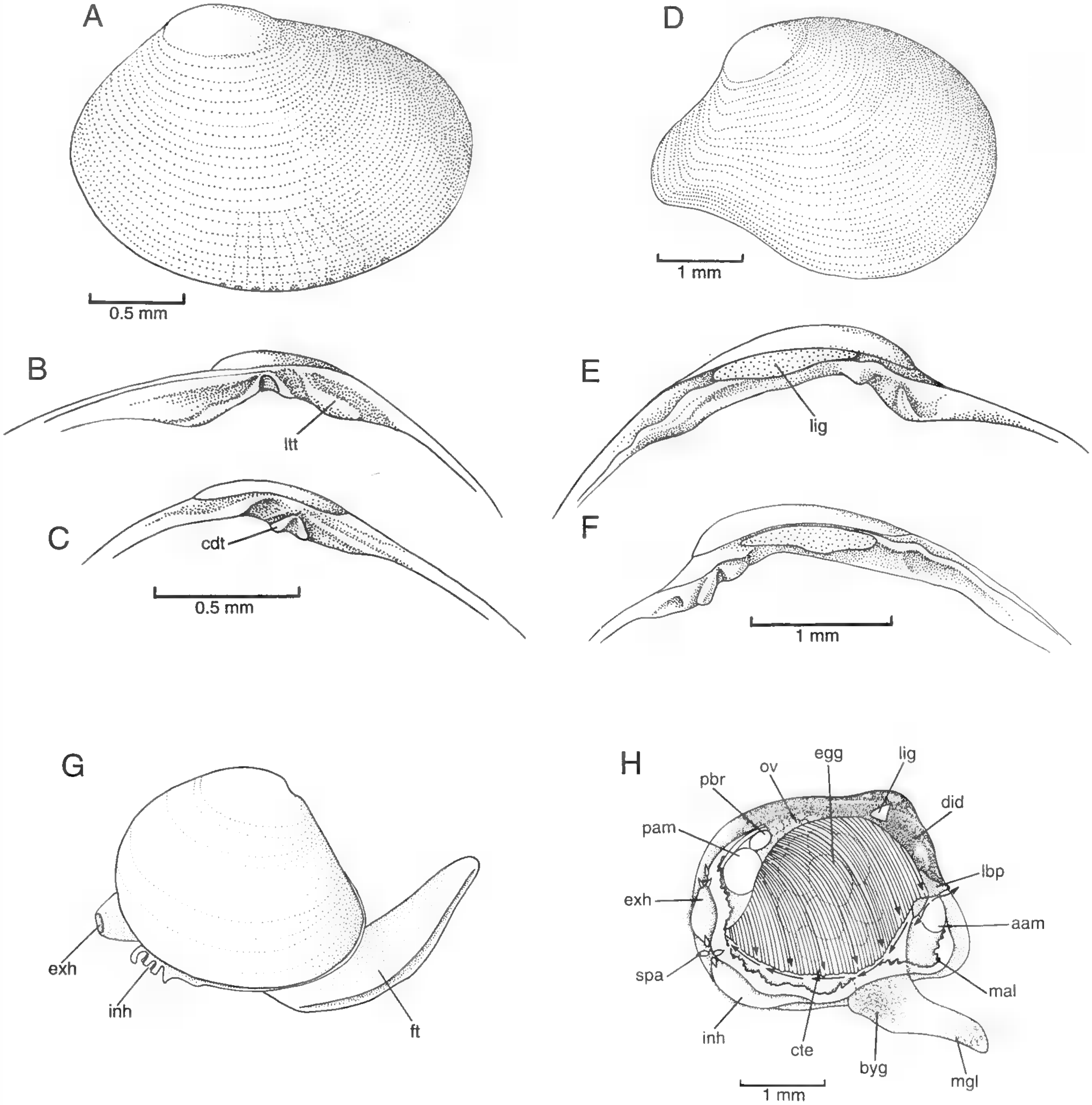


Figure 8.9 Family Cyamiidae. **A–C**, *Cyamiomactra communis*: **A**, right shell valve, external view; **B**, right valve hinge; **C**, left valve hinge. **D–F**, *Gaimardia (Neogaimardia) tasmanica*: **D**, right shell valve, external view; **E**, right valve hinge; **F**, left valve hinge. **G**, *Cyamiomactra* sp., animal from Albany, Western Australia, lateral view. **H**, *Gaimardia (Neogaimardia) finlayi*, internal organs, right view, showing the ciliary currents of the ctenidium, right mantle lobe and shell valve removed. **aam**, anterior adductor muscle; **byg**, byssus gland; **cdt**, cardinal tooth; **cte**, ctenidium; **did**, digestive diverticula; **egg**, an incubating egg; **exh**, exhalant aperture; **ft**, foot; **inh**, inhalant aperture; **lbp**, labial palp; **lig**, ligament; **ltt**, lateral tooth; **mal**, cut edge of mantle; **mgl**, mucous gland; **ov**, ovary; **pam**, posterior adductor muscle; **pbr**, posterior byssal retractor muscle; **spa**, sensory papilla. (H, after Morton, B. 1979b) [A–G, S. Weidland; H, C. Eadie]

Shells are small to medium-sized (usually less than 40 mm in length), equivalve, rounded to elongate, thin-shelled, sometimes inflated, equilateral to inequilateral, colourless or with orange to red colour, and smooth or with weak radial sculpture (Fig. 8.9A, D, G). Shells are aragonitic and have the outer and inner fine granular homogenous layers separated by a prismatic, pallial myostracum (Taylor *et al.* 1973). Umbones are generally near central in position (Fig. 8.9B, C, E, F). The cardinal teeth are elongate and diverging, one of them bilobate in some genera. The lateral teeth are separated from the cardinal teeth and, in some Gaimardiinae, all teeth may be reduced. The ligament is external or sunken and opisthodetic. Species of *Perrierina* have several oblique, subparallel, taxodont-like folds resembling lateral teeth. The pallial sinus is very shallow.

Aspects of the internal anatomy are illustrated in Figure 8.9H. The adductor muscles are subequal, the anterior sometimes reduced in size. Anterior and posterior pedal retractor muscles are present. The foot is small to moderate in size and usually has a byssal gland and a ventral groove, most species being byssally attached to varying degrees of permanence, especially in the Gamardiinae. Locomotion is achieved by crawling, although this can be slow and somewhat laborious in adult Gaimardiinae but faster in small individuals (Morton, B. 1979b). Free living members of the Cyamiidae (for example, species of *Cyamiomactra*) are efficient crawlers and shallow burrowers (W.F. Ponder personal observation) whereas *Gaimardia* lives byssally attached to algae.

The mantle edges are usually papillate posteriorly, but not antero-ventrally (Fig. 8.9G). There are three pallial apertures: a postero-dorsal exhalant aperture, a postero-ventral inhalant aperture, and a broad antero-ventral pedal aperture. There are no siphonal retractor muscles. The outer demibranch (if present) is reflected over the gill axis and is shorter than the inner demibranch. It is not clear if food grooves are present on both demibranchs. The only species studied in detail is the New Zealand *Gaimardia (Neogaimardia) finlayi*, which only has an inner demibranch (Morton, B. 1979b).

In cyamiids the ciliary currents of the mantle are directed forward dorsally. Ventrally they are directed downwards and backwards into a major rejectory tract on each lobe (Fig. 8.9H). Pseudofaeces pass along these rejectory tracts and eventually are discharged from the dorsal section of the inhalant aperture and not from the ventral region of the inhalant siphon, which is typical for most eulamellibranchs (Morton, B. 1979b). The labial palps are very small. The style sac is sometimes briefly conjoined with the midgut and the stomach has no accessory caeca (Morton, B. 1979b).

The heart has the ventricle traversed by the rectum and has paired auricles. The renal organ has two parts, a long, narrow proximal portion and a distal sac-like portion, usually conjoined (Morton, B. 1979b).

The sexes are separate, and a few large eggs are incubated (Fig. 8.9H). Larval development is direct and the young bivalves are nurtured to the crawl away stage. The site of release of the juveniles is not known but it is presumed to be the exhalant siphon (Morton, B. 1979b), at least in *Gaimardia*.

Gaimardiines live attached to intertidal or shallow subtidal algae (Cotton 1961; Fleming 1969; Ponder 1971a; Morton, B. 1979b). Free-living cyamiids such as *Cyamiomactra* live as shallow-burrowers in soft sediments from the low intertidal to the continental shelf.

This family has a southern distribution with several genera restricted to the Australasian region. *Cyamiomactra* is represented in Australia by at least seven species and also occurs in New Zealand, the Antarctic and Subantarctic. *Perrierina* is represented by one species in Australia. *Gaimardia (Neogaimardia)* has two Australian species. *Eugaimardia*, based on a South Australian species, differs from *Gaimardia* in lacking a ventral sinuosity and an anterior rostrum, and is of uncertain affinities.

The oldest fossils attributed to this family, are in the genus *Cyamiocardium* from the Late Palaeocene of Victoria, Australia (Darragh 1994). The fossil genus *Dicranodesma* has been recorded from the Miocene of North America (Chavan 1969c).

Family Neoleptonidae

Neoleptonids are small marine, equivalve bivalves which superficially somewhat resemble galeommatoideans in shell morphology, but lack a byssal gland and have a shallow pallial sinus and a pair of posterior branchial openings. Like other members of the superfamily they lack pedal protractor muscles. The outer demibranch is reduced and sometimes the ascending lamella is lost. Neoleptonids differ from cyamiids mainly in hinge characters.

This group was originally included in the Galeommatoidea but was later placed in the Cyamioidea by Thiele (1929–1935), who also established this family. Anatomical accounts by Soot-Ryen (1960) and Ponder (1969) form the basis for our knowledge of the family. Almost nothing is known of the taxonomy of this group in Australia – neither the number of species, nor even of genera is known. Micropolidae is a junior synonym of Neoleptonidae.

Shells are small (less than 20 mm in length), equivalve, typically rounded to subequilateral and usually slightly thickened (Fig. 8.10A, D). The valves are sometimes higher than long and are smooth or commarginally (concentrically) sculptured. Each valve has an inner and outer layer, separated by a prismatic pallial myostracum (Boss 1982). The hinge plate is broad and arched, the central umbonal resilium bordered by one or more cardinal teeth (Fig. 8.10B, C). The lateral teeth are elongate and the submarginal teeth are lamellar and typically hooked over the internal ligament.

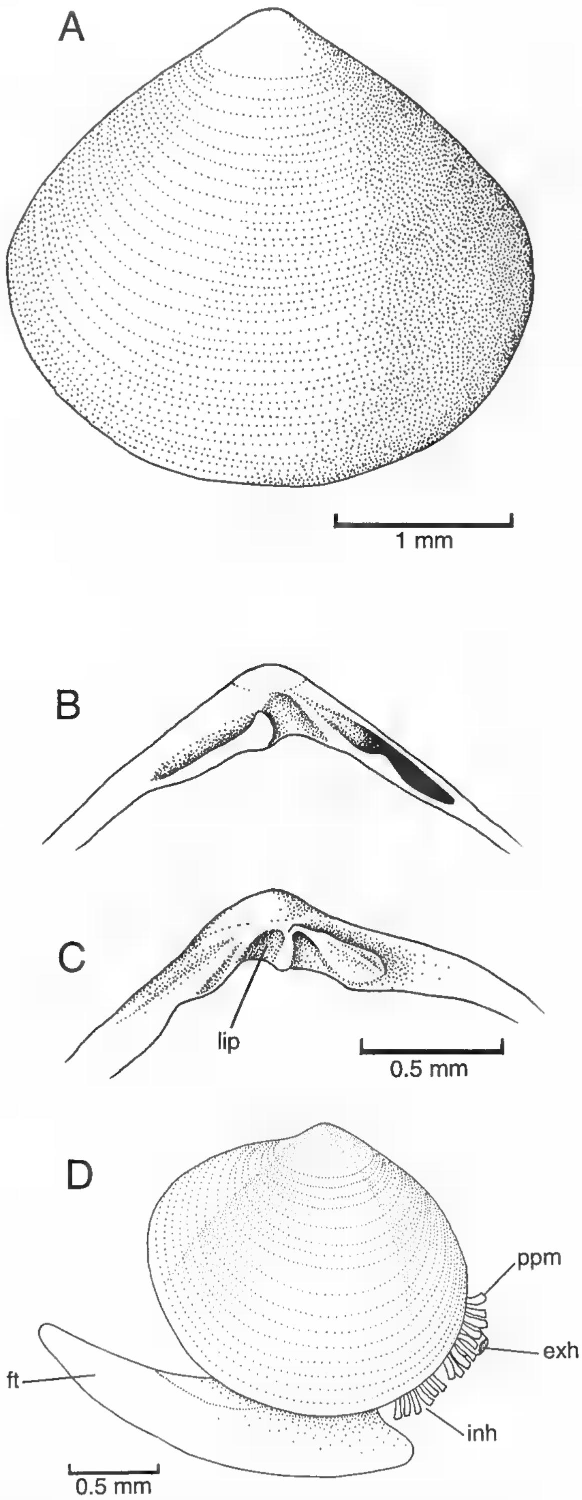


Figure 8.10 Family Neoleptonidae. **A–C**, *Neolepton* species: **A**, left shell valve, external view; **B**, right valve hinge; **C**, left valve hinge. **D**, *Neolepton* species, from Sydney, animal, lateral view. **ft**, foot; **exh**, exhalant aperture; **inh**, inhalant aperture; **lip**, ligament pit; **ppm**, papillate mantle margin.
[S. Weidland]

The adductor muscles are subequal and, although there are no pedal protractor muscles, both anterior and posterior retractor muscles are present. The shell is usually held upright during locomotion (Fig. 8.10D) and the foot is extended in one of two ways. It can be used as a creeping sole, moving by minute contractions in its anterior margin, or extended and withdrawn in a series of jerks, to pull the shell along (Ponder 1969). The foot has a heel, but no byssus pore, permanent sole or ventral groove. A sticky mucus is produced by the pedal glands in the foot which helps these bivalves to adhere temporarily to algae.

The mantle is usually slightly extended around the whole shell margin and, in *Neolepton* species, is glandular above the ventral margin and weakly papillate. There is an antero-ventral pedal aperture and short postero-dorsal exhalant and postero-ventral inhalant siphons, each fringed by moderately long tentacles. The ctenidium has two demibranchs, the outer one reduced. The ciliary currents produced are similar to those of most other eulamellibranchs (Ponder 1969).

Neolepton species do not brood their eggs, and sexes are separate (Ponder 1969). In the tiny (0.9 mm) New Zealand *Pachykellya minima*, four relatively very large larvae are brooded in the mantle cavity (Ponder 1969). Similar species occur in southern Australia, although no observations have been made on their reproductive biology.

All species are marine, living in the intertidal to sublittoral zones, some down to several hundred metres. *Neolepton antipodum*, present throughout New Zealand, has a wide bathymetric range (intertidal to over 300 m; Dell 1952), and is especially common in the intertidal zone among coralline algae. It has been reported from Victoria, but most Australian records are probably referable to *N. novacambrica*, a very similar species.

The taxonomy of Australian members of this family is so poorly known that only very tentative statements can be made about the faunal composition. This family is largely Australasian, but the type species of *Neolepton* occurs in Europe and the Mediterranean, and other genera occur in the Falkland Islands (*Neodavisia*) and Andaman Islands (*Jousseaumiella*). *Notolepton* and the New South Wales genus *Micropolia* are probable junior synonyms of *Neolepton* (on the basis of an examination of living material of the type species of all three nominal genera; W.F. Ponder personal observation).

The oldest recorded fossils in Australasia are from the Miocene of New Zealand. The oldest Australian fossils are probably also from this time (Chavan 1969c)

Family Sportellidae

This family contains small, quadrate to narrowly ovate bivalves which lack pedal protractor muscles and usually have a marginal ligament. A byssal gland and groove in the foot is absent or present, and the gill lacks food grooves on the reduced outer demibranch. The anterior and posterior adductor muscles are subequal. Some species are known to be commensal.

Members of this poorly known family have often been included in the Galeommatoidea but differ from that group in having the inhalant siphon located posteriorly. The only comprehensive review is that of Chavan (1969c) who listed the genera. Very little anatomical information is available, the most comprehensive being that of Ponder (1971a) who described the gross anatomy of a New Zealand species.

Shells are equivalve, small (usually less than 10 mm in length), thin to thickened, inequilateral, quadrate to elongate-ovate and usually with a submedian, prominent umbo (Fig. 8.11). They are typically white and the surface is smooth, pustulate or granulate. The well-developed hinge plate is, at most, only slightly hollowed by the internal resilifer (Fig. 8.11B, C). The trigonal cardinal teeth are well separated from the marginal lateral teeth. The resilium is small and the ligament is usually marginal, mostly external and rests on a nymph. There is a shallow pallial sinus and the adductor muscle scars often have an internal ridge on their inner side.

The adductor muscles are subequal, and anterior and posterior pedal retractor muscles are present. The foot has a byssal gland and groove in *Sportella*, but these are absent in *Anisodonta*.

The mantle edge is smooth or papillate anteriorly and ventrally, and there are typically numerous small, well-developed tentacles posteriorly around the posterior inhalant and exhalant apertures. The inner mantle lobes beneath the exhalant and inhalant apertures are fused ventrally. The ctenidia are loosely bound, that is synaptorhabdic (Boss 1982), and the labial palps are small.

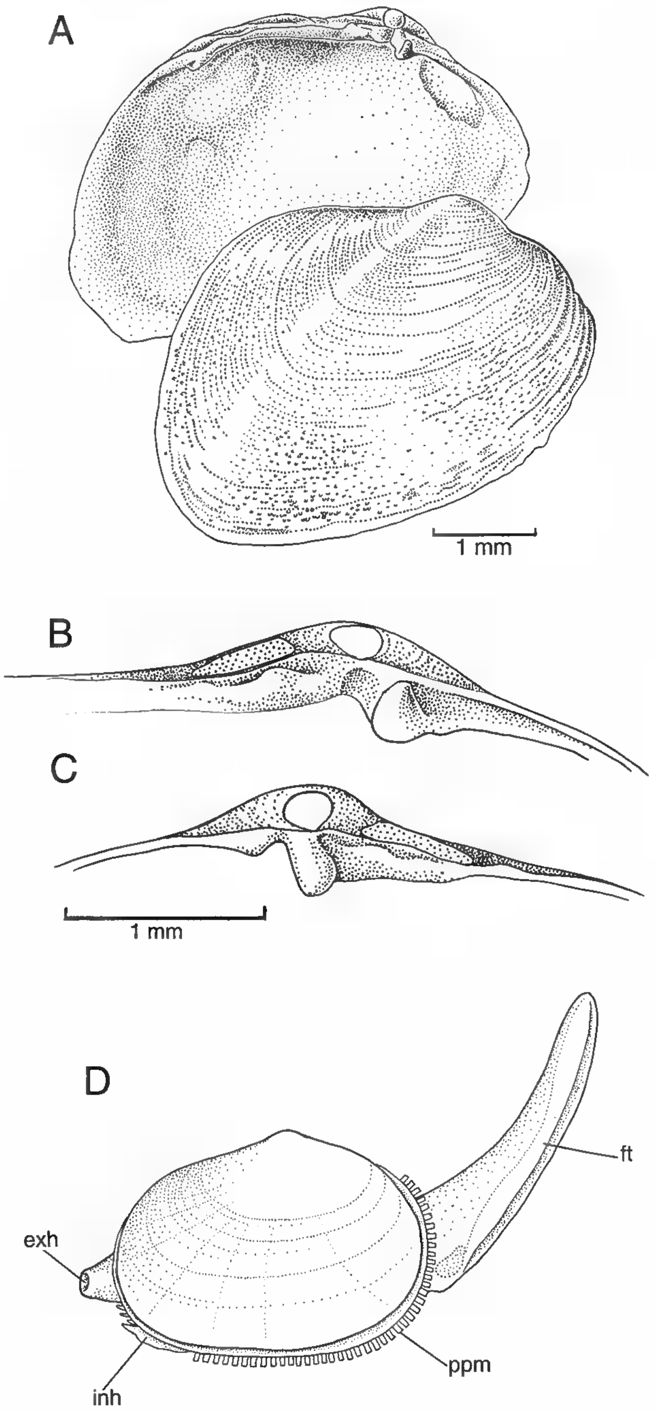


Figure 8.11 Family Sportellidae. **A–C**, *Anisodonta subalata*: **A**, shell valves, left valve in internal view, right valve in external view; **B**, right valve hinge; **C**, left valve hinge. **D**, *Sportella* sp., from Lizard Island, Queensland, animal, lateral view. **exh**, exhalant aperture; **ft**, foot; **inh**, inhalant aperture; **ppm**, papillate mantle margin. [A, A.J. Hill; B–D, S. Weidland]

Food particles are carried ventrally across the descending limb of the outer demibranch, then around the ventral edge, postero-dorsally to the gill axis, where they move in an antero-dorsal direction, to the upper edge of the inner demibranch, there being no discernible food groove on the outer demibranch (Ponder 1971a).

Ponder (1971a) found a few shelled larvae attached by byssal threads at the posterior end of the pedal opening of *Anisodonta alata*. No other information is known about their reproductive biology.

Although members of this small family have an almost worldwide distribution in temperate to tropical seas, they are rarely seen. They mainly frequent intertidal and sublittoral areas. Kay (1979) reported a Hawaiian species, *Anisodonta angulata*, living in the mud tube of a polychaete worm in tide pools on rock benches and on fringing reefs.

Some genera, such as *Basterotia* and *Anisodonta*, are virtually cosmopolitan in distribution, although there are no recorded Australian species of the former genus. *Anisodonta* is represented in Australia by two named species, *A. subalata* (Fig. 8.11A–C; Ponder 1971a), a species previously included in the Hiatellidae and *A. caledonica*. Two species are referred to *Sportella* (Fig. 8.11D) in Australia. This genus has mostly elliptical, flattened and thickened, smooth shells with a long callous nymph, whereas *Anisodonta* shells have a granulose surface with internal ribs on the inner side of the muscle scars.

The earliest fossil sportellids are from the Jurassic (Chavan 1969c). Palaeocene species of *Sportella* are known from Europe and North America. This genus is represented in Australia by a few Recent unnamed taxa and *S. jubata*, which has also been recorded from the Pliocene of South Australia (Ludbrook 1955). *Anisodonta* is known from the Palaeocene of France.

Superfamily CARDITOIDEA

The origin of this superfamily, which consists of the extant families Carditidae and Condylocardiidae, and the extinct family Permophoridae, lies in the Devonian (Chavan 1969d) or possibly even in the Silurian (Allen 1985). This Palaeozoic origin places the Carditoidea among the oldest of the bivalve superfamilies. It experienced a period of moderately high diversity in the Permian and this diversity reached a peak during the Cainozoic.

All living members of the superfamily Carditoidea are marine though Chavan (1969d), in the most comprehensive recent account of the group, very tentatively included in it the non-marine Permian genus *Yavorskiella*. The habitats and habits of carditoideans vary widely and the species range in size from minute to about 100 mm in length.

The major distinguishing shell characters of this superfamily are the generally strong radial sculpture, the generally crenulate internal margins of the valves and the absence of a sinus in the pallial line. The stomach has a long major typhlosole which is distally coiled (Boss 1982).

In general carditoideans are equivalve, and range in shape from trigonal to mytiliform, with the posterior area of the shell of many forms demarcated by a rib or angulation. The shell is aragonitic in substance and solid in structure. The inner complex crossed-lamellar layer and, in some, the outer crossed-lamellar layer of the shell may incorporate straight radial riblets and tubules. Separating these layers is a discontinuous pallial myostracum (Taylor *et al.* 1973). The shell is generally covered by a conspicuous, often ornamented periostracum. External shell sculpture is generally predominantly radial, with commarginal (concentric) elements subsidiary. If the shell structure and its radial ribs are strong then the valve lips may be crenulate. Minute or thin-shelled deep-water species more commonly have smooth lips. A posterior area may be defined by a rib or an angulation. The generally rounded, prosogyrous beak is often situated well in front of the mid-point. The lunule, if present, is small and commonly is depressed, non-symmetrical and/or demarcated by a deep narrow groove which may terminate anteriorly at an internal pustule. An escutcheon, if present may be narrow and/or ill-defined. The ligament may be internal or external and is inserted on well-formed nymphs.

The families and subfamilies comprising this superfamily are differentiated mainly on characters associated with the hinge structure. Cardinal teeth may number two or three, and laterals may be present or absent. If present, the lateral teeth are close to the cardinals. The more distal cardinals may be feeble or may even coalesce with the valve margins or with the ligamental nymphs. These hinge teeth are usually finely striate.

The anterior and posterior adductor muscles are basically similar though their relative sizes are related to shell shape. The more inequilateral, mytiliform species are less isomyarian than are more equilateral forms. Pedal muscle scars are distinct in most forms and the pallial line is entire, lacking a sinus. This simple pattern of pallial muscle attachment reflects the non-siphonate condition of carditoideans. The inner mantle folds are fused to form an exhalant aperture, but the inhalant aperture is demarcated antero-ventrally by the apposition of the mantle edges assisted by interlocking cilia (Allen 1985). There is no communication between the inhalant and exhalant mantle cavities as the ascending limbs of the inner demibranchs are held together posteriorly by ciliary intermeshing. Tissue fusion exists between the gills and the visceral mass, the mantle lobes and the posterior area of mantle-fold fusion.

Through the ventral pedal aperture projects the narrow foot which is byssate in juveniles, and at least in those adult carditoideans living on hard substrata. The strength of the byssus and its effect on shell shape vary greatly between carditoidean taxa.

The gills are large with unequal-sized demibranchs. They are eulamellibranchiate with large ostia. Their latero-frontal cilia are of Atkin's (1937a) Type I according to Newell (1965). The ventral tips of the more anterior filaments of the inner demibranchs are inserted into and fused with the distal oral grooves as in Stasek's (1963b) category II. The labial palps are moderately large and the mouth leads to a stomach of Purchon's (1958, 1960b) Type IV. The oesophagus enters the stomach anteriorly, the conjoined style-sac and midgut leave it postero-ventrally and a large sorting area is located anterior to the dorsal hood, against which the crystalline style rotates. All carditoideans are suspension-feeders.

Carditoideans are dioecious and at least some species are incubatory (Dall 1903), their larvae brooded in the atrium of the ovary or in the exhalant pallial chamber, including the interlamellar spaces of one or both sets of demibranchs. These larvae are retained at least until the prodissoconch stage is reached.

Members of this superfamily are, in general, shallow-water inhabitants of the continental shelf, though some minute forms have been collected from depths of over 1500 m (Yonge 1969). Carditoideans are particularly well-represented in the tropical Indo-West Pacific region. Carditids and condylocardiids can be separated on size (the condylocardiids being minute) and on the position of the ligament, which is internal in condylocardiids.

The extinct permophorids were cosmopolitan in distribution, with Mesozoic fossils of the genera *Kalentera* and *Triaphorus* occurring in New Zealand, and earlier Permian fossils of *Stutchburia* in both eastern and western Australia (Dickins 1963). Permophorid shells can be distinguished from those of other carditoideans by their smooth non-crenulate inner margins, their marginal ligament, their generally large size and the conspicuously thick buttress supporting the scars of the anterior adductor and pedal muscles.

Family Carditidae

The Carditidae arose during the Devonian, with the development of the now-extinct subfamily Palaeocarditinae, and was relatively homogeneous before undergoing phases of diversification in the Cretaceous and more particularly during the Cainozoic. Older fossils are found in areas now in the high latitudes. More tropical groups are among those of apparently more recent origin. The family now inhabits all except the polar seas, with greater diversity in warmer waters (see Chavan 1969d). Its Australian fossil record extends back to the early Eocene (T. Darragh personal communication). However, the evaluation of this record is hampered by a need for a revision of Australian and other extralimital taxa, both extinct and extant.

Carditids are small to medium-sized, of up to about 100 mm in shell length. In shell shape they range from rounded to mytiloid, and have equal valves (Fig. 8.12A–D) except in individuals deformed as a consequence of their nestling habit. In general, the sculpture is radial, usually consisting of strong ribs which may be crossed by commarginal elements forming nodules or scales. The shell is solid, and of crossed-lamellar or of complex crossed-lamellar microstructure (Taylor *et al.* 1973). It is covered by a periostracum which, in some species, is thick and dark.

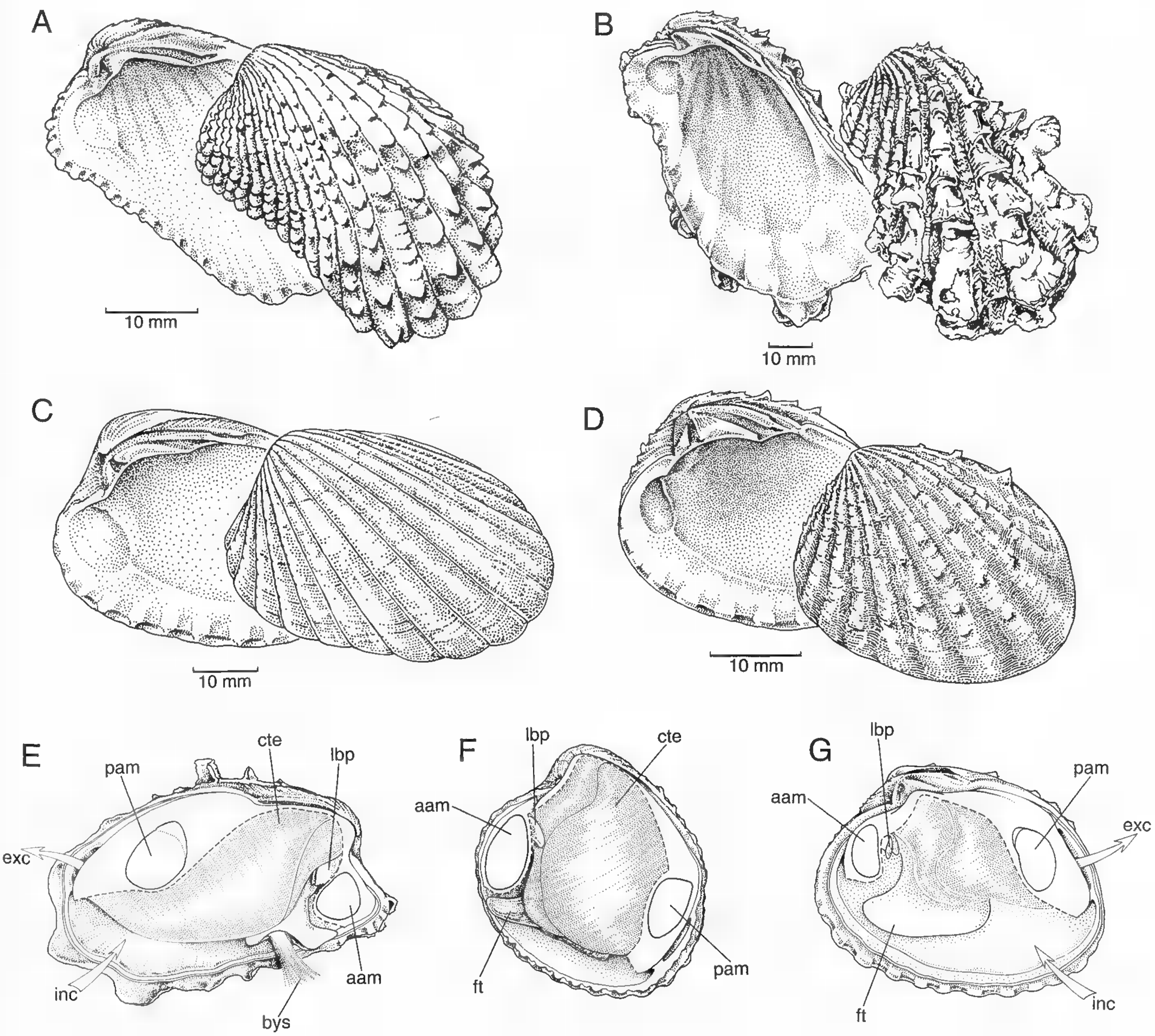


Figure 8.12 Family Carditidae. **A–D**, shell valves, right valve in internal view, left valve in external view: **A**, *Cardita calyculata*; **B**, *Cardita crassicosta*; **C**, *Megacardita incrassata*; **D**, *Cardiocardita (Bathycardita) raouli*. **E–G**, pallial organs: **E**, *Cardita crassicosta*, right view; **F**, *'Venericardia' rosulenta*, left view; **G**, *Cardiocardita (Bathycardita) raouli*, left view. **aam**, anterior adductor muscle; **bys**, byssus; **cte**, outer demibranch of ctenidium; **exc**, exhalant current; **inc**, inhalant current; **ft**, foot; **lbp**, labial palp; **pam**, posterior adductor muscle. [R. Plant]

The prosogyrous shell beaks of carditids are prominent and usually closer to the anterior end. They are more strongly incurved in those forms with a marked tangential component of growth. Anteriorly the typically small, deep lunule is usually defined by a marginal groove, whereas the posterior escutcheon is, in some forms, not so distinctly defined. The ventral edge of the posterior shell area is generally marked by a prominent rib or by an angulation. In most forms the parivincular ligament incorporating the resilium is external. However, in more rotund forms with incurved beaks, a strong tangential growth component and an inter-umbonal growth of the shell margin, it may be split anteriorly under the umbones. In such forms the resilium may be sunken or even completely internal. This condition is more obvious in some American forms (Yonge 1969) and, to a lesser extent, in Australian forms such as *'Venericardia' quoyi*.

The hinge is of the lucinoid pattern with two left and three right oblique cardinal teeth, though the anterior right cardinal may be reduced or absent in some groups. The posterior cardinal teeth are parallel to the dorsal shell margin and are lengthened to extend below the ligament. These cardinal teeth are usually lamellar in shape and transversely striated. The lateral teeth are generally better developed in those forms in which the ligament is feeble, though the anterior left lateral tooth may be represented by only a pustule. The ventral margins of the valves are generally crenulate internally, with the crenulations corresponding to the external radial ribbing in their precise alignment.

The oval adductor muscle scars are almost equal in triangular forms, but the anterior is relatively smaller in species of more pronounced mytiloid shape. The posterior adductor scar may be set on a platform raised anteriorly from the internal shell surface. Pedal retractor muscle scars may be obvious dorsal to the adductor muscle scars, though these may be concerned only with the byssus in firmly attached forms such as *Beguina* species (Yonge 1969). The pallial line is usually entire, lacking a pallial sinus. As in other carditoideans only a posterior excurrent aperture is formed by tissue fusion of the fringed inner pallial folds. An incurrent aperture is only temporarily defined by the apposition of the inner mantle folds. The inhalant area is situated postero-ventrally in carditid species examined by Yonge (1969), although Allen (1968) had indicated that an anterior inhalant area was present in at least some carditids. The foot, which is byssate for at least part of the life span of most groups, protrudes ventrally (Fig. 8.12F, G).

Within the pallial cavity the large, coarsely reticulate, non-plicate, eulamellibranchiate gills (Fig. 8.12E–G) are usually united only by ciliary connections behind the foot. Oral-ward currents are produced on the ventral margins of the inner demibranchs, on the gill axes and at the junctions of the outer demibranchs and the pallial lobes as in Atkins (1937a) Type D (Morton, B. 1982b). The gill/labial palp junction is of Stasek's (1963b) category II and the carditid stomach fits Purchon's (1958, 1960b) Type IV and Dinamani's (1967) section III Group A.

Carditid females produce relatively few, large, yolky ova. The fertilised eggs are surrounded, in at least some species, by an unusually thick capsule (Burne 1920). Fertilisation within the pallial cavity and brooding of the young occurs in many, if not all, species. Eggs may be incubated in the atrium of the ovary or within the interlamellar spaces of the one or both sets of demibranchs (Burne 1920; Jones, G.F. 1963). In the genera *Thecalia* and *Milneria*, which are not found in Australian waters, incubation occurs in a special ventral fold of the mantle. Brooding of carditid larvae may continue until the prodissoconch and part of the nepionic shell have been secreted, so that the young are released as benthic juveniles. In some species of *Cardita*, these juveniles may then attach to the parent's shell by byssal threads (Jones, G.F. 1963).

The blood of at least some carditids contains haemoglobin (Franc 1960; Manwell 1963; Patel & Patel 1969; Yonge 1969). There appears to be some variation within the Carditidae in the blood vascular system. Burne (1920) records that the ventricle of the New Zealand species, *Purpurocardia purpurata* is penetrated by the rectum, as in most members of the order Veneroida. However, White (1942) states that the carditid ventricle lies beneath the rectum. This latter condition is seen in the heart of *Beguina variegata* in which processes from the posterior angles of the ventricle run alongside the rectum. The auricle walls contain pericardial glandular tissue and the kidneys, which in *Cardites antiquata* open from the anterior corners of the pericardium (White 1942), communicate with one another, as in astartids.

Carditids range in habit from byssally attached forms sheltering under boulders as in the Indo-Pacific *Cardita variegata*, to nestlers between rocks and rubble (for example, *Glans* species), byssally attached in crevices in rocky reefs or coral bombies (for example, *Beguina semiorbiculata*; Yonge 1976) to shallow burrowers in soft substrata (for example, *Megacardita incrassata*). Yonge (1969) discerned an evolutionary trend from infaunal freedom towards byssal attachment in juveniles, and even in adults, and believed that this is accompanied by an adaptation in shape tending towards elongation and heteromyarianism. However, Allen (1985) maintained that evolution in the reverse direction is just as possible.

The most comprehensive review of the species of this family is still that of Lamy (1922a), although there has been some updating of generic-level taxa following the review of Chavan (1969d).

This old and diverse family has been subdivided into seven subfamilies, six of which include living forms. Of about sixteen extant genera recognised by Chavan (1969d), at least eleven are represented in the living Australian fauna, with the greatest diversity in northern waters. However, difficulties in working with the diverse Australian fauna using Chavan's system indicate the urgent need for a revision of this family.

Sixteen species, most of relatively medium to large size, are included in the Australian carditid fauna as described by Lamprell & Whitehead (1992). Of these, seven have a northern Australian distribution, among them common Indo-West Pacific species such as the small, nestling *Cardita variegata* and the large coral crevice-dwelling *Begunia semiorbiculata*. Six of the species belong to the fauna of the southern temperate waters. Of these, both the small byssate rock-dweller *Cardita excavata*, and the similarly sized sand-dwelling *'Venericardia' rosulenta* inhabit waters between the south of Western Australia and the central eastern coast of Australia. This latter species, together with a few others, is of uncertain generic placement. However, four of the six southern species listed have distributions centred on the south-eastern coast, including *Cardiocardita (Bathycardita) raouli* (Fig. 8.12D) and *'V.' quoyi* which live in sand in depths to about 70 m. Two species, *'V.' cavatica* and *Glans ? hirasei* have been taken only in deeper waters and sandy substrata off the central eastern coasts (Lamprell & Whitehead 1992). The large, heavily scaled *Cardita crassicosta* (Fig. 8.12B) is unusual in having been recorded from all Australian coasts. Another six genera, approximately, have been recorded from Australian waters, particularly in southern Australia. These are all medium to small in size and all belong to the subfamily Carditamerinae. The most speciose and also most abundant seems to be *Cyclocardia (Vimentum)*. *Pleuromeris* is also recorded from New Zealand. Other genera in this group are *Arcturellina* (small to medium, from deeper shelf waters), *Cardita (Carditellona)* and *Choniocardita (Carditellopsis)*.

Family Condylocardiidae

The Condylocardiidae were divided into the two subfamilies Condylocardiinae and Cuninae by Chavan (1969d). However, Beu & Maxwell (1990) now regard each as having familial rank. The history of the Condylocardiidae is apparently confined to the Cainozoic with its greatest diversity among the Recent forms. Three and perhaps four of the oldest genera have survived in Australian and New Zealand waters since the Eocene – Australian fossils assigned to the genus *Cuna* being recorded from the late Eocene, and some assigned to the genus *Condylocardia* from the Late Miocene (T. Darragh personal communication).

Condylocardiids are small to minute, generally being less than 3 mm in length. They are marine forms with relatively thick and solid shells and with little variation in shape (Fig. 8.13). Most are triangular, being generally higher than long, with a few being trapezoid to ovate. Sculpture is generally radially ribbed, but commarginal sculpture is always present to some degree, even as weak growth lines on otherwise smooth shells. The valves may differ in the development of their dorsal margins. In *Cuna* the right antero-dorsal and the left postero-dorsal margins overlap those opposite.

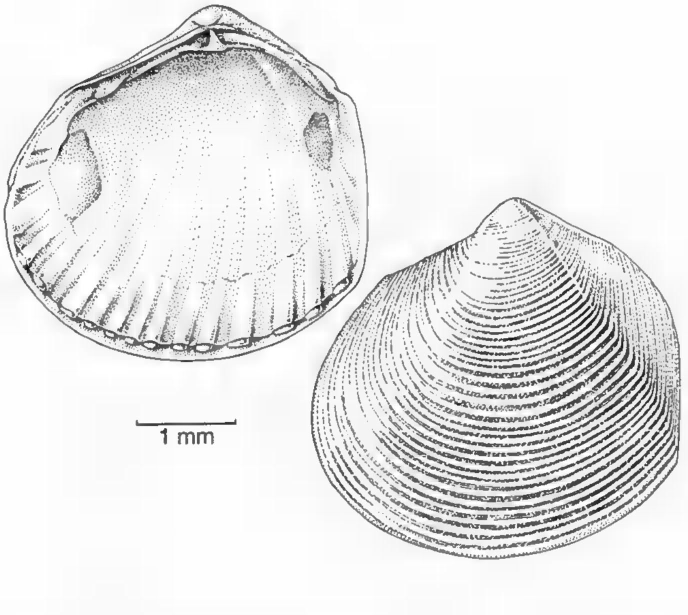


Figure 8.13 Family Condylocardiidae. *Cuna particula*, shell valves, right valve in internal view, left valve in external view. [R. Plant]

The prodissoconch, which is retained at the umbo of most adult shell valves, is large relative to the ultimate size of the adult shell. It tends to be saucer-shaped in the Condylocardiinae and rounded, though often ill-defined, in the Cuninae.

The ligament may be weak and the central resilium may be sunken or internal so that its edge may partly obliterate the left central cardinal tooth. The hinge of adult condylocardiids tends to show features characteristic of those of juvenile carditids (Suter 1913; Franc 1960), commonly with the cardinal and lateral teeth merged. This has lead to various opinions on the allocation of a number of genera between these two families. In the past, some genera, mostly of the subfamily Cuninae, have even been placed in the superfamily Crassatelloidea. The hinges of condylocardiine species resemble those of spondylids with their straight margins and long, hooked lateral teeth. In the Cuninae, the hinge margin is more rounded with the lateral teeth weak or even rudimentary.

Little is known of the soft parts of condylocardiids, but the shell's simple pallial line indicates that, as in other carditoideans, siphons are lacking.

Few observations on the reproduction of condylocardiids have been made. Pelseneer (1911) indicated that *Condylocardia* species are not hermaphroditic and that the young are incubated. Salas & Rolan (1990) remark that young are incubated in all taxa for which developmental information is available. They and Salas & Cosel (1991) described five new species from the Atlantic, each of which broods small numbers of young. Moore (1961) records the eastern American *Cuna dalli* producing young of up to 300 m in length. These burrowed into the substratum immediately after release.

Most of the currently recognised genera of the Condylocardiidae are from temperate waters, with Australasian forms predominant. There are about 47 named species in southern Australian waters (S. Boyd personal communication). Only a few species are known from north-eastern Australian waters. Some authors have placed some of these in other families, such as the Crassatellidae and the Carditidae. Of the genera currently recognised in the Australian fauna, those placed in the subfamily Condylocardiinae include *Micromeris*, *Particondyla*, *Radiocondyla*, *Cunanax Condylocuna* and *Benthocardiella* – the last three are also represented in the New Zealand fauna, and all but the first being confined to Australasia. The Australian representatives of the subfamily Cuninae belong to the genera *Cuna*, *Hanacuna*, *Saltocuna* and *Volupicuna* – again, all but the first being confined to Australasia. A detailed revision of this family may indicate that excessive splitting at the generic level has occurred.

The history of generic and even familial placement of Australian species of this group has been complicated. After Hedley (1902) erected the genus *Cuna* for his new species, *C. concentrica*, from southern New South Wales, other new genera were proposed by Iredale (1936), Cotton (1931) and Laseron (1953). Most authors clearly recognised the cohesiveness of *Cuna* and related genera – Laseron separating them from the family Condylocardiidae as a '*Cuna* group', and Allan (1950) and Cotton (1961) even placing them within the family Crassatellidae. Macpherson & Gabriel (1962) united the two groups within the Condylocardiidae. These groupings were re-assessed by Chavan (1969d) to produce the classification adopted here.

The genera of the subfamily Condylocardiinae are distinguished mainly by size and shape of the protoconch, the outline and proportions of the shell valves, by the gross and finer details of the radial (and, to a smaller extent, of the commarginal) sculpture and on the detail of the hinge margin and teeth.

Research on the condylocardiid fauna of Australia has been largely concentrated upon south-eastern waters. The studies and reviews of Laseron (1953), Cotton (1961), Iredale & McMichael (1962) and Macpherson & Gabriel (1962) largely overlap. Similar studies are still to be carried out on the faunas of the north and west of the country.

Very abundant and seemingly ecologically important local populations of some species have been recorded in Sydney Harbour, New South Wales (W.F. Ponder personal communication), and in Port Phillip Bay, Victoria (R. Burn personal communication). They lie on the surface of shallow subtidal sand flats and are preyed on by some shelled opisthobranchs. Many fossil specimens from the Pleistocene beds of Western Australia show evidence of predation by boring gastropods (G.W. Kendrick personal communication). Other species are more typically found in deep water, and have been taken only by dredging.

Superfamily CRASSATELLOIDEA

Most species of this totally marine superfamily are inhabitants of the shallow areas of the continental shelf, with only a few species living in the deeper waters of the continental slopes (Allen 1983). Yonge (1969) maintained that members of this group are, with carditoideans, the most primitive of modern eulamellibranchs. Extant species belong to three families, of which only one, the Crassatellidae, is represented in the Australian fauna. The Cardiniidae consists of only one extant genus, *Tellidorella*, which is restricted to Central American waters. The family Astartidae, although represented in the Australian fossil fauna, is now largely restricted to temperate and cold waters of the Northern Hemisphere, with only a few species recorded from southern oceans.

Crassatelloidean shells have a periostracum and two inner aragonitic layers (Taylor *et al.* 1973). The valves are generally strong though of varied shape, ranging in outline from triangular to trapezoidal to almost circular. The shell margins of most crassatelloideans fit closely together, though a few have a slight gape to accommodate a fine byssus. Shell sculpture, if present, is predominantly commarginal with a few forms also having fine radial riblets and/or oblique ribs. The strength of this sculpture may decrease during growth. In some forms internal radial riblets, formed within the inner shell layers, may emerge at the shell margins to form crenulations. Such crenulations may also occur in species lacking true internal radial structure.

The beaks are generally prosogyrous and pointed, and may be noticeably flattened. A lunule and an escutcheon are usually well developed and, in some forms may be very depressed. The ligament may be either external and attached to nymphs, though it is often deeply sunken between the steeply sloping sides of the indented escutcheon, or internal and attached to a resilial pit on the hinge plate below the umbo of each valve.

The hinge of crassatelloideans is generally strong, providing a considerable resistance to sheering forces. It is located on a wide, strong hinge plate and is generally of the lucinoid type with two cardinal teeth on each valve, and with the anterior cardinal on the left valve located medially below the beak. Lateral teeth are present and are thin and blade-like in many forms. In the extant families Astartidae and Crassatellidae there are no posterior cardinal teeth on the right valve.

The scars of the adductor muscles, which are almost equal in size, are well marked, as are the more dorsally located scars of the pedal retractor muscles. The simple pallial line which joins the adductor muscle scars rarely shows even a faint indication of a pallial sinus and reflects a relatively simple pallial structure.

The pallial lips, edged with papillae or a few short tentacles, are either fully open or have the inner mantle folds fused at one point only to form a non-siphonate exhalant aperture. The gills within the pallial chamber are of Atkin's (1937a) Type I and have unequal demibranchs, the external being much less extensive than is the internal one. The association between the gills and the labial palps is, in some crassatelloideans, of Stasek's (1963a) Type I and in others of his Type III (Newell 1965).

The superfamily Crassatelloidea is one of the oldest of the extant bivalve superfamilies with its origin as far back as the Silurian (Allen 1985) or perhaps the Ordovician (Chavan 1969e), about

400–500 million years before present. The period of its greatest diversity occurred during the Mesozoic and particularly in the Cretaceous. In Australia, fossil crassatellids, astartids and, probably, cardiniids, are known from the Permian of Western Australia (Dickins 1956, 1963) and also from later deposits (Cox 1961b; Skwarko 1966, 1974). It has been generally agreed that, apart from the three extant families, the superfamily Crassatelloidea also contains the extinct families, Myophoricardiidae and Hippopodiidae (Chavan 1969e; Cox 1969b; Cox & Chavan 1969a, 1969b). However, an alternative grouping has been supported by F.R. Bernard (1983) and Vaught (1989) in which the Astartidae and Cardiniidae are place into a separate superfamily, the Astartoidea. A diphyletic origin of the Crassatelloidea was proposed by Boyd & Newell (1968) on the basis of the hinge structure pattern. Taylor *et al.* (1973) detected differences between the shell structure of crassatellids and that of astartids which tend to support this hypothesis.

Family Crassatellidae

Crassatellids have relatively robust to heavy shells which vary in size from a length of less than 10 mm in some *Talabrica* species to more than 120 mm in some *Eucrassatella* species from Australia (Fig. 8.14). The shell outline varies from triangular to nearly quadrangular with the posterior end often lengthened into a rostrum. Sculpture, if present, is predominantly commarginal though some forms are very finely radially striate and some have oblique ribs. The non-nacreous shell has a homogeneous inner layer which, in almost all species examined, is separated from the crossed-lamellar outer layer by an unconformity, but not by a layer of pallial line myostracum (Taylor *et al.* 1973). The periostracal layer is often thick. Radial riblets within the internal shell layers may emerge on the interior of the close-fitting valve margins as nodulose or elongate crenulations.

The hinge is strong and is borne on a flat, heavy hinge plate. The two divergent right cardinal teeth interlock strongly with the three on the left valve, though the posteriormost of these may be almost obliterated by the internal ligament in some species. The lengths of the anterior and posterior lateral teeth are, in general, appropriate to the shape of the shell. Some or all teeth may be transversely, and more or less finely, striate. Such a strong hinge structure would greatly assist crassatellids to resist valve rotation and dislocation upon attack by large predators.

A distinct lunule and, in some, a large escutcheon, are often indented on the dorsal areas of the shell. The ligament is essentially internal with the internal resilium attaching inside pits on the hinge plate below or just behind the pointed beaks. Posterior and dorsal to these resilial pits lie narrow ridges or nymphs to which the short lamellar layer of the ligament attaches. In some forms, this section of the ligament is visible from the exterior.

The adductor muscles of most crassatellids are approximately equal in size and attach to well-marked scars. Dorsal to the anterior scar is a separate and obvious attachment-scar of the anterior pedal retractor muscle, whereas the scar of the posterior pedal retractor is contiguous with the postero-dorsal part of the posterior adductor muscle scar. In the umbonal recess, lateral to the hinge plate, is the well-marked scar of the pedal elevator muscle. Ventrally, an obvious pallial line marks the zone of insertion of the strong pallial muscles. There is no pallial sinus but, in most species, a slight change in curvature of the pallial line marks the position of a posterior exhalant aperture formed by the fusion of the inner fold and adjacent tissues of the pallium.

Few anatomical studies have been made of crassatellid species. Woodward (1866) described and figured the pallial organs of a Queensland specimen of a *Eucrassatella* species. Pelseneer (1911) described and figured the pallial organs of an unlocalised *Siboga* specimen, presumably of *Bathytormis radiatus* (but labelled *Crassatella indica*). Harry (1966) and Allen (1968) described the anatomy of north-western Atlantic species of *Crassinella*.

Around the non-siphonate exhalant aperture, when present, is the cone valve, which also occurs in other 'lower heterodonts' (Harry 1980). Just anterior to this area of pallial fusion, the inner mantle folds of *Eucrassatella* species usually bear papillae and/or tentacles, marking the area of the inhalant water flow. However, Allen (1968) described an anterior inhalant area in the apparently primitive American genus *Crassinella*. This arrangement is associated with a long anterior adductor muscle projecting into the mantle cavity. In general, there are large glandular areas on the inner surface of the pallium adjacent to the inhalant area, whether anterior or posterior.

The foot is laterally compressed, and is large and rectangular or anteriorly pointed (Fig. 8.14D, E). In some forms, the foot produces a few fine byssal threads in the adult stages.

Lateral to the visceral mass and foot are the non-plicate eulamellibranchiate gills. These gills are almost dorso-ventrally aligned and have their larger inner demibranchs extending well anterior of the outer ones. In the small American *Crassinella* species only the inner demibranchs are present (Harry 1966). Where both demibranchs are present, the distal edge of each bears a food groove. The anterior filaments of these inner demibranchs are typical of Stasek's (1963a) category III and are not inserted into the distal oral grooves. However, in some species the ends of a few anterior filaments may be fused to the folds of the inner labial palps. Anteriorly, the ascending limbs of the gills are fused to the pallial folds laterally and to the visceral mass medially except in the more primitive *Crassinella* in which attachment is only by interlocking cilia (Allen 1968). More posteriorly, apparently in all groups, interlocking cilia less firmly attach the gills to one another, to the visceral mass, to the pallial lobes and to the zone of pallial fusion. The inhalant and exhalant pallial chambers are functionally separated (Fig. 8.14D, E).

The mouth is bordered by wide lips that are enlarged laterally to form variably sized labial palps. The stomach of most species is large and is surrounded, anteriorly at least, by the digestive gland. The ventral loop of the intestine is surrounded by gonadal tissue.

The heart, situated dorsally well behind the beaks, has a long tubular ventricle pierced by the rectum, and large lateral auricles which White (1942) recorded as having pericardial glandular tissue incorporated in their thick walls. The blood plasma and also some of the tissue cells of some species of the American genus *Crassinella* are reported by Harry (1966) to contain haemoglobin.

No wide-ranging revision of this family at the subgeneric level has been attempted since that of Lamy (1917). Darragh (1964) revised the extant Australian species in the nominate subgenus of *Eucrassatella* and, in the following year revised the species of this subspecies and of *E. (Spissatella)* in the south-eastern Australian Tertiary fauna.

Crassatellids generally live partly buried in sand or rubble with their postero-ventral inhalant and exhalant areas protruding. They are, in some areas, heavily preyed upon by octopuses which smother them, by boring gastropods or by shell-crushing sharks and rays. The robust shells of large southern Australian *Eucrassatella* species have been used traditionally as hand tools by Aboriginal hunter-gatherers.

In 1982, Boss estimated the family to contain about 30 species worldwide. Vaught (1989) listed eight genera of which four are present in Australian waters. The genus *Eucrassatella* is the most diverse of these, with *E. kingicola* (the type of the genus), *E. donacina* and *E. pulchra* and *E. cumingii* living off the tropical to subtropical coasts of Australia. Little is known of the other Australian taxa that have been allocated to this family. In southern Australian waters, the genus *Talabrica* is represented by perhaps five species of about 10–15 mm in length. However, the relationship of these to some seven or so smaller species that have been placed in the genus *Salaputium*, has not been resolved. The generic placement of the Indo-West Pacific species, commonly known as *Crassatina ziczac* (Fig. 8.14E), living along the northern coast, is even in doubt. At least the type species of the small

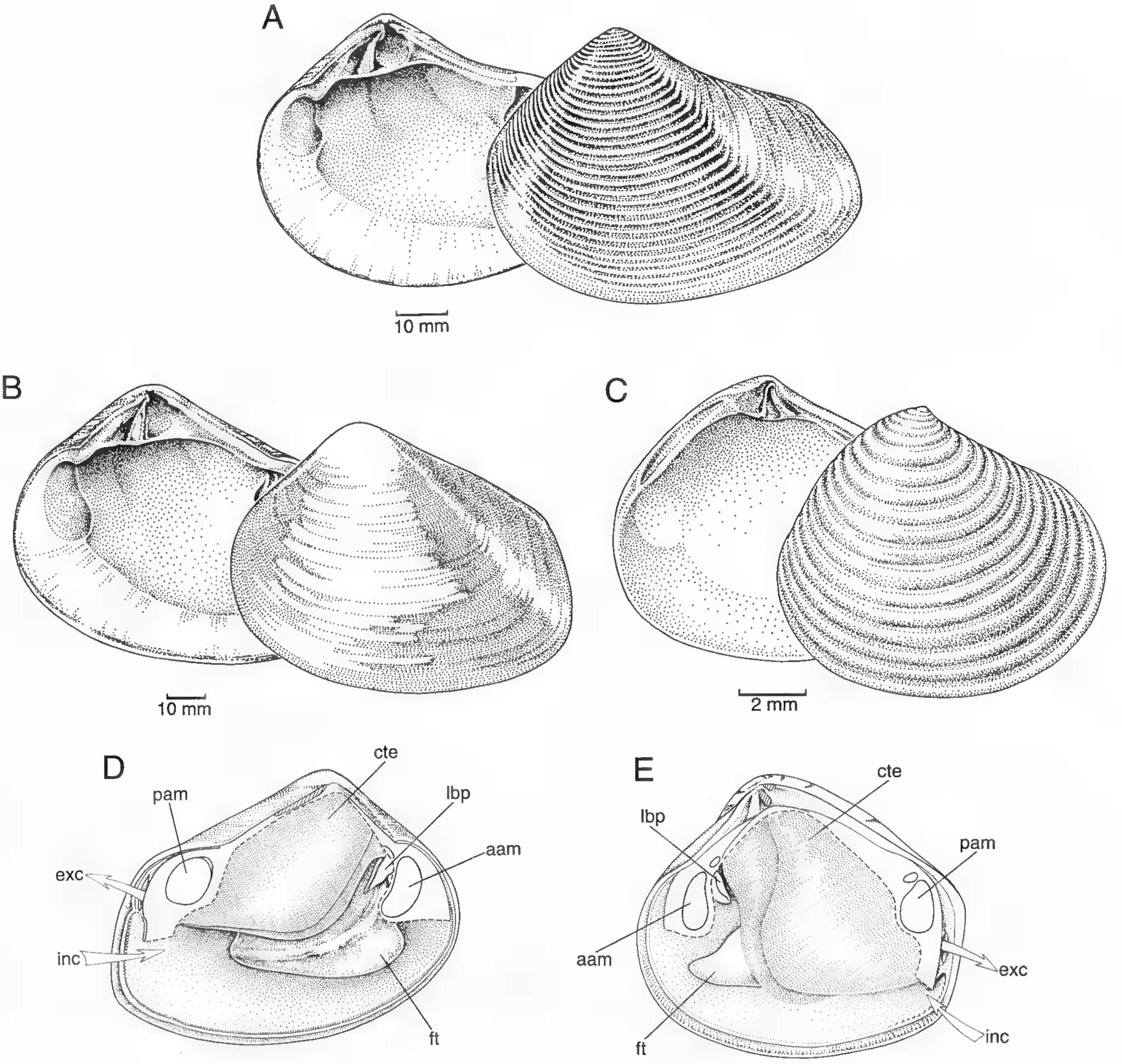


Figure 8.14 Family Crassatellidae. A–C, shell valves, right valve in internal view, left valve in external view: **A**, *Eucrassatella pulchra*; **B**, *Eucrassatella decipiens*; **C**, *Salaputium fulvidus*. **D**, **E**, pallial organs: **D**, *Eucrassatella decipiens*, right view; **E**, *Crassatina ziczac*, left view. **aam**, anterior adductor muscle; **cte**, ctenidium; **exc**, exhalant current; **ft**, foot; **inc**, inhalant current; **lbp**, labial palp; **pam**, posterior adductor muscle. [R. Plant]

eastern Australian genus *Fluctiger*, *F. royanus*, seems better placed here on the basis of shell and anatomical characters than in the Veneridae where it was originally placed.

Though arising in the Devonian, this family apparently underwent little diversification until the Cretaceous. A similar level of diversity has continued from then until the present (Chavan 1969e), as has the family's wide geographic distribution. However, cold water taxa now seem to be more restricted than formerly, whereas warm groups appear to be more abundant.

Perhaps the earliest evidence of the presence of the family Crassatellidae in Australia is provided by fossils of the extinct genus *Oriocrassatella* from Permian deposits in Western Australia (Dickins 1956, 1963). The extant genus *Salaputium* goes back to the Lower Eocene (T. Darragh personal communication), *Eucrassatella* has an extensive fossil record back to the Oligocene (and perhaps the Upper Eocene) of south-eastern and southern Australia (Darragh 1964, 1965a), and *Spissatella* has been recorded from the Lower Oligocene and Lower Miocene of southern Australia (Darragh 1965a, personal communication). Closely related to *Salaputium* is the southern Australian *Talabrica* which is represented in the Pliocene–Quaternary of south-western Australia (G.W. Kendrick personal communication). No fossil record exists for the small eastern Australian genus *Fluctiger*, nor is there any for the genus *Crassatina* presently found in northern Australian waters. The paucity of fossil deposits in northern Australia may contribute to the lack of an Australian fossil record for this latter genus. The genera *Eucrassatella*, *Spissatella*, *Salaputium*, *Talabrica* and *Crassatina* all occur in the fossil and/or living faunas of New Zealand (P. Maxwell personal communication).

Family Astartidae

Members of the Astartidae do not form part of the extant fauna of Australia, but a few species which may be circum-Antarctic in distribution have been found in the cool deep waters off southern Africa and southern South America and some others have been taken in the low latitudes east and west of Africa. Antarctic and Subantarctic species include *Astarte longirostris* and *A. africana*.

The earliest reliable records of this family are from the Devonian. However, fossils of the extinct genus *Matheria* from the Middle Ordovician of North America have been tentatively placed in this family by Chavan (1969e). From the period of greatest astartid diversity in the later part of the Mesozoic, only one subfamily, the Astartinae, has survived until the present. The subfamily is largely restricted to the temperate and cold waters of the Northern Hemisphere. The fossil record indicates that, in the past, this family has had a much more widespread distribution.

Australian representatives have been recorded from the Lower Permian (Dickins 1963) and Lower Cretaceous (Cox 1961a) of the Carnarvon Basin, and from the Middle Jurassic of the Perth Basin in Western Australia (Skwarko 1974). Skwarko (1966) also tentatively recorded astartids from the Lower Cretaceous of the Northern Territory. Darragh (1994) has described the first Australian Tertiary astarid, *Astarte notailis*, from the Late Palaeocene of Victoria.

Astartids are regarded as relatively conservative descendants of a group of bivalves from which the rest of the Heterodonta arose (Nicol 1954). Their moderately compressed shells have outlines ranging from triangular to circular to almost quadrangular. External sculpture is of commarginal striae or ribs, but coarse sculpture may be restricted to the earlier-formed parts of the shell. The shell is slightly inequivalve in that the right lunular area overlaps the left, and the escutcheon rim of the left valve slightly overlaps that of the right (Nicol 1954). Internal shell layers may have a radially ribbed structure.

Living species of this family can be distinguished from those of the Cardiniidae by the lack of a posterior cardinal tooth in the right valve. They can be distinguished from crassatellids by the lack of an internal resilium and of a resilial pit on the hinge plate, and by the presence of a layer of myostracum left behind by the pallial line between the two inner shell layers (Taylor *et al.* 1973).

The anatomy and biology of Northern Hemisphere astartids has been studied in detail by Saleuddin (1965, 1967). The ventral tips of the anterior filaments of the inner demibranch are inserted into but not fused with the distal oral groove, so fitting into Stasek's (1963a) category I. Cone valves are present around the inhalant aperture (Harry 1980). The pericardium and heart are elongate with the tubular ventricle surrounding the rectum. There is no communication between the auricles, the walls of which contain a mass of pericardial gland tissue. Patches of similar tissue are located in the ventral part of the mantle (White 1942). Extracellular haemoglobin is present in the haemolymph of at least some species (see Bonaventura & Bonaventura 1983).

Research on cool-water European and American species indicates that these astartids are sluggish, shallow burrowers that are active at night. The posterior end of the shell, housing the non-siphonate exhalant aperture and the inhalant area, protrudes from the soft substratum (Saleuddin 1964). At least some of these species exhibit sexual dimorphism with the larger females producing large eggs that adhere to the substratum close to the parent (Saleuddin 1964). Non-pelagic larvae are typical of cold water species, but the larvae of temperate and tropical species seem to be typically pelagic (Ockelmann 1958 *fide* Mackie 1984).

Superfamily CARDIOIDEA

Cardioid shells usually have radial sculpture, sometimes with a change of sculptural pattern on the posterior area. The hinge of each valve usually has two cardinal teeth: those of the left valve are of unequal size (the anterior tooth is the larger). In the right valve, the cardinals may be fused to some extent. The laterals may be distant from or close to the cardinals. In some genera anterior laterals are lacking.

Pallial siphons are lacking and the pallial line is entire without a sinus (except in some fossil estuarine forms). There are no cruciform muscles. Anterior and posterior adductor muscles are subequal. The postero-ventral mantle gape representing the inhalant aperture is separated from the ventral pedal gape by a zone of mantle fusion. Ctenidia are plicate with both inner and outer demibranchs, although the latter are shorter than the former.

The superfamily originated in the Upper Triassic. Four families are recognised, three of them extant and one extinct. The Lahilliidae is an extinct family that ranged from the Upper Cretaceous to the Miocene in the Southern Hemisphere. It is represented in the Australian, New Zealand, Antarctic and South American marine fossil faunas by the genus *Lahillia*. The Lymnocardiidae are brackish-water bivalves of Eurasia with a known time range from the Miocene to the Recent and three living genera in the Caspian Sea. The Cardiidae is the oldest and largest family in the group, originating in the Upper Triassic. It radiated in the Tertiary and is a speciose and cosmopolitan marine family in modern times. The Hemidonacidae originated in the Middle Tertiary, apparently in northern Australia, and comprise a single genus. The inclusion of this family within the Cardioidea has been problematical, but in a review, Ponder, Colman, Yonge & Colman (1981) demonstrated that this is the most appropriate place for it.

Family Cardiidae

Cardiids are popularly known as cockles or, more definitively, as heart cockles on account of their heart-like outline in end view. The Cardiidae are a well-defined family of small to medium-sized, shallow-burrowing, suspensory-feeding, infaunal marine bivalves.

Cardiids have equivalve, ovate to quadrate and usually tumid shells with prosogyrate umbos, a short parivincular ligament and a cyclodont hinge (Figs 8.15, 8.16A–C). There are usually two non-bifid cardinal teeth in each valve which are cruciform in arrangement and may be separate or joined at their dorsal ends. Lateral teeth are usually strong with one anterior and one posterior lateral in the left valve, and one or two anterior and one or two posterior laterals in the right valve. Adductor muscle scars are subequal and the pallial line is entire. Externally the shell valves are sometimes smooth, but usually sculptured with nodulose, rugose, squamose or spinose radial ribs. There may be secondary sculpture in the interspaces. A smooth or hirsute periostracum is usually present.

Cardiid animals have no pallial siphons, only gapes between the mantle lobes fringed by middle lobe thickenings that are not capable of extensible and contractile movement. There are no siphonal contractile muscles. Consequently, a pallial sinus is lacking. The inhalant and exhalant gapes are surrounded by sensory papillae or tentacles which, in some species, bear minute 'eyes'. The foot is large and geniculate (sickle-shaped) and capable of rapid digging (Fig. 8.16C).

The ctenidia are plicate and include both inner and outer demibranchs. The outer demibranchs are short, reaching only about half the depth of the inner, and have a supra-axial extension. They lie closely appressed to the descending lamellae of the inner demibranch, suggesting that food particles are transferred to the ventral food groove of the latter for carriage to the mouth. The free edges of the inner ascending lamellae are not fused to the visceral mass but behind the visceral mass those of the left and right sides fuse together medially forming a broad, thin septum. The labial palps have extended bases and lie well below the antero-posterior ctenidial axis just ventral to the anterior adductor muscle.

The earliest descriptions of Australian cardiids are of three species of the genus *Fragum*, described by Linnaeus (1758), and all from central Indo-West Pacific localities. The majority of northern Australian species were described by European authors during the 19th century, also from Indo-West Pacific localities. Lamarck (1815–1822) named *Cardium tenuicostata* (= *Fulvia*) from 'Timor et a la Nouvelle Hollande', his original material almost certainly coming from King George Sound in southern Western Australia. Since the beginning of the 20th Century, six Australian species have been described by Australian authors, all species apparently endemic. There has been no modern revision of the family, although Fischer-Piette (1977) published an account of museum specimens

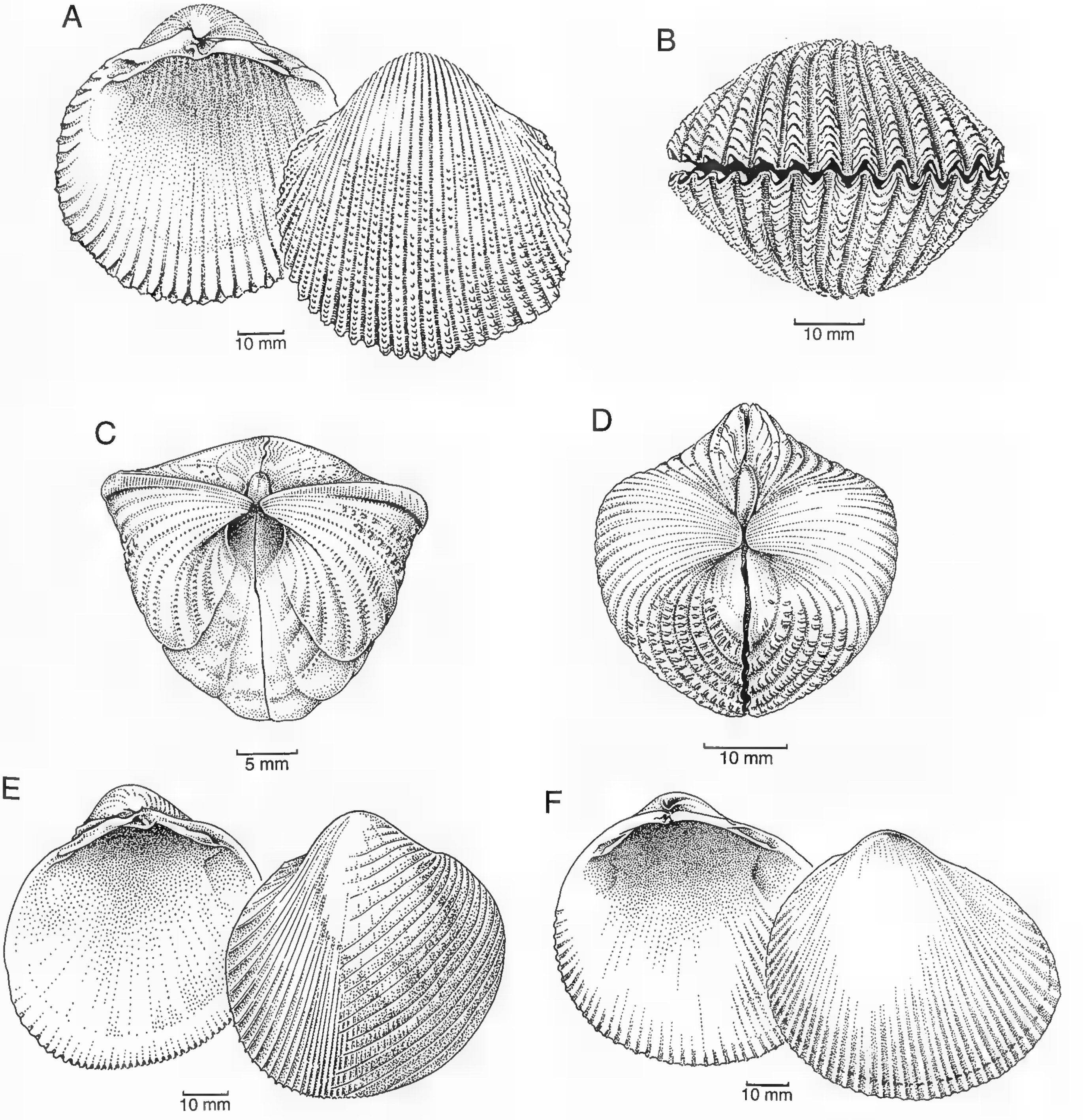


Figure 8.15 Family Cardiidae. Shell valves: **A**, *Vepricardium multispinosum*, right valve in internal view, left valve in external view; **B**, *Acrosterigma reeveanum*, paired valves in ventral view; **C**, *Fragum retusum*, paired valves in dorsal view, posterior uppermost; **D**, *Fragum unedo*, paired valves in dorsal view, posterior uppermost; **E**, *Nemocardium lyratum*, left valve in internal view, right valve in external view; **F**, *Fulvia tenuicostata*, right valve in internal view, left valve in external view. [R. Plant]

known to him. Lamprell & Whitehead (1992) provide an account of most of the Australian cardiids, and a review of the Western Australian cardiids was published by B.R. Wilson & Stevenson (1977). The latter study includes a key to the genera. Poutiers (1992) studied the Australian Protocardiinae. Revisions of the American taxa by Dall (1901b), Keen (1937), McLean (1939), Clench & Smith (1944), and an account of the cardiids described by Lamarck published by Lamy (1942) are useful for comparison. Schneider (1992) has made a preliminary cladistic analyses of the Cardiidae.

No Australian studies on the anatomy, physiology or ecology of cardiids have been made, although Pelseneer (1911) described the anatomy of several Indo-West Pacific species that are represented in the northern Australian fauna. Information on the anatomy of non-Australian cardiids may be found in Kishinouye (1894), Johnstone (1899), Zugmayer (1904), Kupfer (1915), Roche (1925), Kawaguti (1950) and Braun (1954).

Cardiids live in soft substrata ranging from muds to moderately coarse sands. They are shallow burrowers, standing more or less vertically in the substratum with the posterior edge of the shell just below the surface so that the short siphons (Fig. 8.16A, B) project very slightly into the water above. In many species the posterior area of the shell is flattened and lies parallel to the surface.

With the animal in its vertical position the distal part of the thick and strong, sickle-shaped foot points downwards and forms an anchor for vertical movements. The animals are also capable of modest lateral movement and may leave short tracks in the substratum as they go. When attacked by predators, exposed cardiids are able to press the tip of the foot against the substratum and, by means of a sudden contraction, flip themselves several centimetres sideways. Starfish and rays are important predators of cardiids on northern Australian cockle-beds.

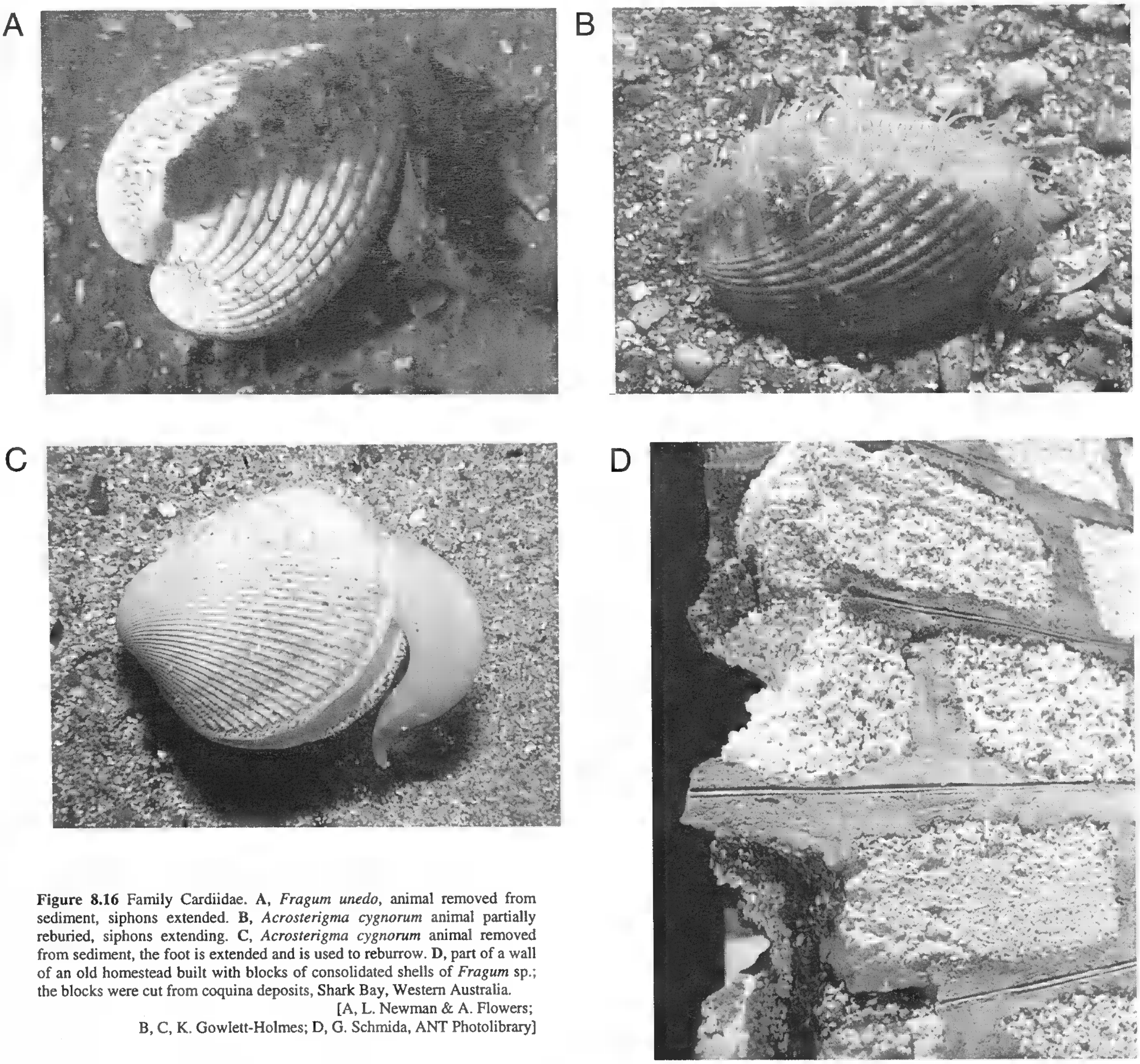


Figure 8.16 Family Cardiidae. **A**, *Fragum unedo*, animal removed from sediment, siphons extended. **B**, *Acrosterigma cygnorum* animal partially reburied, siphons extending. **C**, *Acrosterigma cygnorum* animal removed from sediment, the foot is extended and is used to reburrow. **D**, part of a wall of an old homestead built with blocks of consolidated shells of *Fragum* sp.; the blocks were cut from coquina deposits, Shark Bay, Western Australia.
[A, L. Newman & A. Flowers;
B, C, K. Gowlett-Holmes; D, G. Schmida, ANT Photolibrary]

The pallial eyes of the northern Atlantic species *Cardium edule* are complex structures, each with a multicellular lens, a thin cornea, and a retina of the inverse type (Barber & Wright 1969). Pallial eyes have also been described in *'Cardium' muticum* of the North Pacific (Kishinouye 1894). Cardiid eyes are associated with ciliated sensory tentacles (Zugmayer 1904; Kupfer 1915; Roche 1925). There is no information on whether pallial eyes are present in all cardiids and whether their structure is similar throughout the family.

Kawaguti (1950) described zooxanthellae in the mantle lobes of the Indo-west Pacific *Corculum cardissa*. In this species, the posterior areas of the valves which are exposed to the light when the animal lies half buried in the substratum are translucent which may be regarded as circumstantial evidence that this bivalve may supplement its nutrition from the photosynthetic activity of its symbionts.

Cockles may be extremely abundant in their preferred habitats. The small *Fragum erugatum* may number thousands per square metre in the shallow carbonate sands of hypersaline or mesosaline bays in Shark Bay. When the animals die their shells are washed ashore in countless billions, sorted by the wind, and form an almost pure *Fragum* shell beach. Older beaches of this type become consolidated and form the famous coquina deposits of Shark Bay which are sawn into blocks and used as a building material (Fig. 8.16D). Larger species are rarely as abundant as this but many species may occur in such numbers that they may be fished commercially. Although no Australian species is commercially used in modern times, *Fragum unedo* which is abundant intertidally in northern Australia, was an important element in the subsistence economy of Aboriginal communities in earlier times. *Fragum fragum*, a very common coral lagoon species, is widely used in the Indo-West Pacific region for making necklaces and in other shell crafts.

The family Cardiidae comprises about 200 living species. It is cosmopolitan, but the majority of species are found in the tropical and subtropical latitudes. A summary of the distribution of the Australian species is given by B.R. Wilson & Allen (1987). There are about 35 species in the Australian fauna, representing nine genera. Of these, 29 are tropical species found in northern Australia, three are endemic to the central west coast of Western Australia and three are endemic in the temperate waters of southern Australia.

The majority of the northern species are widespread throughout the Indo-West Pacific region. One of them, *Acrosterigma reeveanum*, occurs across northern Australia from New South Wales to Geographe Bay in Western Australia, but is not found beyond Australian shores. Another, *Plagiocardium frazeri*, is known only from central and southern Queensland and the far north of Western Australia. One widespread Indo-West Pacific species, *A. rugosa*, is found in Queensland, but not in Western

Australia. Three tropical species appear to be endemic to the north coast of Western Australia although further study may show them to be present in the Queensland fauna as well. Eleven of the Indo-West Pacific species reach only as far south as North West Cape in Western Australia whereas nine extend onto the west coast as far south as Shark Bay or the Houtman Abrolhos.

Two of the west coast endemics, *Acrosterigma vlamingi* and *A. marielae*, are restricted to the central coast between North West Cape and Cape Naturaliste. The third, *Fragum erugatum*, has an unusual living distribution from the Dampier Archipelago on the North West Shelf to Fremantle, but it has a fossil range (Quaternary) as far east as the Yorke Peninsula in South Australia. Apparently the southern end of range of this species is unstable and responsive to climate changes.

The northern Australian species, *Acrosterigma reeveanum*, also extended further into the temperate zone during the Quaternary with fossil records in South Australia. One of the north-western endemics, *A. dupuchense*, has Late Quaternary fossil records in Shark Bay but is restricted now to the North West Shelf. The distribution of these species demonstrates a Recent contraction of range of the northern fauna.

All three temperate endemic cardiids are widespread across southern Australia. *Nemocardium thetidis* ranges from North West Cape to southern Queensland, *Fulvia tenuicostata* ranges from about Fremantle to southern Queensland, and *Acrosterigma cygnorum* ranges from about Fremantle to New South Wales. Each of these species has antecedents in the fossil faunas of the south-eastern Australian Tertiary.

The current classification is based entirely on shell morphology (Keen 1969b). Five subfamilies are recognised. The Cardiinae (eight living genera worldwide, two genera in Australia – *Vepricardium* with one species and *Plagiocardium* with two species) have the hinge long and nearly straight, with the left posterior cardinal tooth high; the ribs have ornamentation on the crests, never on the sides, and the posterior margin is digitate or crenulate. The Trachycardiinae (three living genera worldwide, one in Australia – *Acrosterigma* with 19 species) have the hinge short, wide, and angulate to straight; and the posterior area of the shell has spinose ribs and a dentate margin. The Fraginae (six living genera worldwide, five in Australia – *Fragum* with five species; *Corculum* with one species; *Ctenocardia* with three species; *Microfragum* with one species; *Afrocardium* with two species) have a shell with the posterior area distinctly demarcated by an angulate radial ridge; and a rib sculpture of commarginal nodes or scales. The Protocardiinae (five living genera worldwide, four in Australia – *Nemocardium* with one species; *Lyrocardium* with one species; *Pratulum* with one species; *Frigidocardium* with two species) have a rounded or quadrate shell with a long, arched hinge; the posterior area of the shell is defined by an angulate radial ridge and has coarse raised ribs, usually spinose. The Laevicardiinae (five genera worldwide, two in Australia – *Laevicardium* with three species; *Fulvia* with two species) have elliptical-oblique-shaped shells with the posterior area smooth or weakly sculptured; the ribs are never spinose.

This classification, based solely on shell characters, is subjective and future anatomical review is likely to result in change the subfamilial and generic arrangement.

It appears that all the Australian species and genera have Tethyan affinities, including the southern endemics. Several of the Indo-West Pacific cardiids found in northern Australia have apparently close relatives in the tropical Western Atlantic. For example, the Indo-West Pacific species *Acrosterigma elongata* is barely distinguishable from the Western Atlantic *A. magna*. The Indo-West Pacific *Ctenocardia fornicata* closely resembles the Western Atlantic *Trigoniocardia media* (which brings into doubt the status of *Trigoniocardia*). These relationships exemplify the common relict Tethyan affinities of the Indo-West Pacific and Western Atlantic molluscan faunas.

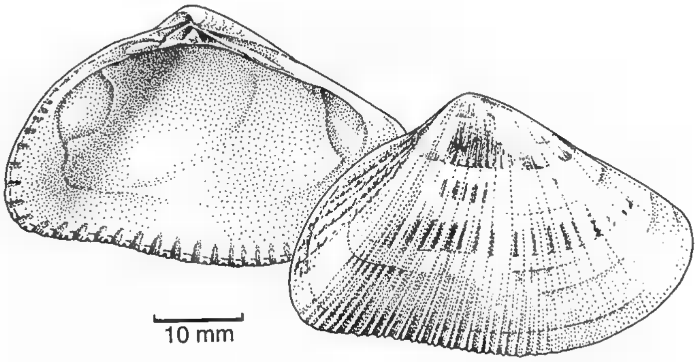


Figure 8.17 Family Hemidonacidae. *Hemidonax pictus*, shell valves, left valve in internal view, right valve in external view. [R. Plant]

Family Hemidonacidae

The Hemidonacidae are a small marine family comprising a single genus, *Hemidonax*.

Hemidonacids shells are small to moderate in size, rather solid, elongately trigonal, radially sculptured, lack a pallial sinus, and having interlocking crenulations around the margins (Fig. 8.17). They are differentiated from shells of the Cardiidae by a bifid anterior cardinal in the left valve, lateral teeth located close to the cardinals, and the ligament lying within the dorsal part of the hinge plate. The ligament is opisthodetic and has anterior and posterior secondary extensions. Anatomically the family is characterised by a non-geniculate foot that lacks a byssal groove, a small pedal gape that is separate from the inhalant aperture, and a lack of siphons, pallial eyes, cruciform muscles and pallial sinus.

Shells of this family were apparently first collected in eastern Australia and the Philippines and taken to Europe for study late in the 18th Century. The confused early nomenclatural history was discussed by Ponder *et al.* (1981). Until the late 19th Century the known species were classified as either *Cardium* or *Donax*, that is until Mörch (1871) introduced a distinct generic name for them. Subsequently, the classification of the genus was problematical, with authors placing it variously in the Cardiidae, Crassatellidae or Donacidae, until Iredale & McMichael (1962) erected a new family name for it. Pelseneer (1911) provided the first information on anatomy (based on South-East Asian material) and referred the genus to the Crassatellidae. Boss (1971) reviewed the classification and concluded that *Hemidonax* should be placed in the Cardiidae. Ponder *et al.* (1981) resolved the classification issue with a taxonomic and morphological survey of the living and fossil species, confirming the distinctness of the family but allying it with the Cardiidae in the superfamily Cardioidea.

There is a moderate degree of mantle fusion in this family, but there are no siphons, the inhalant and exhalant apertures being mere gaps. The slightly thickened mantle edge around the apertures scarcely projects beyond the shell margins, except for the ventral part of the exhalant aperture which has an extensible edge protruding like a short tentacle. The pedal gape is rather short and well separated from the inhalant aperture. The middle mantle folds are greatly reduced. The inner mantle lobes bordering the exhalant and pedal apertures bear short, simple tentacles and the inhalant aperture is surrounded by complex, branching tentacles. Unlike cardiids, hemidonacids lack pallial eyes.

The foot is wide, thin, compressed and simple and lacks a byssal groove and gland. The adductor muscles are subequal, the pedal muscles are thin and do not encase much of the visceral mass (as they do in the Cardiidae). Foot retractor muscles are lacking and there are no cruciform muscles (as in the Donacidae). Neither are there siphonal retractors, there being no siphons, and hence no sinus in the pallial line.

The ctenidia are plicate and resemble those of the Cardiidae with a small outer demibranch bearing a supra-axial extension, and a much larger inner demibranch. The free edge of the outer demibranch reaches only to about the middle of the descending surface of the inner demibranch to which it is closely applied. This suggests that there is direct transfer of food particles to the food groove along the free edge of the inner demibranch. The ascending lamellae of the inner demibranchs are not fused to the visceral mass (as they are in the Cardiidae) but behind the visceral mass they maintain a weak ciliary connection to each other. The labial palps lie level with the anterior end of the ctenidial axis and the dorsal side of the anterior adductor muscle.

There is no information on reproduction or larval development of hemidonacids. However, it is likely that they are dioecious spawners like the cardiids. Nor are there any details on feeding or niche preferences among the species.

As far as is known, hemidonacids are superficial burrowers in the shallow sublittoral zone. They live in clean sand with the posterior apertures just level with the surface of the substratum. The compressed foot suggests that they are active burrowers.

The family is confined to the central Indo-West Pacific and Australian regions. One species in the Philippines–Indonesian region (*H. donaciformis*), has a subspecies in northern Australia (*H. d. australiensis*) and four other extant species are known – two in eastern Australia (*H. pictus*, *H. dactylus*), one in the north-west (*H. arafurensis*), and one in the temperate south (*H. chapmani*). The one named fossil species, *H. dixoni* (Miocene-Pleistocene), is described from south-eastern Australia. *Hemidonax*, is believed to have originated in the tropical north of Australia and to have speciated into the temperate south during the Pliocene.

Superfamily TRIDACNOIDEA

Tridacnoideans ('giant clams') are medium-sized to very large marine bivalves that live either on or in close association with shallow-water coral reefs (Pl. 14). The group comprises a single family, the Tridacnidae and two extant genera, *Tridacna* and *Hippopus*. Aside from their importance in reef ecosystems, they are significant for including the largest bivalves ever to have existed (Rosewater 1965; Yonge 1975). Although the Tridacnoidea are today confined to the Indo-Pacific region, fossil species are known from the West Indies, northern Africa (Egypt) and Europe (Rosewater 1965; Keen 1969c).

Tridacnoideans are characterised by large, thick to extremely thick, equivalve shells which exhibit prominent ribs, sometimes with scales or short spines, a hinge of two oblique lamellar cardinal teeth and one or more lateral teeth (usually no anterior lateral teeth), and often a byssal gape (Rosewater 1965; Keen 1969c). At the microstructural level the shell is aragonitic, with a crossed-lamellar outer layer and complex crossed-lamellar inner layer (Boss 1982; Belda, Cuff & Yellowlees 1993). The ligament is completely external and positioned posteriorly. Internally, muscle scars are principally associated with the large posterior adductor muscle (the monomyarian condition) and the posterior pedal retractor muscle. The pallial line is simple, without a pallial sinus. Tridacnoideans differ from most other bivalve molluscs in having the hinge orientated ventrally against the substratum and the internal organs repositioned to accommodate the specialised positioning of mantle and siphons dorsally (the so-called 'rotated' nature of the organs actually produced through differential growth ventrally, Stasek 1962, 1963c; Lucas 1994). The greatly hypertrophied siphonal tissue adjoining the outer edges of the shell valves is orientated dorsally. Inner and outer demibranchs of the gill are narrow, curved (J- or S-shaped) and the filaments show distinct nodes (Yonge 1980; Boss 1982). Development of the outer demibranch is variable, ranging from complete (*Hippopus hippopus*, *Tridacna gigas*) to incomplete (other species of *Tridacna*) (Rosewater 1965). Other internal anatomical features of tridacnoideans include: an anteriorly situated mouth; elongate, variably developed labial palps; a stomach conforming to Type V of Purchon (1960a); unification of the style sac to the midgut; penetration of the ventricle of the heart by the elongate rectum; absence of an anterior adductor muscle; posterior positioning of the byssal orifice and the incurrent siphonal orifice; and an elongate kidney (Purchon 1955a; Rosewater 1965; Yonge 1980; Boss 1982; Norton & Jones 1992).

The mantle edge either exhibits discrete hyaline structures (the so-called 'hyaline organs' of *Tridacna*) or is translucent (*Hippopus*) and always contains vast numbers of the symbiotic dinoflagellate algae, of the genus *Symbiodinium* (Lucas 1994). The only other bivalve molluscs that have symbiotic algae are the cardiids *Corculum cardissa*, *Fragum fragum*, and *Fragum unedo* (Kawaguti 1983), but in none of these is the symbiosis as significant as in tridacnoideans. Tridacnoideans are not gonochoristic as sometimes stated (for example, Boss 1982), but in fact are typically hermaphroditic (Rosewater 1965; Braley 1988). Fertilisation is external in all species.

Although the present study follows Keen (1969c), Kafanov & Popov (1977) and Boss (1982), in assigning the Tridacnidae to its own superfamily, the Tridacnoidea, it is generally accepted that tridacnids are very closely related to the Cardiidae; they are sometimes included in the Cardioidea (see Yonge 1980). Schneider (1992) in fact has reduced the Tridacnidae to a subfamily of the Cardiidae based on his preliminary cladistic analysis of cardiid-tridacnid shell and anatomical features.

Family Tridacnidae

The characteristics of this family are as outlined above for the Tridacnoidea. One of the two extant genera, *Tridacna*, often has brightly coloured mantles which, when extended, protrude laterally from the edge of the shell, in all but one species. The other genus, *Hippopus*, has a generally duller appearance to the mantle, and the mantle does not extend beyond the inner edge of the shell. The mantles are generally exposed to sufficient sunlight which supports the giant clams' symbiotic relationship with zooxanthellae (the dinoflagellate algae, *Symbiodinium* sp.). The two genera and three subgenera of *Tridacna* (principally derived from Keen 1969c) can be defined by the following features. *Tridacna sensu lato* has the shells large to massive; ribs few, strong; and anterior lateral teeth absent. *Hippopus* has shells moderately large; ribs more numerous than *Tridacna*; no byssal gape; and anterior lateral teeth present. *Tridacna sensu stricto* has the umbones almost central; valves almost equilateral; and is unattached, but set among reef corals in adults. *Tridacna (Persikima)* has umbones posterior to the midline; and valves strongly inequilateral. *Tridacna (Chametrachea)* has umbones anterior to the midline; sculpture tending to be scaly; and often bores into coral. Linnaeus (1758) provided the first valid binominal names for *Tridacna gigas* and *Hippopus hippopus*. The most complete taxonomic revision was that of Rosewater in 1965, who later (1982) described an additional species, *Hippopus porcellanus*. Thus, the species described by 1982 were *Tridacna (Tridacna) gigas*, *Tridacna (Persikima) derasa*, *Tridacna (Chametrachea) squamosa*, *Tridacna (Chametrachea) maxima*, *Tridacna (Chametrachea) crocea*, *Hippopus hippopus* and *Hippopus porcellanus* (for colour illustrations of shells of most of the above species see Lamprell & Whitehead 1992). A new species, *Tridacna tevoroa*, was named and later more fully described by Lucas, Ledua & Braley (1990, 1991) from the islands of Tonga and Fiji. Another new species, *Tridacna rosewateri*, was named from shell specimens alone taken from the Saya de Malha Bank in the western Indian Ocean (Sirenko & Scarlato 1991).

Figure 8.18C shows a general diagram of the left valve and half the tridacnid soft parts. Lucas (1994) reviewed the controversy of whether tridacnid shells have rotated with respect to the soft body to account for the unusual mantle structure as Yonge (1936, 1980) argued, or have grown in the morphologically posterior direction compared with typical bivalve molluscs, which show growth in a ventral direction, as argued by Stasek (1962, 1963c). Lucas (1994) indicated that the evidence from juvenile tridacnid development (La Barbera 1975) supports Stasek's concept.

The shells of large *Tridacna gigas* are massive (> 400 kg), whereas smaller species attain a maximum of an order of magnitude less in weight than *T. gigas* (Lucas 1994). Shell shape ranges from semicircular to sub-oval, fan-shaped, elongate, ovate triangular or triangular. An anterior lateral tooth is absent with the exception of the genus *Hippopus*. Sculpture consists usually of well-developed ribs often ornamented with broad scales or short, stout spines. Positioning of the umbones in respect to the anterior or posterior extremities of the valves is one of the most useful diagnostic features of the three subgenera of *Tridacna*, as is the development of the byssal gape (prominent in *T. (Chametrachea)*. Shell microstructure of the giant clam was described by Belda *et al.* (1993). The species of giant clam (excluding *Tridacna rosewateri* and *T. tevoroa*) are illustrated in Figures 8.19 and 8.20 (after Norton & Jones 1992).

The posterior adductor muscle and posterior pedal retractor muscle are located subcentrally. Their scars on the shell valves are adjoining. The anterior adductor muscle is absent. The pallial line on each valve is the scar of the long, wide mantle retractor muscles. The foot is truly functional only in juvenile clams, and subsequently atrophies. Atrophy of the byssus occurs only in the larger species of *Tridacna* and in *Hippopus*. The byssal gape in the shell valves is pronounced in species of the subgenus *Tridacna (Chametrachea)*, all of which rely on a combination of byssal threads and coral boring/wedging for attachment to the substratum. The demibranchs, labial palps and digestive tract (including the crystalline style) generally adhere to the basic bivalve design, so that although symbiosis is one source of nutriment for giant clams, they also obtain food by filter-feeding and by uptake of dissolved organic matter (reviewed in Lucas 1994). Rosewater (1965) draws attention to the fact that only in *Hippopus* and *Tridacna (Tridacna) gigas* is the outer demibranch of the gills complete. Other species of Tridacnidae show varying degrees of reduction of the outer demibranch. Some of the potential food material is rejected at the mouth and disposed of as pseudofaeces, as occurs in other bivalve molluscs when the density of particles in the water column is too high.

The symbiotic relationship with zooxanthellae appears to supply a majority of older clams' carbon requirements, but young juveniles still rely heavily on supplementing their food supply with particulate matter (Klumpp, Bayne & Hawkins 1992). Glucose is the main photosynthate produced by the zooxanthellae and this is taken up by the host clam. Other photosynthates, in decreasing amounts, are glutamate, aspartate, succinate, alanine, and glycerol (Griffiths & Streamer 1988; Fitt 1993). For many years the zooxanthellae were believed to occur extracellularly in the bloodstream where they concentrated in 'haemal spaces' (Yonge 1936, 1953; Morton, B. 1978b) near the surface of the mantle, though a complex tube system had been observed in one study that might have established a link between the stomach and mantle edge (Mansour 1946). Mansour's tube system has now been confirmed, these tubes being essentially tertiary extensions of the gut (Norton & Jones 1992) in which the zooxanthellae occur extracellularly.

The kidney in giant clams is large and contains phosphate concretions (Trench, Wethey & Porter 1981). The large kidney may act as a storage for some indigestible products from the zooxanthellae (Yonge 1980), though Fitt (1993) questions whether quantitative data support the hypothesis that tridacnid kidneys are unusually large compared to other bivalve molluscs. Respiration via the gills is similar to other bivalves but during the daily period of maximum sunlight, excess oxygen generated by photosynthesis of the entrapped zooxanthellae is eliminated via the gills (R.K. Trench personal communication 1982). Sensory organs include hyaline organs (eyes) and ultraviolet receptors in the eye (Wilkens 1984). The nervous system is poorly developed as in other bivalve molluscs, but some integrated behaviour is shown as in the spawning response (Braley 1984, 1985; Heslinga *et al.* 1984; Trinidad-Roa 1988). Reproduction has been investigated (Stephenson 1934; Wada 1954) increasingly due to interest in mariculture of giant clams (Beckvar 1981; Gwyther & Munro 1981; Braley 1984; Heslinga *et al.* 1984; Crawford, Nash

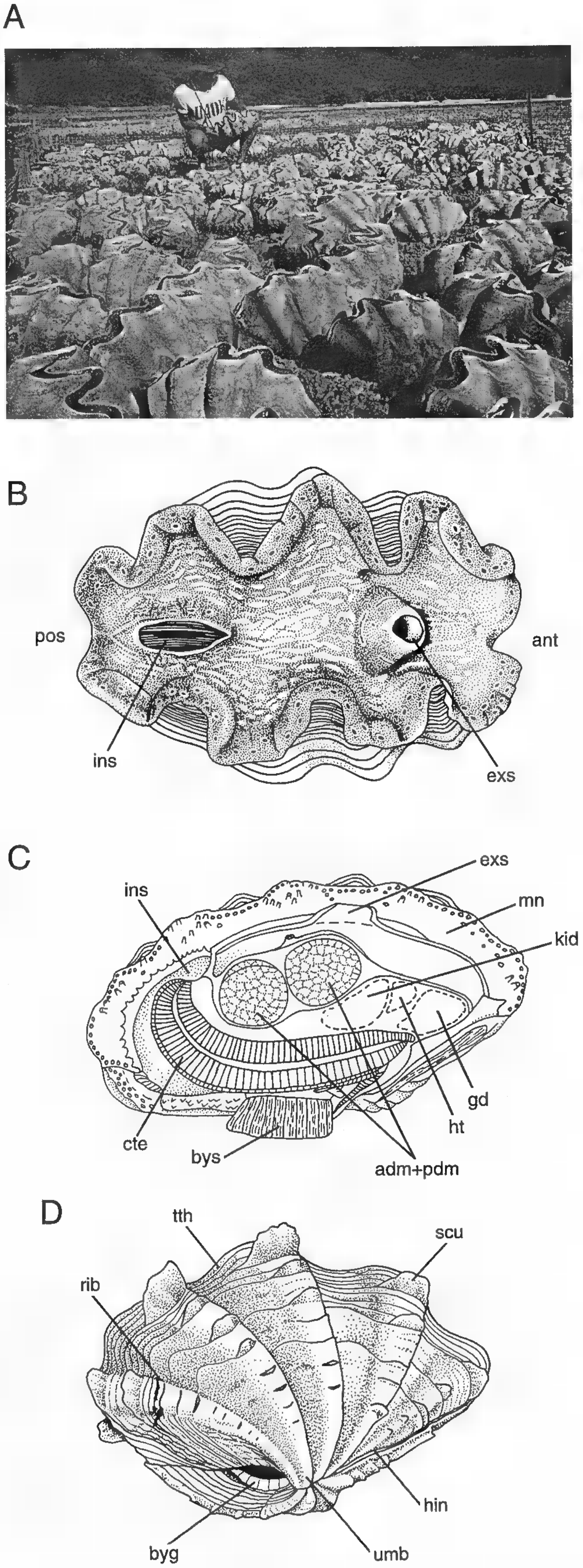


Figure 8.18 Family Tridacnidae. A, five and six-year-old *Tridacna gigas* in intertidal culture at Orpheus Island, Great Barrier Reef. **B–D**, tridacnid features: **B**, shell, mantle view; **C**, internal anatomy, right valve removed; **D**, shell, right lateral view. **adm**, adductor muscle; **ant**, anterior; **byg**, byssal gape; **bys**, byssus; **cte**, ctenidium; **exs**, exhalant siphon; **gd**, gonad; **hin**, hinge; **ht**, heart; **ins**, inhalant siphon; **kid**, kidney; **mn**, mantle; **pdm**, pedal retractor muscle; **pos**, posterior; **rib**, rib; **scu**, scute; **tth**, teeth; **umb**, umbo. (B–D, from Calumpong 1992) [A, J.S. Lucas; B–D, J. Legaspi]

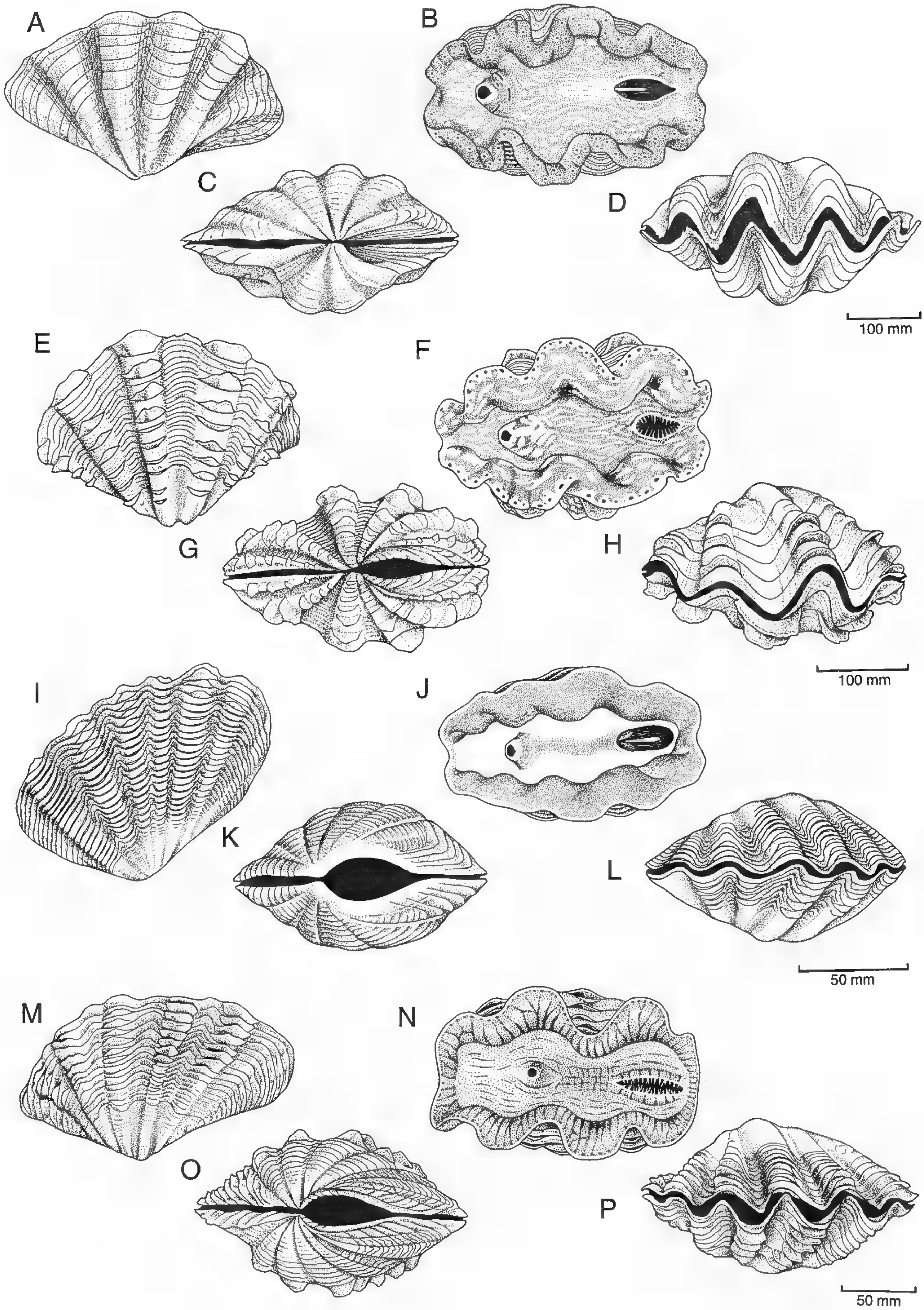


Figure 8.19 Family Tridacnidae. Shell valves, lateral, mantle, ventral and dorsal views: **A–D**, *Tridacna gigas*; **E–H**, *Tridacna squamosa*; **I–L**, *Tridacna crocea*; **M–P**, *Tridacna maxima*. **A**, **E**, **I**, **M**, lateral views; **B**, **F**, **J**, **N**, mantle views; **C**, **G**, **K**, **O**, ventral views; **D**, **H**, **L**, **P**, dorsal views. (From Calumpong 1992) [J. Legaspi]

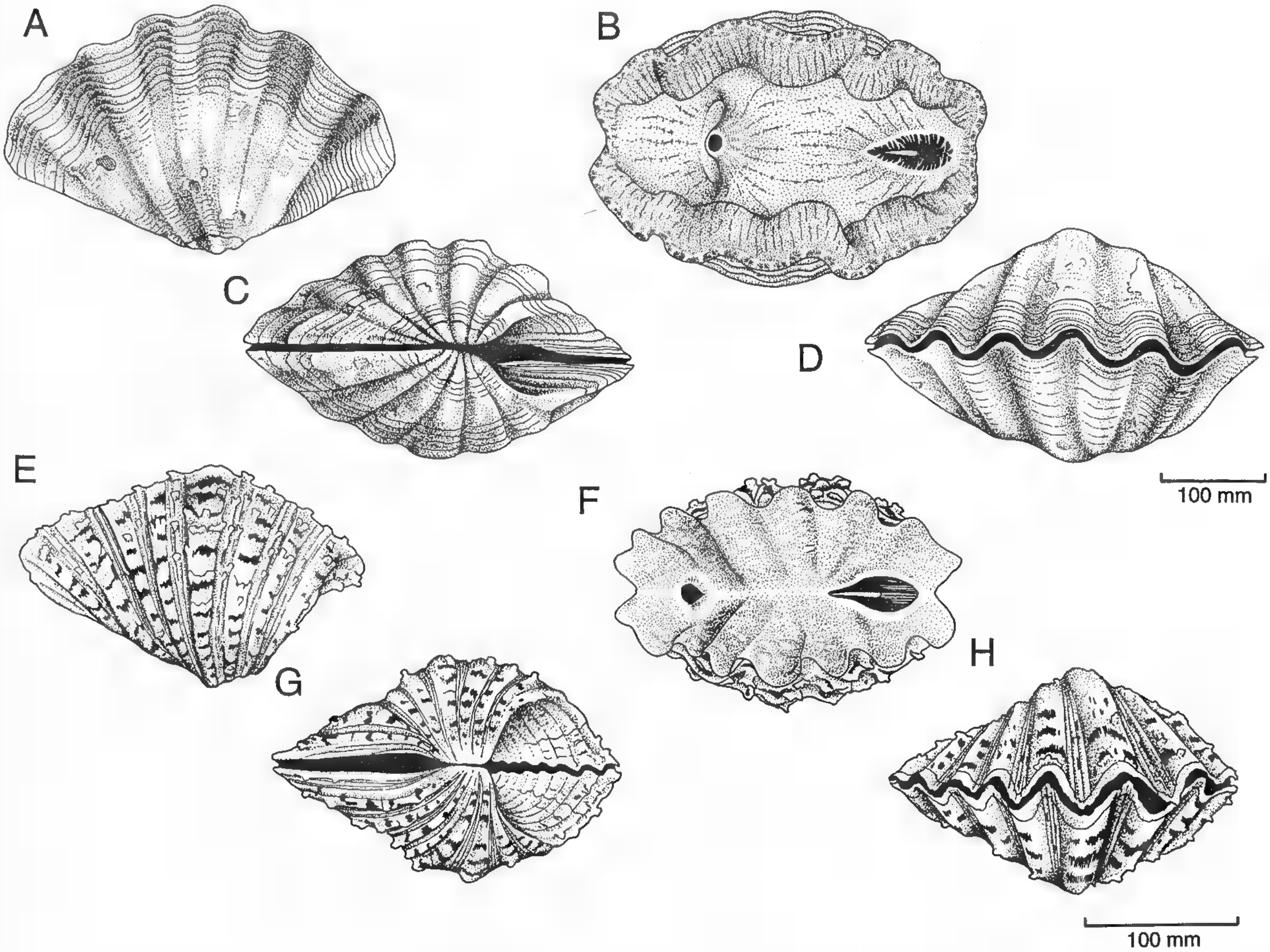


Figure 8.20 Family Tridacnidae. Shell valves, lateral, mantle, ventral and dorsal views: **A–D**, *Tridacna derasa*; **E–H**, *Hippopus hippopus*. **A**, **E**, lateral views; **B**, **F**, mantle views; **C**, **G**, ventral views; **D**, **H**, dorsal views. (From Calumpong 1992) [J. Legaspi]

& Lucas 1986). Their sessile habit has allowed *in situ* studies on spatial distribution and gonad biopsy samples of discrete giant clam populations over annual periods (Braley 1987a, 1988).

Giant clams are initially protandrous and then simultaneous hermaphrodites, but *Tridacna (P.) derasa* appears to display hermaphroditism much less often than the other species (Braley 1988). Individuals of the larger species become reproductively mature as males in four to five years. Maricultured *Tridacna (T.) gigas* in the Philippines matured as females at about 10 years and were induced to spawn (M.J.T. Roa personal observation, 1995). During spawning, sperm release precedes the spawning of eggs. This spawning is diel (mid to late afternoon) in the larger giant clam species, but lunar periodicity and reproductive season appear to vary with locality (Braley 1984; Heslinga *et al.* 1984). Larvae are planktotrophic for about one week, then settle at a size of 200 µm. Although about 1000 million eggs have been spawned by an individual *T. (T.) gigas* in a hatchery situation (J.S. Lucas personal observation), the tremendous potential fecundity is not realised in natural recruitment (Pearson 1977; Yamaguchi 1977; Braley 1987b). Australia's Great Barrier Reef has the largest natural populations of the most heavily exploited species, *Tridacna (T.) gigas* and *T. (P.) derasa*, in their existing ranges. Here, some reefs support high density populations of these species (>30 per ha) which would be more likely to assure successful fertilisation than the typically sparse densities encountered on most reefs (Braley 1984, 1987b). *Tridacna (T.) gigas* is more common in the northern half of the Great Barrier Reef, but other species appear to be distributed more evenly over its length. The distribution of all giant clam species, with the exception of the two most recently described species, is centred around eastern Indonesia and the southern Philippines. The ranges of the heavily exploited species have become reduced, particularly in the Pacific islands and in much of Asia. Only two species, *Tridacna (C.) maxima* and *T. (C.) squamosa*, range widely from eastern Africa to the central Pacific islands. Due to the symbiosis with zooxanthellae, giant clams are restricted to shallow depths (*ca* 10 m) in coral reef areas, though two species, *Tridacna (P.) derasa* and *T. (P.) tevoroa*, can be found at moderate depths (20–35 m) in very clear tropical seas.

Although giant clams are sessile, as juveniles they are capable of short distance movement by discarding old byssal threads, moving with the foot and placing new byssal threads on the substratum. Adult *Tridacna (T.) gigas*, which are abyssate, can right themselves if they have been rolled on their side by rapid opening or closing of the valves which shifts the point of equilibrium of mass (Fankboner 1971). A jet of water through the excurrent siphon is used to deter grazing fish (Stasek 1965). The only consistently boring giant clam species is the small *Tridacna (C.) crocea*. However, the next smallest species, *Tridacna (C.) maxima*, may be found partially or deeply embedded in reef substrata. *Tridacna (C.) crocea* is fully embedded in the coral so that only the edge of the shell protrudes. It has been suggested that this species not only physically deepens its hole by the shell scraping the coral, but that the byssal gland secretions may assist with deterioration of the coral in the hole (Hamner & Jones 1976).

Diseases or parasites can affect populations (Alder & Braley 1989; Braley 1992; Norton & Jones 1992) but definitive causes of such phenomena are poorly understood at present. Predators on small clams include octopods, fish, rays, turtles, as well as an array of gastropod molluscs such as *Cymatium* sp., muricids, pyramidellids (Calumpong 1992), but for large individuals humans are the main predator. Heavy exploitation of giant clam populations in the late

1960s and early 1970s, particularly by Taiwanese fishing vessels, affected not only the Pacific and Asia but even previously untouched reefs of the central to northern Great Barrier Reef (Pearson 1977). The adductor muscle of giant clams is a much-prized delicacy in South-East Asia, Hong Kong and Taiwan where the price ranges upwards from US$20 per kilogram. It has been estimated by two market studies (Dawson & Philipson 1989; Shang, Tisdell & Leung 1991) that the Taiwanese market alone could absorb between 100–240 tonnes/year of adductor muscle. Tisdell & Wittenberg (1992) estimated a potential market of up to 3000 tonnes/year of whole meats amongst the Pacific islander populations in New Zealand alone. Shells are also valuable for the tourist trade and the aquarium trade is being supplied now with maricultured clams. An ACIAR (Australian Centre for International Agricultural Research) project on the Culture of Giant Clams took place between 1984 and 1992. Numerous publications resulted from that project, and hatcheries and farms in the Pacific, the Philippines and Australia were developed. Figure 8.18A is an impressive photograph of the grow-out phase of intertidal culture of *Tridacna gigas* from James Cook University's field station on Orpheus Island, North Queensland. Likewise, the MMDC (Micronesian Mariculture Demonstration Centre) project in Palau (Heslinga, Perron & Orak 1984; Heslinga, Watson & Isamu 1990) and ICLARM (International Center for Living Aquatic Resources Management) in the Solomon Islands (Munro, Gilkes, Gervis & Hambrey 1993; Munro, P 1993) have been important centres for giant clam culture research. The mariculture of giant clams can include both commercial production for food as well as the production of juveniles for restocking of depauperate reefs.

Derivation of neither the Cardiidae (Keen 1980) nor the Tridacnidae (Allen 1985) from the Carditoidea can be maintained in view of the distinctive sperm morphology of the Carditoidea-Crassatelloidea-assemblage (Healy 1995, 1996). It seems more likely that the Cardiidae-Tridacnidae group arose from a source closer to the Veneroidea or from that group's direct antecedent.

Although authors differ as to whether the Tridacnidae should be placed into their own superfamily – Tridacnoidea (Keen 1969c; Kafanov & Popov 1977; Boss 1982) – or included in the Cardioidea (Yonge 1980; Schneider 1992), they are in general agreement that tridacnids and cardiids are closely related. Stratigraphically, the Cardiidae appeared earlier (Triassic) than the Tridacnidae (possibly upper Cretaceous, definitely from the Eocene onwards) (Keen 1969c). Yonge (1980) has suggested that tridacnids may even have arisen to partly fill the ecological gap available following the extinction of the sedentary rudist bivalves at the Mesozoic–Cainozoic boundary. Recently, Schneider (1992) reduced the Tridacnidae to the level of subfamily within the Cardiidae, based on a cladistic analysis of shell and anatomical features. His study revealed a number of shared derived features of the Fraginae and *Tridacna* (for example, tentacle pattern, positioning of the style sac and caecum, structure of the stomach floor, presence of a large valvule). The closeness of this relationship is further strengthened by the fact that the only recorded occurrences of symbiotic algae within the tissues of the Bivalvia are among members of the Fraginae (*Fragum*, *Corculum*; Kawaguti 1983) and the Tridacnidae (Rosewater 1965; Yonge 1980). Although in the present account we have retained the Tridacnidae as a family within its own superfamily, primarily because of the specialised mode of life of these bivalves and the shell and anatomical changes associated with that mode of life, Schneider's results suggest strongly that the family should probably be included among the Cardioidea.

Stasek (1962) has suggested that both *Hippopus* and *Tridacna* arose separately from an ancestral form resembling the extinct genus *Byssocardium*. Rosewater (1965) supported separate origins of *Hippopus* and *Tridacna*, but also stressed that *Hippopus* appears to be the more primitive of the two genera: the shell more closely resembling that of *Byssocardium*; and the lack of discrete hyaline 'organs'. Authors differ as to their interpretation of the least specialised species within the genus *Tridacna*. Rosewater (1965) argued that the presence of a complete outer demibranch in *T. (T.) gigas* indicates that it is less highly derived than either *T. (Persikima) derasa* or any species of *T. (Chametrachea)*, all of which lack a complete outer demibranch. Alternatively, Yonge (1980) favoured species of *T. (Chametrachea)* (*T. (C.) maxima*, *T. (C.) squamosa*) as being the least specialised of all tridacnids because they maintain their byssal attachment to the substratum throughout their lifespan – the large size of *T. (T.) gigas* and *T. (P.) derasa* here being perceived as an advanced feature associated with replacement of byssal attachment with sheer weight. Fossil tridacnids elsewhere other than in the Indo-Pacific are rare. Three *Tridacna* species are known from the mid- to late Tertiary of Europe and Egypt and a single species, possibly belonging to the genus *Hippopus*, has been recorded from the lower Miocene of Florida (Rosewater 1965). Three extinct genera each containing two or three species are known from the Eocene of France and Jamaica (*Avicularium*, *Byssocardium*, *Goniocardium*). The extinct genus *Sawkinsia* was recently transferred from the Tridacnidae back to its original position among the Cardiidae by Schneider (1992) because of the absence of critical tridacnid shell features.

Superfamily MACTROIDEA

Mactroideans are shallow-water, infaunal-burrowing bivalves that occur, sometimes abundantly, in estuarine and marine habitats. Their shells are equivalve and porcellaneous with a prominent resilifer (sometimes projecting – chondrophore), typically paired lateral teeth (absent in Cardiliidae) and a distinctive inverted V-shaped arrangement of cardinal teeth (single deltoid cardinal on left valve, paired almost dorsally joined cardinals on right valve). The anterior cardinal of the right valve may be closely associated with or even combined with the anterior lateral in some Mesodesmatidae. A lamina sense organ occurs on the inner wall of the mantle behind the siphons (Cotton 1961).

Conchologically the Australian Mactroidea are well known, but from the anatomical viewpoint they remain virtually unstudied. Most of the commoner or widely distributed species were described by European workers including Lamarck, Reeve, Deshayes and Gmelin in the late eighteenth to mid-nineteenth centuries. It was not until the first half of this century that Australian workers such as Iredale turned their attention to descriptions and revisions of the local Mactroidea. Australia has an especially rich array of Mactridae, to which, even relatively recently, new species have been added (Lamprell & Whitehead 1990; Healy & Lamprell 1992).

Mactroidean shells are porcellaneous, aragonitic, and composed of inner and outer (complex) cross-lamellar layers (Taylor *et al.* 1973). The large internal ligament is contained by a resilifer, whereas the external ligament, if present, is very reduced and supported by narrow nymphs. Lateral teeth are present in most mactroideans, but may be poorly developed or even absent in certain genera. Similarly the inverted V-shaped configuration of cardinal teeth (anterior to the resilifer) may sometimes be secondarily reduced (for example, many Mesodesmatidae). Shells of most mactroideans are trigonal or subtrigonal in shape and close-fitting. In taxa with elongate shells (for example, the mactrid subfamily Lutrariinae) a pronounced shell gape occurs anteriorly and posteriorly. The brown to translucent periostracum is commonly eroded in mature or gerontic specimens. Anterior and posterior adductor muscle scars are equal to markedly unequal and connected by a pallial line which usually shows a distinct sinus. Anterior and posterior pedal retractors are associated with anterior and posterior adductors, respectively (Boss 1982). Adult mactroideans lack a byssus. Only the Mactridae (Fig. 8.21) and Mesodesmatidae are known anatomically. The spade-shaped or angular foot which projects from an antero-ventral gape in the mantle, enables rapid burrowing through the substratum. Siphons are either joined (Fig. 8.21; Mactridae) or separate (Fig. 8.23A; Mesodesmatidae), and are papillate distally (Allan 1959; Cotton 1961).

Feeding in mactroideans, as in most bivalves, involves filtration and concentration of particulate matter by the gills and subsequent ciliary transport of food onto the labial palps. The palps assist in sorting food and directing it to the mouth. The paired labial palps (partially united in the Mactridae) are elongate and narrow (Fig. 8.21) but not inserted into the distal oral groove (Boss 1982). A rejection channel for pseudofaeces is often formed from the mantle folds (Yonge 1948). The stomach conforms to the Type V of Purchon (1960a), except that the style-sac and midgut are separated and the minor typhlosole is absent.

The circulatory system consists of a heart (thin-walled auricles and an elongate, dilated ventricle) and anterior and posterior aortae, the latter having a postventricular dilation. The hindgut passes through the ventricle to the anus (Allen 1975; Boss 1982).

The gills are eulamellibranchiate, with smooth, plicate or synaptorhabdic ctenidia, inner and outer demibranchs and interlamellar septa (Boss 1982). Gills may also serve to regulate salts and uptake of amino acids in some species (Anderson 1975).

Studies of reproductive biology and larval survival in the Mactroidea are limited largely to Atlantic and New Zealand species of commercial importance (Rapson 1952; Longo & Anderson 1970; Cain 1975). Mactroideans are dioecious and larviparous (Boss 1982). Spermatozoa are of the aquasperm type, that is to say are composed of a short head (acrosome and nucleus), short midpiece and a flagellum (Longo & Anderson 1969). Temperature appears to be a major factor in initiating gamete formation, and in some estuarine species (for example, *Rangia cuneata*) synchrony of spawning may be salinity dependent (Cain 1975).

Mactroideans inhabit marine or estuarine environments, preferring areas of shifting sand or sandy mud in the littoral zone. Certain species exhibit wide adult salinity tolerances (from nearly 0–33 ‰ in the American mactrid *Rangia cuneata*; Cooper 1981).

By their very abundance, the Mactroidea constitute an ecologically important group of bivalves. Much of our current knowledge of the habits and anatomy of these animals derives from work on commercial American, New Zealand and European species. Detailed studies on the biology and ecology of Australian or Indo-Pacific mactroideans are lacking.

The superfamily comprises approximately 200 species distributed between four families: the cosmopolitan Mactridae and Mesodesmatidae and the rare Indo-Pacific Cardiliidae and Anatinellidae (Keen 1969d; Boss 1982). Of these, the Mactridae, Mesodesmatidae and Cardiliidae are known to occur in Australian waters, the Mactridae in particular being well represented both in terms of species (45) and genera (8).

Significant problems concerning the phylogeny and composition of the Mactroidea remain. Thiele (1929–1935) tentatively placed the Cardiliidae in the Mactroidea. Saul (1973) argued that the Mactridae may have been derived polyphyletically from various lines of Arcticidae during the Jurassic and Cretaceous. Allen (1985) included the Mesodesmatidae in its own superfamily and considered this group to be 'a small, highly specialised superfamily paralleling the tellinoidean donacids in form, habits and habitat' (p. 382). He also suggested that the Tellinoidea and Mesodesmatoidea may share a common origin. Anatomically however, the Mactridae and Mesodesmatidae are closer to each other than to the Tellinoidea or other heterodonts (Purchon 1987b), and similarities between mesodesmatids and tellinoideans (or cardioideans) must be regarded as convergences (Yonge & Allen 1985). In the absence of comparative soft part morphology for the Anatinellidae or Cardiliidae, the Mesodesmatidae are here treated as a member family of the Mactroidea.

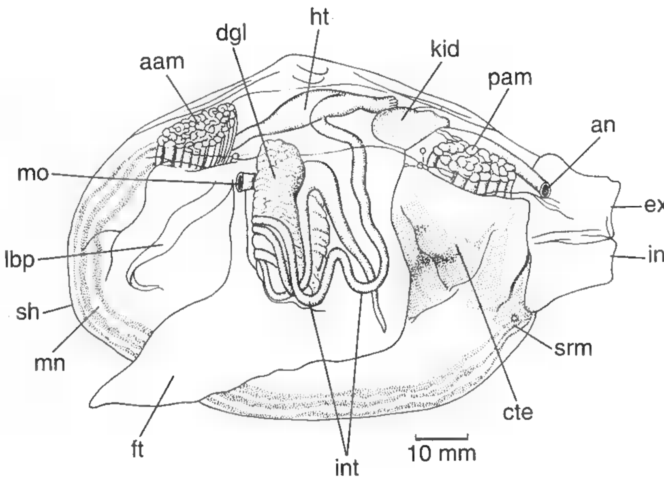


Figure 8.21 Superfamily Mactroidea. Mactroidean anatomy, based on the European mactrid, *Mactra (Mactra) glauca*. **aam**, anterior adductor muscle; **an**, anus; **cte**, ctenidium; **dgl**, digestive gland; **exs**, exhalant siphon; **ft**, foot; **ht**, heart; **ins**, inhalant siphon; **int**, intestine; **kid**, kidney; **lbp**, labial palp; **mn**, mantle; **mo**, mouth; **pam**, posterior adductor muscle; **sh**, shell; **srm**, siphonal retractor muscle. (After Milne-Edwards in Fischer 1880–1887) [S. Weidland]

Family Mactridae

Commonly known as surf clams or trough shells, mactrids are important components of the marine and estuarine fauna around the coastlines of mainland Australia and Tasmania (Kershaw 1958; Allan 1959; Cotton 1961). They are medium to large burrowing bivalves with smooth, equivalve, often trigonal shells and a well-developed hinge which features a large resilifer, a prominent and inverted V-shaped cardinal tooth on the left valve, an angular pair of cardinals joined or almost joined dorsally on the right valve, and often elongate lateral teeth. The siphons are joined and usually enclosed within a periostracal sheath.

Many of the larger, tropical mactrids occurring in Australia were described by Deshayes and Reeve in the early 1850s from material supplied by the English shell collector Hugh Cuming. Thirty years earlier, Lamarck had described species gathered from the southern and western coasts, including the circum-Australian *Spisula (Notospisula) trigonella* (for this and other early references see Lamprell & Whitehead 1992). E.A. Smith (1914) listed all known species from Australia, including one new species (*Mactra queenslandica*), and their principal synonyms. Through checklists and books subsequent authors have added to, illustrated, or briefly discussed the mactrid fauna of Australia or of the individual states (Allan 1959; Cotton 1961; Iredale & McMichael 1962; Lamprell & Whitehead 1992). With the exception of the endemic *Diaphoromactra*, most of Iredale's (1930a) genera were placed as subgeneric divisions of *Mactra* (*Austromactra*, *Nannomactra*, *Electomactra*) or *Spisula* (*Notospisula*) by Keen (1969d). Gill & Darragh (1963) revised the living and fossil Australian Zenatiinae. Most of the valid species and genera of the Mactridae occurring in Australian waters have been diagnosed and illustrated photographically by Lamprell & Whitehead (1992), including their relatively recently described (1990) species *Mactra (Mactra) westralis* and *Spisula (Notospisula) austini.*

The Mactridae are divisible into four subfamilies: Mactrinae (most mactrids), Lutrariinae, Zenatiinae and Pteropsellinae, and there are about twenty valid genera (Keen 1969d). All four subfamilies are represented in the extant Australian fauna. These comprise the following genera (approximate number of local species indicated): subfamily Mactrinae – *Mactra* (27 species), *Diaphoromactra* (endemic, one species), *Mactrinula* (one species in Lamprell & Healy in preparation), *Spisula* (seven species); subfamily Lutrariinae – *Lutraria* (three species), *Heterocardia* (one species), *Meropesta* (one species); subfamily Pteropsellinae – *Raeta* (three species); subfamily Zenatiinae – *Zenatina* (endemic, 1 species). Boss (1982) estimates that the family contains approximately 150 species worldwide. Of these, 46 species (33 endemic) from

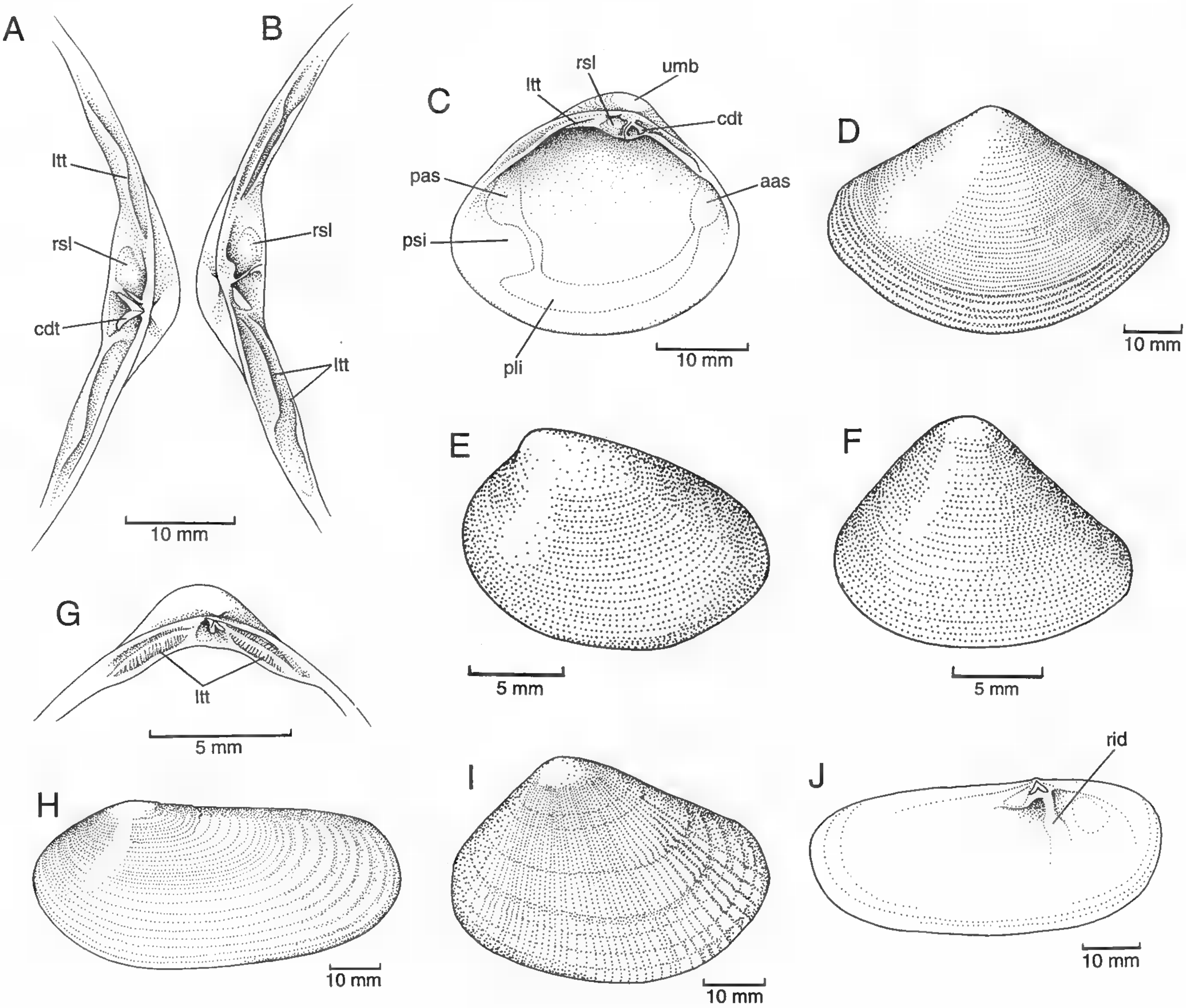


Figure 8.22 Family Mactridae. **A**, **B**, *Mactra (Mactra) eximia*, hinge detail, left (**A**) and right (**B**) valves. **C**, *Mactra (Mactra) abbreviata*, left valve, internal view. **D**, *Mactra (Austromactra) contraria*, left valve, external view. **E**, *Diaphoromactra versicolor*, left valve, external view. **F**, **G**, *Spisula (Notospisula) trigonella*: **F**, left valve, external view; **G**, , hinge, showing striations of lateral teeth on left valve. **H**, *Lutraria rhynchaena*, left valve, external view. **I**, *Meropesta nicobarica*, left valve, external view, showing radial ribbing. **J**, *Zenatina victoriae*, left valve, internal view, showing strengthening internal ridge. **aas**, anterior adductor muscle scar; **cdt**, cardinal teeth; **ltt**, lateral teeth; **pas**, posterior adductor muscle scar; **pli**, pallial line; **psi**, pallial sinus; **rid**, internal support ridge; **rsl**, resilifer; **umb**, umbo.
[S. Weidland]

nine genera (two endemic genus, four endemic subgenera) have been recorded from Australia (Lamprell & Whitehead 1992; Lamprell & Healy in preparation).

Typical mactrid shells are inflated, relatively thin in proportion to their size, with a well-developed, triangular to oblong resilifer (Fig. 8.22; Pl. 15.4). The A-shaped cardinals and often the lateral teeth are characteristically well developed (Fig. 8.22A, B, G). Shell sculpture is usually commarginal and weak (for example, Fig. 8.22D), but in the Indo-Pacific genus *Meropesta* (Fig. 8.22I) and European *Eastonia* (both in the subfamily Lutrariinae), prominent radial ribbing is present. Mactrids have a strong, angular foot (Fig. 8.21) and are capable of rapid burrowing. The joined inhalant and exhalant siphons (Pl. 15.5) can be retracted into the shell valves in the Mactrinae, but remain outside the permanently gaping valves in the Lutrariinae and Zenatiinae.

The mactrid stomach generally conforms to Purchon's Type V (see superfamily treatment) and differs from that of the Mesodesmatidae by having fewer sorting areas and by having the postero-ventral portion of the gastric shield emarginated (Purchon 1960a).

According to Boss (1982), mactrids are dioecious and larviparous. To date, reproduction has not been studied in any species of the family occurring in Australia. Longo & Anderson (1969, 1970) have covered in detail the ultrastructure of spermatogenesis and fertilisation of the American surf clam *Spisula (Hemimactra) solidissima*. Sperm of *S. (H.) solidissima* and the Australian species, *S. (Notospisula) trigonella*, resemble those of other heterodonts (Healy 1989, unpublished data).

Aside from the work of B.R. Wilson & Kendrick (1968) and A.R. Jones, Murray & Skilleter (1988) on *Spisula (Notospisula) trigonella*, published data on the biology or ecology of Australian mactrids are limited to brief notes in otherwise taxonomic works (Cotton 1961; Ludbrook 1984) or popular field guides (Allan 1959; Rippingale & McMichael 1961; Macpherson & Gabriel 1962; Coleman 1975). This is surprising considering that these bivalves are often very common and in some instances form a dominant component of littoral communities (Kershaw 1958; Allan 1959). In Moreton Bay (Queensland) for example, piles of shell grit may consist almost entirely of *Spisula (Notospisula) trigonella* (Fig. 8.22F, G). The same species has rapidly colonised estuaries in Western Australia (Wilson, B.R. & Kendrick 1968). In contrast, another endemic mactrid, *Diaphoromactra versicolor* (Fig. 8.22E), has a very restricted distribution, occurring only in marginal marine lakes of South Australia (for example, Lake MacDonnell; Cotton 1961) and Western Australia (vicinity of Israelite Bay; Ludbrook 1984).

Comparative studies on the internal anatomy, reproductive cycles and population structure of the Australian Mactridae remain to be carried out.

Although mactrids constitute a significant food resource in the United States and Japan (Habe 1971; Abbott 1976) they are not collected commercially in Australia. Given that population dynamics of larger Australian mactrids have never been investigated, it seems unlikely that any significant fishery for these bivalves will develop in the near future. Analyses of shell middens indicate that in Queensland, larger mactrids such as *Mactra eximia*, *M. abbreviata* (Fig. 8.22C), *M. rufescens* and *Lutraria rhynchaena* (Fig. 8.22H) were important to Aboriginal communities, providing a source of nutriment, the empty shells becoming handy scraping or scoop-like utensils (Allan 1959; Macpherson & Gabriel 1962).

Undisputed mactrid genera such as *Aliomactra*, *Cymbophora* and *Mulinoides* are known from the upper Cretaceous of North America (Keen 1969d). The earliest recorded appearance of the Mactridae in Australia is in the early Miocene of Victoria (*Zenatiopsis*). *Mactra* (*Mactra*, *Austromactra*) and *Spisula* (*Notospisula*) have been recorded from the Pleistocene of Western Australia and South Australia (Ludbrook 1978, 1984). Gill (1963) used *Zenatiopsis* and the venerid genus *Placamen* to determine the age of ironstone strata of Red Bluff in Victoria. Gill & Darragh (1963), in their review of the Australian Zenatiinae, erected the genus *Zenatina* for the living endemic species *Zenatina victoriae* (Fig. 8.22J), and restricted usage of *Zenatiopsis* to various Australian fossil species.

Family Mesodesmatidae

Mesodesmatids, or wedge clams, can be distinguished from the Mactridae by their compressed often cuneiform shell shape, narrower resilifer, simpler cardinal teeth (inverted V-shaped less conspicuous), usually posteriorly directed umbones and separated siphons (Fig. 8.23).

Much has been written on the nomenclature of Australian and New Zealand mesodesmatids, especially in relation to the correct application of generic names for the Australian species (Dawson 1959; Beu 1971a; Beu & de Rooij-Schuiling 1982). The family has also been known as Amphidesmatidae, Donacellidae and Paphiidae. Data pertaining to the external morphology, habits and relative abundance of certain Australian mesodesmatids have been provided by Allan (1959), Cotton (1961) and Roberts (1984b), but comparative studies within the group are still required.

In comparison with the often large-sized New Zealand species (60–110 mm), shells of Australian mesodesmatids are small (typically under 33 mm in length; see Lamprell & Whitehead 1992) (Fig. 8.23). Dentition is variable throughout the family. Anterior and posterior laterals are usually strongly developed (Fig. 8.23C) and, with the exception of the American subgenus *Paphies (Mesodesma)*, always smooth. Cardinals are often simple rather than deltoid. The right valve has two cardinal teeth, the anterior one is often combined with the anterior lateral. A pallial sinus is well developed in *Paphies (Amesodesma)* (Fig. 8.23B) and absent in *Anapella* and *Davila* species. Allan (1959) and Cotton (1961) briefly described and/or illustrated the shape of the foot, mantle papillae and siphons of *Paphies (Amesodesma) elongata* (see Fig. 8.23A).

Adductor, pedal retractor and siphonal retractor muscles are as described for the superfamily.

The stomach is essentially of Type V construction, with a greater number of sorting areas than in the Mactridae (Purchon 1960a, 1987b). The family is gonochoristic and larviparous (Boss 1982) with spawning occurring in autumn (March–June) in the Australian species *Paphies (Amesodesma) cuneata* (Roberts 1984b). Rapson (1952) found that spawning in the New Zealand toheroa (*Paphies ventricosa*) could range from continuous to erratic and that larval settlement in the littoral region was influenced by phytoplankton abundance.

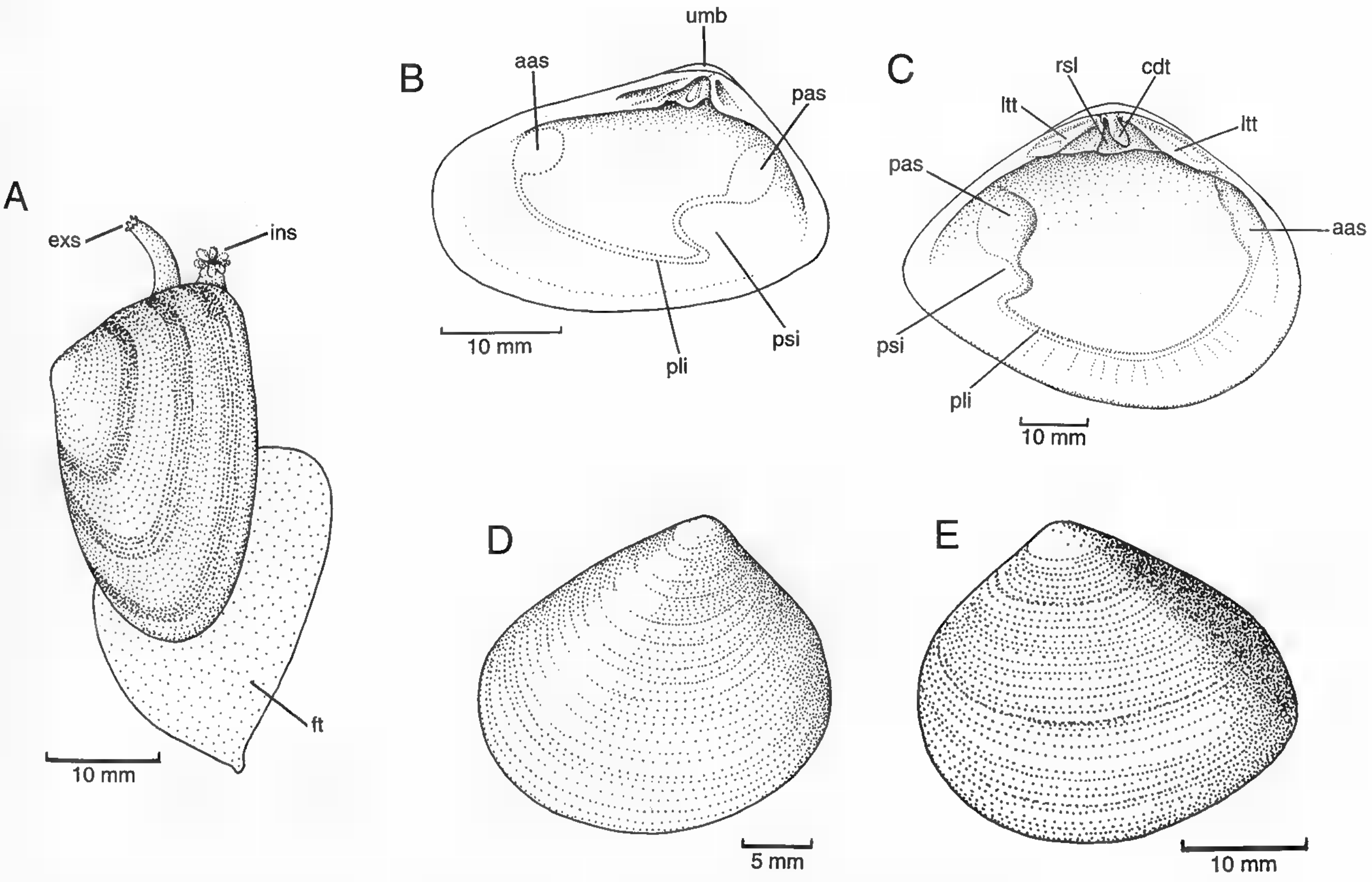


Figure 8.23 Family Mesodesmatidae. **A**, **B**, *Paphies (Amesodesma) elongata*: **A**, animal showing shell, foot and siphons, left view; **B**, right valve, internal view. **C**, *Atactodea striata*, left valve, internal view. **D**, *Davila plana*, left valve, external view. **E**, *Anapella cycladea*, left valve, external view. **aas**, anterior adductor muscle scar; **cdt**, cardinal teeth, **exs**, exhalant siphon; **ft**, foot; **ins**, inhalant siphon; **ltt**, lateral teeth; **pas**, posterior adductor muscle scar; **pli**, pallial line, **psi**, pallial sinus; **rsl**, resilifer; **umb**, umbo. (A, after Cotton 1961) [S. Weidland]

In Australia, mesodesmatids are common inhabitants of the surf zone of sandy beaches – for example species of *Paphies (Amesodesma)*. Others occur on mudflats – for example, some species of *Anapella* – and in shallow tropical lagoons – for example, species of *Atactodea*, *Davila* (Allan 1959; Cotton 1961). Cotton (1961) stated that local mesodesmatids are an important source of food for fish and sea birds. The high incidence of round bore-holes in shells of some species such as *Paphies (Amesodesma) elongata* (Allan 1959) indicates that these bivalves also form a major prey item for naticid sand snails. Roberts (1984b) estimated the density of *Paphies (Amesodesma) cuneata* in Prince Royal Harbour, Western Australia, to be 30 individuals m^{-2}.

Allan (1959) described the ability of *Paphies (Amesodesma) elongata* to re-burrow rapidly when uncovered by wave movement along the shore. In general, mesodesmatids are more active than mactrids and some species, for example, *P. (A.) elongata*, leave obvious burrowing tracks between tide marks (Cotton 1961).

Unlike the toheroa or tuatua of New Zealand, *Paphies* species, Australian mesodesmatids are too small to be of commercial significance. Whereas in New Zealand the common name 'pipi' is applied to *Paphies australis*, in Australia the name usually refers to the tellinoidean *Donax (Plebidonax) deltoides* (Allan 1959; Willan, this Chapter).

Two subfamilies of Mesodesmatidae are now recognised – the Mesodesmatinae and the Davilinae – both of which occur in Australian waters. A third subfamily, the Erviliinae, has recently been shown by B. Morton & Scott (1990) to belong to the Tellinoidea (family Semelidae). In total, the Australian fauna includes 11 species distributed between the genera *Paphies* (eight species; two subgenera *Amesodesma* and *Actactodea*), *Atactodea* (listed as a subgenus of *Paphies* in Lamprell & Whitehead 1992; Lamprell & Healy in preparation) in the subfamily Mesodesmatinae, and *Davila* (one species) and *Anapella* (two species) (Lamprell & Whitehead 1992) in the subfamily Davilinae. Only *Anapella*, which Cotton (1961) included in the Mactridae, is endemic to Australia (Fig. 8.23E).

In Australia, fossil Mesodesmatidae are recorded only from the Pleistocene and include the still extant *Paphies (Amesodesma) elongata*, *P. (A.) angusta*, *Anapella cycladea* and the extinct *Anapella variabilis* (Ludbrook 1978, 1984).

Much remains to be learned of the habits of Australian mesodesmatids, especially in relation to reproduction, feeding and population biology. Endemic species, although small in size, are sometimes abundant on ocean beaches and would make excellent subjects for ecological studies.

Family Cardiliidae

Members of the Cardiliidae have inflated, dorso-ventrally oblong shells ornamented with radial ribbing. Paired valves are heart-shaped with subspiral umbones. The deep resilifer is flanked anteriorly by an elongate, inverted V-shaped cardinal tooth on the left valve and by a triangular, weaker cardinal on the right valve. The lateral teeth and pallial sinus are absent (Fig. 8.24). The absence of a pallial sinus suggests that cardiliids are not deep burrowers.

Little is known of this small family of a few species in the single genus *Cardilia* (Boss 1982) and some authors (for example, Thiele 1929–1935) even express doubt about its supposed mactroidean status. Hedley (1910) included *Cardilia semisulcata* in his list of Queensland molluscs, and examination of the Australian Museum collection reveals valves of this species from North Queensland (Port Douglas-Tully area) and from 150 to 190 m depth off Port Hedland, Western Australia.

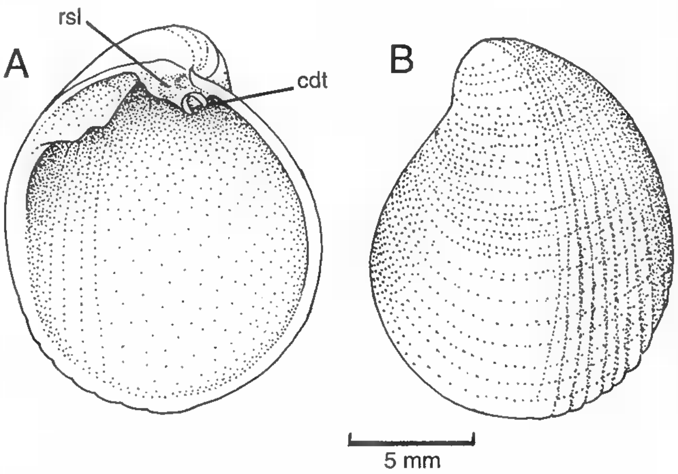


Figure 8.24 Family Cardiliidae. *Cardilia semisulcata*, left valve: **A**, internal view; **B**, external view. **cdt**, cardinal teeth; **rsl**, resilifer. [S. Weidland]

Superfamily SOLENOIDEA

The Solenoidea is a relatively small group of infaunal bivalves. The shells are thin and fragile, narrowly elongate, rectangular, cylindrical or laterally compressed, and they gape widely at each end. Collectively they are often called razor shells or fingernail shells. The shell comprises two aragonitic layers, an outer crossed-lamellar layer and an inner complex crossed-lamellar or homogeneous layer (Boss 1982). The umbones are more or less terminal. Beneath them lies the relatively small hinge with delicate, peg-like cardinal teeth (teeth corresponding to the laterals of other heterodont bivalves are absent) and behind them, the external ligament. The pallial sinus is short. The anterior adductor is larger than the posterior adductor and both are placed dorsally. The anterior pedal retractor usually has two insertions in each valve. A cruciform muscle is absent.

Solenoideans are non-selective suspension-feeders living vertically or slightly obliquely in the substratum in more or less permanent tubes, in which they can ascend or descend. The foot is cylindrical and club-shaped, conical, and dilated towards its end which is blunt. Most solenids burrow so quickly that it can be quite difficult to expose them by digging with a spade (Schiedek & Zebe 1987). Naticid gastropods (Schneider 1982) and nemertine worms are known to prey on solenoideans. Some particularly agile solenoideans escape from such predators by 'leaping' out of their burrows, swimming for a short distance using the foot as a piston, and then reburying very rapidly (McMahon & McMahon 1983).

Knowledge of the anatomy of solenoideans rests on overseas studies (Bloomer 1901, 1902; Ghosh 1920; Yonge 1952; Owen 1959; Pohlo 1963; Morton, B. 1984a), and no comparable works are available for any member of the Australian fauna. Significantly, the style sac and midgut are separate, not united as in the Tellinoidea.

The enlarged and cylindrical foot permits rapid vertical burrowing to a depth of about 300 mm (Drew 1907; Fraenkel 1927). Trueman (1967) investigated the dynamics of burrowing. Those intertidal solenoideans living in poorly aerated substrata can experience environmental anaerobiosis, and during burrowing cycles they can also experience functional anaerobiosis by way of the energy demands of the foot. Physiological investigations of the North Atlantic *Ensis directus* have shown it to be unique among bivalves in producing two different amino acids in response to these different anaerobic stresses – strombine under environmental anaerobiosis and octopine under functional anaerobiosis (Schiedek & Zebe 1987).

Solenoideans inhabit soft substrata, especially seagrass beds and are a food source for wading birds. The larger species are consumed by humans in many parts of the world. Meehan (1982) documented that the Anbarra Aborigines of Arnhem Land eat two species, one *Solen* and one *Pharella*, and that the collective name for these shellfish is ngudgo. *Sinonovacula constricta* is widely cultivated in China (Morton, B. 1984a).

There are about 130 extant solenoidean species living in temperate to tropical waters. The superfamily contains two families, the Solenidae and the Pharidae according to Cosel's (1990) recent review. Within the former family, Cosel recognised four genera (*Solen*, *Ensisolen*, *Solena* and *Neosolen*) and within the latter ten (*Pharus*, *Cultellus*, *Ensis*, *Phaxas*, *Ensiculus*, *Siliqua*, *Neosiliqua*, *Pharella*, *Orbicularia* and *Sinonovacula*, the latter presumably including *Novaculina*. Cosel (1990) endorsed the transfer by B. Morton (1984a) of *Sinonovacula* into this subfamily from the Tellinoidea. Only four of these fourteen genera are known definitely to occur in Australia – *Solen*, *Pharella*, *Cultellus* and *Sinonovacula* – but the taxonomy of the Australian species (probably numbering less than 15) is far from resolved. However, the temperate water species appear to be endemic and the tropical ones widespread in the Indo-West Pacific.

Morphologically and ecologically, two divergent lineages are recognisable within the Solenoidea that cut across the taxonomic divisions. The majority of taxa are actively burrowing marine species with short, fused siphons but *Sinonovacula* (and *Novaculina*), the problematic genera, comprise sedentary freshwater or estuarine species with long separate siphons.

Family Solenidae

The family Solenidae comprises only four Recent genera, *Solen* and *Solena*. *Solen* is the largest, with about 65 species (Cosel 1992). It occurs in Australian waters where it is represented by about ten species. *Solen correctus* and *S. vaginoides* (Pl. 13.4) are widespread in temperate Australian waters, and *S. aureomaculatus*, *S. fonesii*, *S. kajiyamai* and *S. sloani* have been described from northern Australia. *Solen grandis* (Fig. 8.25) is a distinctive tropical species.

Solenids have medium-sized, fragile shells rarely exceeding 150 mm in length, with terminal to subterminal umbones and an anteriorly located hinge consisting of a single cardinal tooth in each valve, and an external, opisthodetic ligament seated on nymphs. Interestingly, the right valve actually projects into the left during growth, but additional internal calcification prevents damage to the hinge (Stasek 1963d). Shells are elongate, equivalve, inequilateral, truncate and gaping at both ends (Fig. 8.25). Externally shells are smooth or weakly sculptured commarginally and covered with a pronounced, smooth, glossy periostracum.

The mantle has a relatively small anterior pedal gape and a large area of ventral fusion caused by fusion of the inner mantle lobe and part of the middle lobe. One Asian species, *Solen* aff. *exiguus*, has a pair of long pallial tentacles that can be protruded through the anterior gape (Morton, B. 1987); these tentacles are presumed to be sensory because they can extend into the substratum well beyond the foot. All members of this family have short stout siphons which are united for their entire length. These siphons, which are formed from the inner and middle mantle lobes, bear papillae distally. They can be autotomised when the animal is under attack (Owen 1959; Hodgson 1984). The gills lie posteriorly in the mantle cavity and are plicate with interlamellar septa. The midgut has a separate style sac and there is no appendix at the posterior extremity of the stomach. The semicircular major typhlosole penetrates deeply into both right and left caeca and terminates in front of the left pouch. Within the stomach, the caecum comes into close association with the orifices of many ducts from the digestive diverticula. The heart consists of two, thin, subtriangular auricles and a larger ventricle through which the rectum runs. The posterior aorta has a bulbus arteriosus.

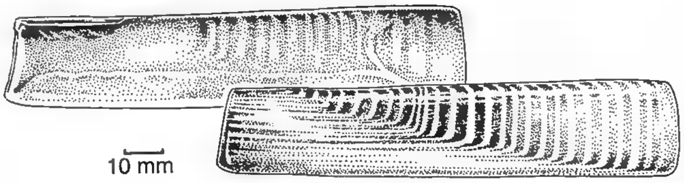


Figure 8.25 Family Solenidae. *Solen grandis*, shell valves, right valve in internal view, left valve in external view. [R. Plant]

Quantities of *Solen correctus* are dug as bait for bream fishing in harbours of south-eastern Australia; it is said these bivalves can be enticed out of the sand by a pinch of salt. Two Australian references mention that species of *Solen* are gregarious (Allan 1962; Coleman 1975).

The fossil record for this family and the next is poor because the shells are extremely fragile (Keen 1969e). Cosel (1990) dates the Solenidae from the lower Eocene. Greatest diversity has been attained at the present time.

Family Pharidae

This family is widely known under the name Cultellidae. About 65 species are known worldwide. Shells are generally similar to those of solenids in their narrow rectangular shape (Fig. 8.26), but they tend to be laterally compressed and wider, and the umbones are generally subterminal (Fig. 8.26A, B). Often the shells are reinforced internally with calcareous rays emanating from beneath the umbones. The right valve has two cardinal teeth and the left valve has only one (Cosel 1990). The foot is laterally compressed and obliquely truncate.

Those anatomical studies that are available provide evidence for the existence of more than one group, the pharids and the two problematic genera *Sinonovacula* and *Novaculina* (see above). There are major differences in the hinges and the siphons (Cosel 1990). Significant works on overseas members of this family are by Atkins (1937b), Graham (1949), Yonge (1952) and Cosel (1990, 1993).

A small additional orifice called the fourth aperture is present between the fused mantle lobes in the genus *Ensis* (Fig. 8.26B; Atkins 1937b). In *Ensis siliqua* there is an enormous posterior sorting area to the stomach which penetrates deeply into the enlarged, backwardly directed dorsal hood (Graham 1949).

The anatomy of the genera, *Novaculina* and *Sinonovacula*, is less well known. B. Morton (1984a) gave a thorough account of *Sinonovacula*. *Sinonovacula* has teeth like *Pharella*, but long, separate siphons. There is no fourth aperture. Sensory tentacles around the pedal gape respond to mechanical disturbance and water can be squirted from the gape, presumably to flush away any source of irritation (Morton, B. 1984a). The labial palps are large compared with the relatively small gills and are clearly the principal sorting area.

The best known Australian species is the brown-spotted *Cultellus cultellus*. No species of *Ensis* occurs in Australian or Indo-Pacific waters, even though the genus is widespread in Europe and America.

Cosel (1990) dates the Pharidae from the upper Cretaceous. The greatest diversity has been attained at the present time.

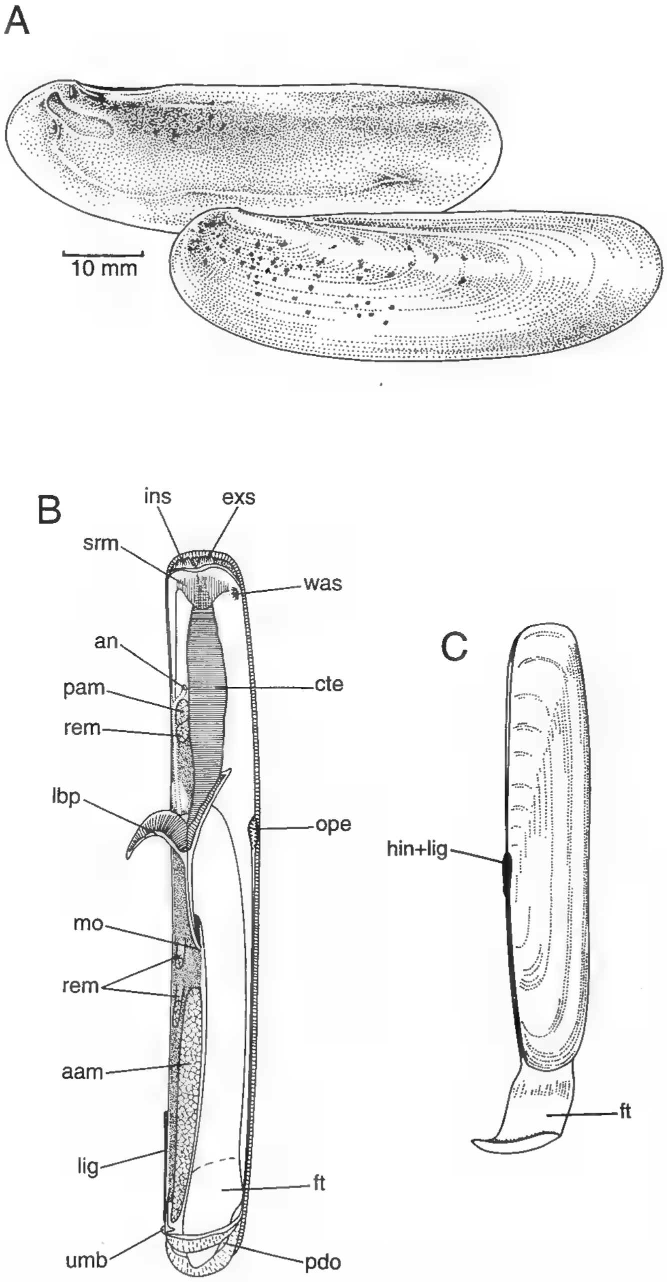


Figure 8.26 Family Pharidae. **A**, *Cultellus cultellus*, shell valves, right valve in internal view, left in external view. **B**, *Ensis arcuatus*, internal anatomy, left valve and mantle lobe removed. **C**, *Pharus legumen*, with foot protruding; note the centrally placed hinge and ligament. **aam**, anterior adductor muscle; an, anus; **cte**, ctenidium; **exs**, exhalant siphon; **ft**, foot; **hin**, hinge; **ins**, inhalant siphon; **lbp**, labial palp; **lig**, ligament; **mo**, mouth; **ope**, fourth opening; **pam**, posterior adductor muscle; **pdo**, pedal opening; **rem**, retractor muscles; **srm**, siphonal retractor muscle; **umb**, umbo; **was**, waste. (B, C, after Yonge & Thompson 1976) [A, R. Plant; B, C, C. Eadie]

Superfamily TELLINOIDEA

Members of this superfamily, the largest numerically in the Bivalvia, have laterally compressed and often inequilateral shells, external ligaments seated on shelly plates called nymphs, narrow siphons completely separated, enlarged palps and complex stomachs. All species are permanently infaunal, living at depths up to several times their shell length, and for the most part, capable of reburrowing rapidly if uncovered. In their specialisation of gills, labial palps and stomachs for handling food, tellinoideans could be considered to represent the culmination of the heterodont radiation.

Despite the large fauna and their ecological significance, Australian tellinoideans have received scant scientific attention, taxonomically, anatomically or ecologically. In contrast, the overseas literature is voluminous. Principal anatomical works are those by Bloomer (1907), Graham (1934), Yonge (1949), Reid & Reid (1969), Wade (1969) and Purchon (1987a). Comprehensive taxonomic studies are those by Bertin (1878), Boss (1966, 1968, 1969b, 1972), Afshar (1969) and Coan (1973a, 1973b, 1988). The largest family is the Tellinidae which, with about 90 nominal genera, has approximately double all the other genera in the superfamily combined. The most complete ecological investigation is that by Trevallion (1971) on the European *Tellina tenuis*.

Even though shell shape is too variable to make any generalisations for the whole superfamily, all shells studied so far are identical in their aragonitic composition and three-layered construction: an outer layer of composite prisms, a cross-lamellar middle layer and a complex cross-lamellar or homogeneous inner layer. The hinge usually has two cardinal teeth and two lateral teeth, one anterior (which is commonly bifid) and one posterior in each valve. The posterior cardinal and both laterals may be obsolete. The ligament is typically external and opisthodetic, and seated on nymphs, but in the Semelidae its resilial portion is sunken into an internal pit between the valves.

Rapid burrowing is accomplished by the enlarged foot, whose actions Trueman, Brand & Davis (1966) have elucidated. The mantle has a broad anterior pedal gape. Posteriorly it is produced into two siphons that are independently mobile and usually long. These narrow tubular siphons are formed by fusion of the inner muscular lobes of the mantle edge. A pair of small muscles, the cruciform muscles (Fig. 8.27), intersects in the form of a cross at the base of the siphons (Graham 1934). These muscles represent a tie for the siphons – the anterior attachments take the strain when the siphons extend and the posterior ones do likewise when they are withdrawn (Yonge & Thompson 1976). There are two sensory organs intimately associated with the cruciform muscles (Frenkiel & Mouëza 1984). Those organs probably monitor water quality (Odiete 1978). The cruciform muscles constitute the chief synapomorphy of the Tellinoidea (Frenkiel 1979). Presence or absence, respectively, of this muscle has necessitated the transfer of genera into or out of the Tellinoidea (Morton, B. 1984a; Morton, B. & Scott 1990; Cosel 1990). Members are dimyarian, often with the two adductor muscles of unequal in size. The pallial line is sinuate with a deeply embayed pallial sinus. In all tellinoideans the stomach has a postero-dorsal caecum which may be lobed (Purchon 1987a).

Larval development has been described by Frenkiel & Mouëza (1979). These investigators found that pediveligers could remain in a 'byssal drifting' state for several weeks if no suitable substratum was available. Webb (1986) investigated the ontogeny of the shell in European representatives of three families. Sufficient ontogenetic studies are now available to conclude that late stage larvae of the Tellinoidea all develop a similar and distinctive triangular shell with an extended anterior end (for example, Chanley 1969).

Even though the Tellinoidea is clearly holophyletic by virtue of its cruciform muscles, postero-dorsal stomach caecum and larval shell, its members inhabit all types of soft substrata and burrow to all depths. Populations often attain densities with enormous biomass, sufficient to sustain an array of predators such as birds, fishes, mantis shrimps, crabs, polychaetes, naticid gastropods and starfishes. The Tellinoidea shows a gradation from deposit-feeding to suspension-feeding – some species press the inhalant siphon to the substratum and ingest deposited material from the sea floor, whereas others orientate the inhalant siphon level with, or above, the substratum and ingest particles filtered form the suspension in the water column (Pohlo 1969).

The superfamily is clearly of tropical origin and species occur everywhere but Antarctica (Nicol 1966). No work has been undertaken specifically on the biogeography of Australian tellinoideans. All five families that constitute the Tellinoidea are considerably more speciose in tropical than in temperate waters. All the Australian temperate species are endemic, but it is possible to recognise some cognate pairs with closely related species in

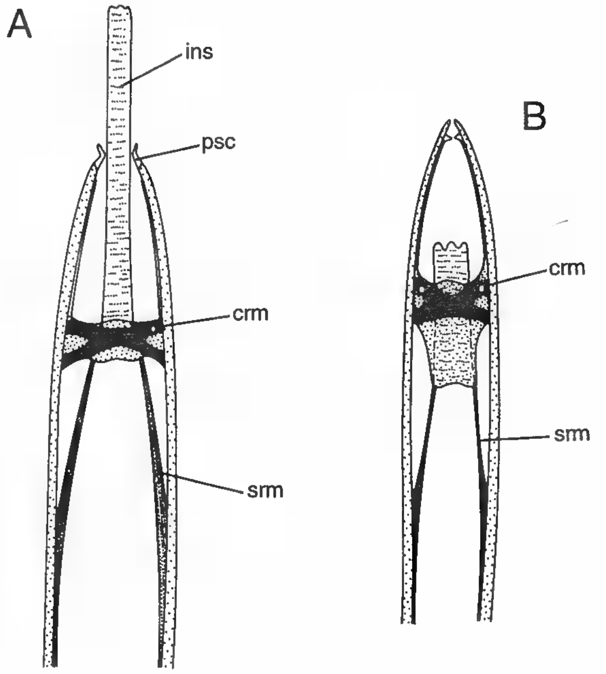


Figure 8.27 Superfamily Tellinoidea. Undersurface of a tellinid showing the base of the separate siphons with the cross tie of the cruciform muscle: **A**, siphons extended; **B**, siphons withdrawn. **crm**, cruciform muscle; **ins**, inhalant siphon; **psc**, periostracum; **srm**, siphonal retractor muscle. (After Yonge & Thompson 1976) [C. Eadie]

New Zealand, for example *Macomona deltoidalis* in Australia – *M. liliana* in New Zealand, and *Soletellina alba* in Australia – *S. siliquens* in New Zealand.

Keen (1969f) dates the superfamily from the upper Triassic.

The families in the superfamily are Tellinidae, Semelidae, Psammobiidae, Solecurtidae and Donacidae, and they all occur in Australia. Some authors place the European genus *Scrobicularia* in a family distinct from the Semelidae.

Family Tellinidae

Shells in the family Tellinidae are markedly laterally compressed and thin, with a distinct flexure and corresponding narrow gape posteriorly (Fig. 8.28A–C; Pls 15.2, 15.3). Tellinids figure prominently in sandy and muddy substrata throughout Australia. Endemic species with wide distributions around the southern half of the continent are *Tellina deltoidalis*, *T. margaritina*, *T. imbellis* and *T. botanica*. The best known of the many wide-ranging Indo-Pacific species with distributions around northern Australia are *Tellina australis*, *T. ovalis*, *T. virgata*, *T. chloroleuca* (Fig. 8.28A), *T. scobinata*, *T. capsoides*, *T. inflata*, *T. foliacea*, *Macoma candida* and *Macalia bruguieri*.

Ponder (1975) presented synonymies for four common Australian species. Lamprell & Whitehead (1992) mention 89 Australian species. There remain, however, many unidentifiable species.

The tellinid classification requires revision. Two subfamilies have been recognised, the Tellininae and Macominae, and a proliferation of genus-group taxa – some 100 or so. Because so little is known of the limits and relationships of these taxa, most workers recognise only a few genera, some of which (for example, *Tellina* and *Macoma*) they subdivide into a large number of subgenera, The most recent genus-group level classifications of the whole family are by Afshar (1969) and Keen (1969f).

Shells of tellinids, or simply tellins, vary between 5 and 125 mm in adult length. Live animals lie obliquely within the substratum on their left valve, and thus the right valve has become correspondingly more inflated and convex. The valve margins are smooth. The shell surface is usually smooth but some species display low, commarginal ridges, a few have prominent radial ribs and others have file-like scales, such as *Tellina scobinata* (Fig. 8.28C). Stanley (1969) discovered that the asymmetrical ridges on shells of *Tellina* and *Strigilla* serve to grip the sand during shell-rocking movements thus aiding sediment penetration. Even more peculiar is the occurrence of sculpture on only one valve; J.G. Wilson (1979) speculated that the presence of diagonal striae on only the right valve of *Tellina fabula* might strengthen that valve against the stresses generated by contraction of the pedal musculature. The shells of many species are brightly coloured, often with the pigmentation arranged in rays; the significance of such colouration in a group of deep-burrowing bivalves is a mystery. Externally the periostracum is thin or obsolete. Both anterior and posterior adductor muscles are always present and the former is often slightly larger than the latter. Two small scars resulting from the cruciform muscle insertions are present postero-ventrally in each valve below the pallial line. The narrow hinge always has two cardinal teeth. Lateral teeth are present in the Tellininae, but are absent in the subfamily Macominae. The pallial sinus is very deep and its outline can differ between right and left valves in some species.

The mantle has a broad antero-posterior gape through which the foot is extended. Postero-dorsally the inner mantle lobes are fused, forming the siphons which are extremely extensible and have papillae distally (Fig. 8.28D). The inhalant siphon ingests deposited organic material from the sediment surface. The 20 mm long European species *Tellina tenuis* can take in as much as 180 ml hr^{-1} in nature (Trevallion 1971). The gills are smooth and have interlamellar septa; the inner demibranch is the larger of the two and the outer demibranch lacks ascending lamellae anteriorly. The surface area of the gills is much reduced in comparison with the labial palps which approach the gills in size. The palps are more or less united posteriorly, and like the anterior filaments of the inner demibranch, are not inserted or fused into the distal oral groove. Pohlo (1973) demonstrated that in *Florimetis obesa* the palps vary intraspecifically in size. Yonge (1949) suggested that much of the incoming deposit material is drawn forward and thrown directly on the surface of the palps; both here and in the stomach sorting must be very rigorous. To perform its triturating function, the stomach combines a massive crystalline style with a heavy gastric shield. R. Reid & A. Reid (1969) attempted to explain the functioning of the intact stomach. The major typhlosole usually penetrates both right and left stomach caeca, but in some species of *Tellina* the typhlosole only penetrates the left caecum, a condition Purchon (1987a) interpreted as a reversion to the ancestral state. The left pouch and left and right caeca are often fused to form a branched 'combined caecum' (Hughes 1977).

The pericardium surrounding the heart is elongate. The posterior aorta has a bulbus arteriosus.

Tellins are dioecious. Nott (1980) provided details of reproduction and successful artificial spawning. Gilbert (1977) found gonadial growth occurred throughout the winter, that spawning was tied to seawater temperature and that variation occurred in the age of sexual maturity. Larvae are always planktonic but some species are lecithotrophic and have a shortened swimming stage. The reproductive ecology of a population of *Tellina mariae* from Victoria is described by Coleman (1982).

In life, tellins bury deeply (to 400 mm) and rest obliquely with their siphons pointing upwards. The siphons extend to the sediment surface where the inhalant one rotates with its tip touching the substratum to ingest organic material and sand grains (Gilbert 1977). The exhalant siphon expels faeces and water while extended more or less horizontally below the surface. Experimentally, low oxygen concentrations, extremes of temperature and lack of food may stimulate both siphons to extend out into the water column (Trevallion 1971). Trevallion (1971) calculated the energy budget for *Tellina tenuis*. In suitable substrata, tellins can attain high population densities; for example,

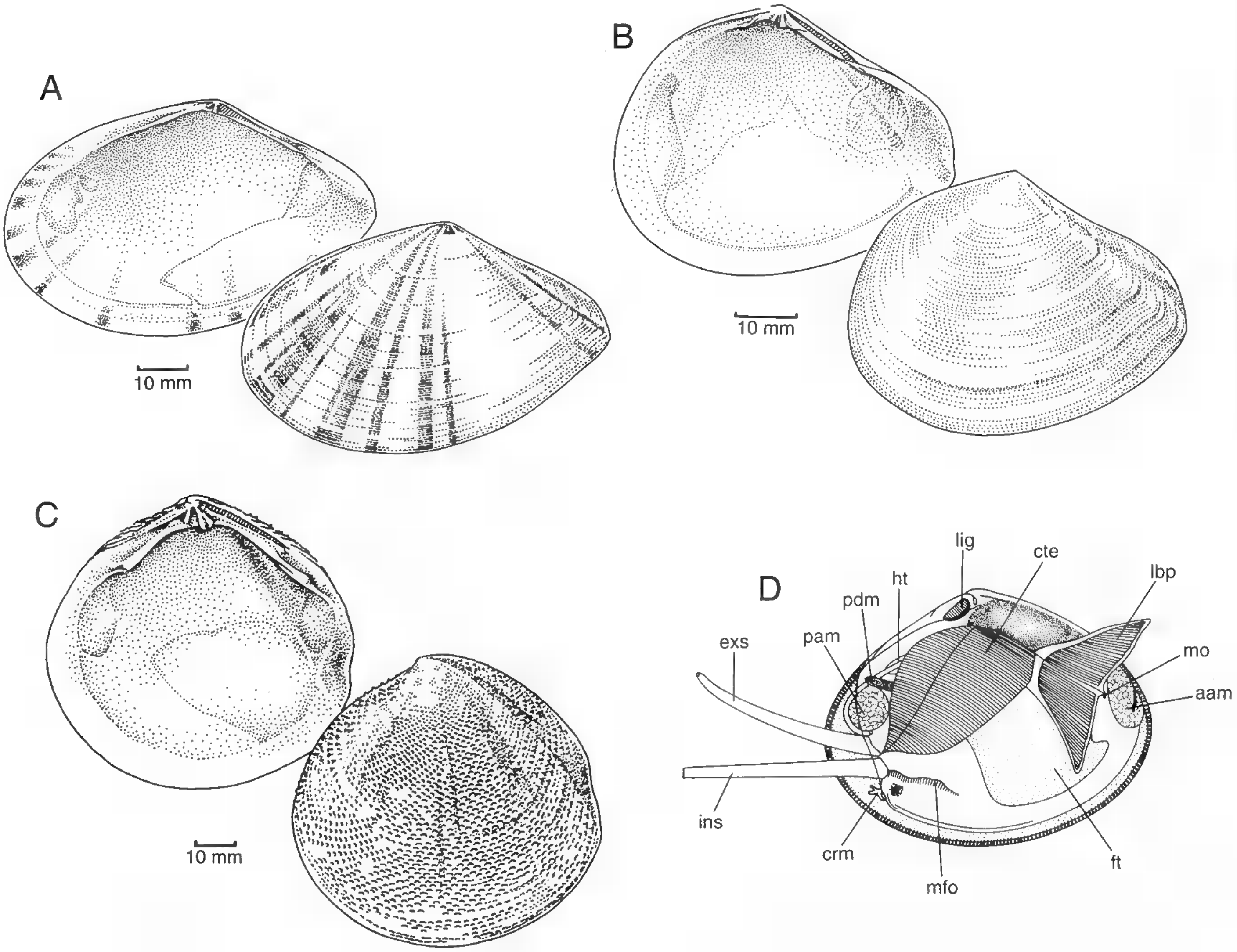


Figure 8.28 Family Tellinidae. A–C, shell valves, right valve in internal view, left valve in external view: A, *Tellina (Laciolina) chloroleuca*; B, *Tellina (Macomona) deltoidalis*; C, *Tellina (Scutarcopagia) scobinata*. D, *Macoma balthica*, internal anatomy of a deep burrower in muddy sand. **aam**, anterior adductor muscle; **crm**, cruciform muscle; **cte**, ctenidium; **exs**, exhalant siphon; **ft**, foot; **ht**, heart; **ins**, inhalant siphon; **lbp**, labial palp; **lig**, ligament; **mfo**, mantle fold; **mo**, mouth; **pam**, posterior adductor muscle; **pdm**, pedal retractor muscle. (D, after Yonge & Thompson 1976) [A–C, R. Plant; D, C. Eadie]

J.L. Bernard (1963) found the southern Californian *Tellina buttoni* to decrease from 476 m^{-2} on deep offshore shoals to 172 m^{-2} on inshore sands. Similarly, Wells & Threlfall (1980) found a maximum density for the Western Australian *Tellina cockburnensis* of 153.3 m^{-2} corresponding to a weight (including shells) of 33.7 gm m^{-2}. Such densities give tellins dominant species status in many soft substratum communities. Their importance lies in their being staple foods for bottom-feeding commercial fishes such as plaice, flounder and whiting.

Family Semelidae

Shells of semelids are very similar to those of the Tellinidae, but differ in having the resilial portion of the ligament enlarged and sunken into a pit on the hinge plate within each valve (Fig. 8.29A). This condition may have evolved independently in several tellinid lineages, as has also happened once in another group of heterodont bivalves, the Mactroidea, so presently there is no certainty as to the monophyly of the Semelidae.

Five genera belonging to this family occur in Australia – *Semele*, *Leptomya*, *Theora*, *Ervilia* and *Abra*. *Ervilia* was recently transferred into the Semelidae from the Mactridae (Morton, B. & Scott 1990). One further genus, *Semelangulus*, has also been included by some workers (for example, by Macpherson & Gabriel 1962), but it is now considered to belong to the Tellinidae (Vokes 1980). None of these genera has been monographed in Australia, so studies on foreign congeners are all that are available. Extensive work has been done on species of *Abra* and *Scrobicularia* (Fig. 8.29B, C), both of which are common and accessible in the North Atlantic Ocean. The total number of species in Australia is about 30.

Semele is the largest genus in Australia, both in size (*S. amabilis* can reach 70 mm in length) and in number of species (12 are currently recognised). Many species in this genus, such as *S. casta* (Fig. 8.29A), are widespread in northern Australia.

The following features of the semelid shell highlight putative distinctions from the Tellinidae: the posterior flexure is only slight; some species have a bark-like periostracum; the hinge exhibits the plesiomorphic tellinoidean set of two cardinal and two lateral teeth, laterals are absent only in *Scrobicularia*; the resilial pit, the chondrophore, can project obliquely or vertically into the valve's interior; the pallial sinus is very deep and well rounded. Purchon (1987a) found nothing in semelid stomach anatomy that is particularly distinct from that of the Tellinidae or Solecurtidae.

Semelids resemble tellinids ecologically, but are less significant throughout Australia. Surprisingly, most ecological information is available for Australia's most diminutive semelid, *Theora lubrica*, because it was introduced accidentally (probably) from Japan where it is an important member of the infauna of muddy bays (Kikuchi & Tanaka 1978; Tanaka & Kikuchi 1980; Imabayashi & Tsukuda 1984). Certainly, *T. lubrica* and the native Australian *T. fragilis* are an important food source for estuarine and shallow-water fishes (R.C. Willan personal observation).

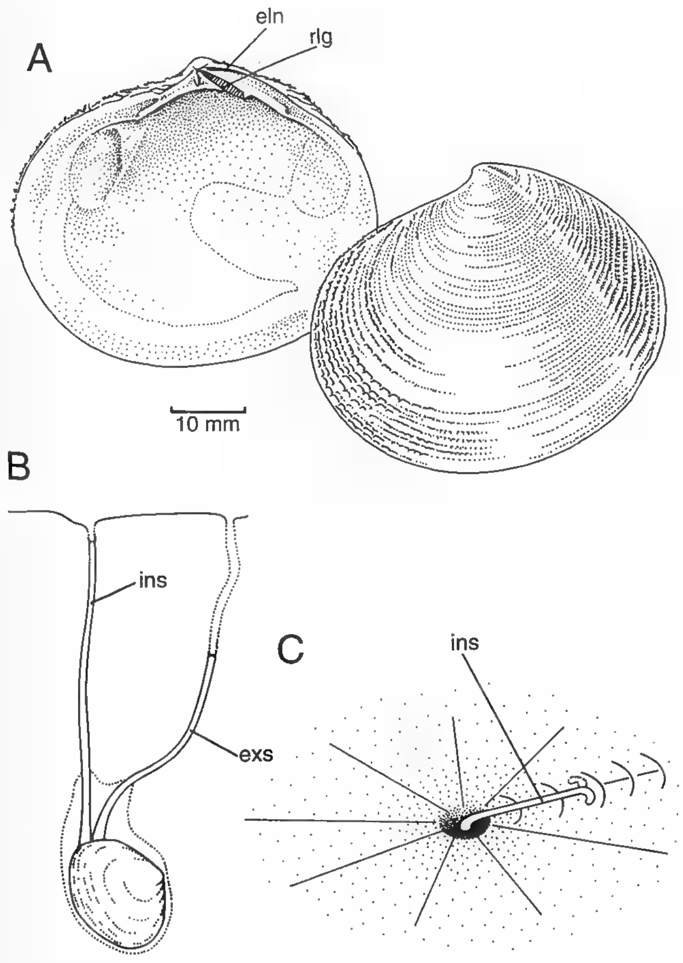


Figure 8.29 Family Semelidae. **A**, *Semele casta*, shell valves, right valve in internal view, left valve in external view. **B**, **C**, *Scrobicularia plana*: **B**, animal *in situ*, showing the position of the inhalant and exhalant siphons; **C**, the inhalant siphon collecting detritus from the surface. **eln**, external portion of ligament on nymph; **exs**, exhalant siphon; **ins**, inhalant siphon; **rlg**, resilial portion of ligament. (B, C, after Yonge & Thompson 1976)
[A, R. Plant; B, C, C. Eadie]

Family Psammobiidae

Psammobiid shells are very similar to those of the Tellinidae, but they lack a posterior flexure and never have lateral teeth. Neither condition represents a synapomorphy and therefore both the monophyly of the group and its status as a distinct family, separate from the Tellinidae, are questionable (Willan 1993).

The name for the family has been settled by the International Commission on Zoological Nomenclature, Psammobiidae taking precedence over Asaphidae, Garidae and Sanguinolariidae (ICZN 1970). The taxonomy of all Australian psammobiids has been reviewed (Willan 1993), and four genera can be recognised – *Asaphis*, *Heteroglypta*, *Gari* and *Soletellina*. *Gari* comprises several distinct subgenera. *Soletellina* continues to be used widely in preference to *Hiatula* because of doubt about the type species of *Hiatula*.

We must rely on overseas studies like those of Bloomer (1911), Graham (1934), Nakazima (1957), Purchon (1960a), Dinamani (1967), Pohlo (1972), Narchi (1980) and Berg & Alatalo (1985) for our knowledge of psammobiid anatomy and biology. Depledge (1985) has investigated the ecophysiology of the widespread tropical Indo-Pacific species *Asaphis violascens*.

Shells of adults are 10–200 mm in length. They are markedly laterally compressed and, like tellins, the right valve is more convex than the left. The valves are elongate with the umbones, which are low, usually near the middle of the dorsal margin (Fig. 8.30). The rear margin is truncate and generally there is a small gape posteriorly. The margins are smooth. Sculpture is often a good generic indicator: in *Soletellina* the shell surface is always smooth; in *Gari* the posterior slope is usually ornamented; in *Asaphis* the whole shell is sculptured in strong radial ribs; in *Heteroglypta* there are four different sculptural sections. The popular name for the family is sunset shells because of the shells' vivid radial colours. As with the scallops (Beautician), each species has an extensive colour range. The periostracum is usually conspicuous, especially so in estuarine forms, but thin and flaky when dry. Both anterior and posterior adductor muscles are always present, and the pedal retractor muscles are located dorsally just in front of the hinge. The hinge itself is relatively narrow and the teeth are delicate, the basic arrangement being two, usually bifid, cardinal teeth in each valve. Reports in the literature of cardinal tooth numbers of other than two are erroneous; they have come about either through post-mortem loss of a cardinal leaving only one apparent tooth, or by false association with the veneroidean family Glauconomidae where three cardinals exist in each valve. The ligament is external and it rests on conspicuous nymphs. The pallial line usually has a deep pallial sinus subtended postero-ventrally by the scars of the cruciform muscles. Frenkiel (1979) described the ultrastructure of the sensory organ associated with the cruciform muscle in *Nuttallia nuttallii*.

Graham (1934) has given a detailed anatomical account of the European species *Gari tellinella*. The mantle has a broad antero-ventral pedal gape. The structure of the foot, siphons, gills, labial palps and heart is exactly as in the Tellinidae. On the basis of gill structure, Graham (1934) considered *Gari* to be one of the more primitive tellinoideans. *Asaphis* has an extraordinarily dilated midgut which Narchi (1980) speculated might serve to boost numbers of micro-organisms prior to their processing by the stomach. The psammobiid stomach has two special features which are shared with the Donacidae – a substantial transverse fold across the floor between the oesophageal orifice and the transverse sector of the intestinal groove (absent in *Soletellina*), and a semicircular flange on the floor like a major typhlosole stretching from the orifice of the style sac towards that of the left pouch (Purchon 1987a).

Individual psammobiids are dioecious. Berg & Alatalo (1985) found that the Caribbean *Asaphis deflorata* reached sexual maturity after two or three years, that larvae developed to the pediveliger stage within 10 to 15 days, and that this stage lasted only one day.

Psammobiids occupy a multiplicity of habitats. *Gari* species burrow deeply in clean sands and *Soletellina* species burrow deeply in muddy sands (Willan 1980). Most species investigated have been found to be essentially deposit-feeders like tellins (for example, Narchi 1980; Tsuchiya & Kurihara 1980), but Pohlo (1972) insisted that *Nuttallia nuttallii* is a non-selective suspension-feeder. Some species of *Gari* and *Soletellina* inhabit mangrove swamps and *Gari crassula* only lives in the estuarine sections of large rivers. *Asaphis violascens* lives buried in gravel or

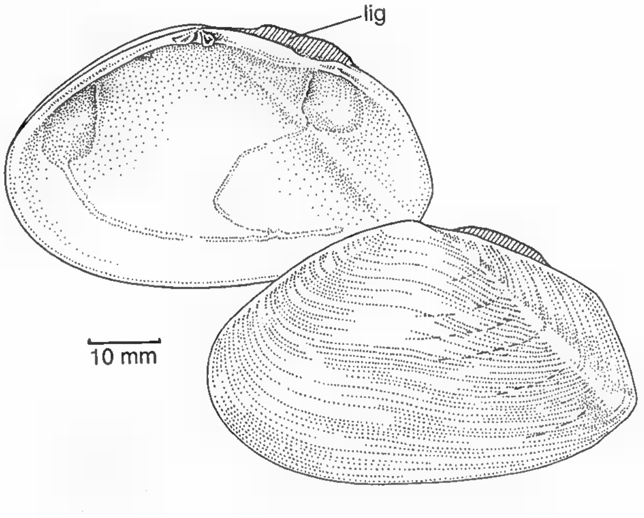


Figure 8.30 Family Psammobiidae. *Gari (Gari) lessoni*, shell valves, right valve in internal view, left valve in external view. **lig**, ligament on nymph.
[R. Plant]

within gravel-filled bedrock crevices at mid-tide level (Britton 1985). It does not desiccate because it keeps its valves tightly sealed during emersion; the estimated lethal dose of emersion was calculated to be 110.76 hours by Day (1980). Ansell (1967) elucidated the escape response of two British species of *Gari*; their leaping cycles involve foot eversion, foot twisting and recovery phases. Owen (1959) noted the capacity of some psammobiid species to autotomise the tips of their siphons. In some parts of the world, species of *Asaphis* are eaten by humans (Fisher 1978).

Thirty-one psammobiid species occur in Australian waters, 26 of them distributed in the tropics (Willan 1993). Four of the five temperate species range widely around the continent's lower half, the exception being the large, thick-shelled *Gari kenyoniana* which is restricted to South Australia, Tasmania and Victoria. B.R. Wilson & Allen (1987) were incorrect with their representation of the distribution of *Soletellina alba* (as *S. donacioides*), and hence their interpretation of that species' relationship to *S. biradiata. Soletellina alba* lives as far north as Hervey Bay on the east coast and is the sister species to the New Zealand *S. siliquens*. The five temperate species are all endemic, and were probably all derived from Indo-Pacific stock during the Tertiary.

Family Solecurtidae

The narrowly rectangular shell shape, with truncate extremities and subcentral umbones (Fig. 8.31), led to confusion of solecurtids with both psammobiids and solenoideans until Graham (1934) studied their anatomy. Shell shape is now regarded as convergent in all three taxa. More recently, B. Morton (1984a) relocated two problematic genera, *Novaculina* and *Sinonovacula*, to the solenoidean family Pharidae to leave only *Solecurtus*, *Azorinus* and *Tagelus* in the family Solecurtidae. Both *Solecurtus* and *Azorinus* occur in Australia, the former with five known species and the latter with two species. No studies have been undertaken on any member of the family in Australia; species of *Solecurtus* and *Azorinus* have been described briefly and illustrated by Lamprell & Whitehead (1992). The most significant overseas publications are all anatomical: Bloomer (1907); Ghosh (1920); Pohlo (1973); Villarroel & Stuardo (1977).

Shells range from 10–80 mm in adult length, and are smooth or sculptured with oblique, frequently divaricating, ribs. They have smooth margins and a well-developed periostracum. There may be considerable variation in the degree of truncation, colour and thickness of the periostracum within a particular species. Both anterior and posterior adductor muscles are present and both are rather narrowly elongate and positioned dorsally. The cruciform muscles are displaced anteriorly. The pallial line has a shallow to deep sinus. The hinge and ligament are the same as those of the Psammobiidae.

The animal in *Solecurtus* species is impressive in greatly exceeding its shell in size (Fig. 8.31) and it probably cannot be accommodated within its shell. The inner mantle folds are extensively folded posteriorly. The siphons, which are annulated and regularly banded with dark pigment for their entire length, have a common basal section. The openings to both siphons are guarded by lobes, and rudimentary straining tentacles are present at the tip of the inhalant siphon. Often the siphons are further protected by internal folds or elongate papillae. *Tagelus* species have large gills with well-developed marginal grooves, an outer demibranch which is not upturned, relatively small labial palps and a large dorsal hood to the stomach (Pohlo 1973; Villarroel & Stuardo 1977).

Most solecurtids live subtidally where they dwell in a permanent vertical burrow in clean substrata. Some species can live as deep as 500 mm below the sediment surface. Dworschak (1987) and Bromley & Asgaard (1990) have described *Solecurtus* burrows and burrowing behaviour. Their orientation in life is vertical. J.E. Morton (1979) reported that *Solecurtus* and *Tagelus* can burrow just as rapidly as solenoideans. The long, annulated siphons of *Solecurtus* are capable of autotomy at any joint, and this happens readily when living specimens are handled. Being tellinoideans, the assumption has been that solecurtids are deposit-feeders, but Pohlo (1973) showed conclusively, by both field and anatomical observations, that *Tagelus californianus* is a non-selective suspension-feeder. Meehan (1982) includes *Solecurtus sulcatus* in a list of shellfish eaten by the Anberra Aborigines of Arnhem Land, but that species constitutes only a very minor part of the diet.

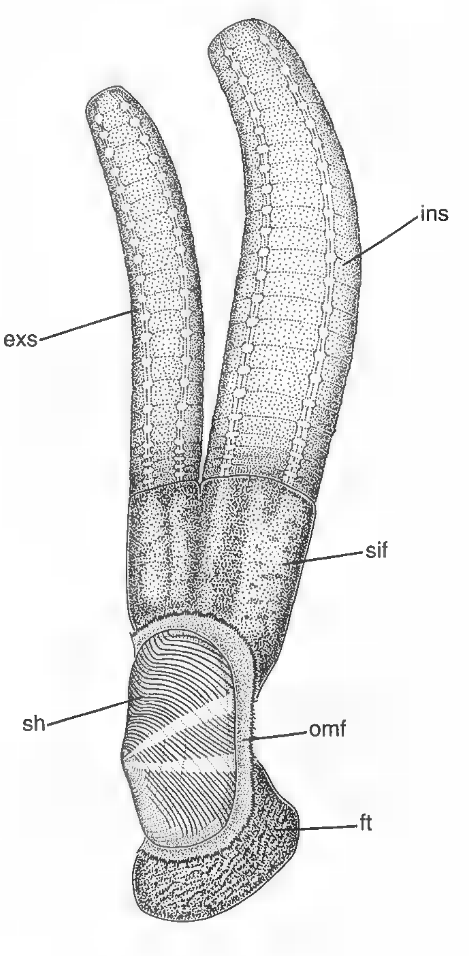


Figure 8.31 Family Solecurtidae. *Solecurtus sulcatus*, animal, lateral view. **exs**, exhalant siphon; **ft**, foot; **ins**, inhalant siphon; **sh**, shell; **sif**, fused base of siphons; **omf**, outer mantle fold. (After photograph by R.C. Willan)
[L. Newman]

The family Solecurtidae is tropical with no Recent representatives in temperate Australian or New Zealand waters; species tend to be widely distributed. This family requires a good deal more study, particularly with regard to intraspecific variation. Ecological investigations will be hampered by solecurtids' comparative rarity, their habit of burrowing very deeply, and their tendency when handled to autotomise their siphons.

Family Donacidae

The Donacidae are a small, but important family of heavy-shelled yet agile tellinoideans modified for life on open sandy beaches (Pl. 15.1). Whereas the distinctions between the other tellinoidean families (Solecurtidae apart) are obscure, the Donacidae are clearly defined by shell, mantle and siphon morphology, presence of a pedal elevator muscle and a relatively simple stomach. There is some debate as to whether the family is basically primitive (Pohlo 1967; Coan 1973b), or advanced through secondary simplification (Wade 1969; Purchon 1987a). As is so throughout the Tellinoidea, there is a need for revisionary studies on all the Australian donacid species. Considering the historical and recreational importance of *Donax (Plebidonax) deltoides*, plus its potential for aquaculture, it is surprising that ecological investigations have only taken place relatively recently (King 1985). In contrast, there is a plethora of overseas publications on the ecology of the family because species of the genus *Donax* are easy to collect in most parts of the world. Some of the more important studies are by Wade (1967a), Penchaszadeh & Olivier (1975), D.A.S. Smith (1975), Donn, Clarke, MacLachlan & duToit (1986) and Vega & Tunnell (1987). Major anatomical works are those by Yonge (1949), Purchon (1960a, 1963, 1987a), Stasek (1963a), Nakazima (1965), Trueman (1966), Pohlo (1967, 1973), Wade (1967b, 1969), Narchi (1972, 1978), Mouëza (1976), Mouëza & Frenkiel (1976) and Ansell (1981, 1985).

Donacids are characteristic of surf beaches where they live buried just beneath the sand. Their orientation in life is vertical. When uncovered by scouring waves, they are able to rebury quickly. In exploiting this high energy habitat, donacids show convergence with bivalves of the mactroidean family Mesodesmatidae.

Most donacid shells are triangular with the anterior end narrow and rounded, and the posterior end broad and obliquely truncate (Fig. 8.32A), qualifying the family for the popular name of wedge shells. A posterior flexure and gape are never present. Shells are solid and equivalve, and the margins close tightly to accommodate the animal wholly within the shell. Adult size among the Australian species ranges from 10 mm to nearly 80 mm for *Donax (Plebidonax) deltoides*, and this size is large for the family by world standards. Sculpture is usually weak, with the posterior slope sometimes differently ornamented and set off by a furrow. Colouration is usually pale and muted, but a given species can be highly polymorphic. The periostracum is extremely thin. Both adductor muscles are present and are approximately equal in size. A pair of pedal elevator muscles inserts dorsally. The pedal protractor muscle inserts near the posterior face of the anterior adductor muscle. The cruciform muscles are postero-ventral to the well-developed pallial sinus. The arrangement of the teeth and ligament is typical of the superfamily, but some species lack lateral teeth in the left valve and others have a small portion of the resilium relocated to a position in front of the umbo.

Aspects of donacid internal anatomy are illustrated in Figure 8.32B. The mantle has a broad antero-ventral pedal gape, the middle lobes having a double inner row and a double outer row of tentacles. Unlike the rest of the superfamily, the siphons are short and stout. Both siphons bear elaborately branched lobes at their extremities. Although the gills are variable in structure within the family, the outer demibranch is always shorter than the inner one. The gills are united posteriorly to reach the septum at the base of the siphons, thus physically separating inhalant and exhalant mantle chambers. The labial palps are small and the anterior filaments of the gill's inner demibranch are not fused with, or inserted into, the distal oral groove; they function primarily for the rejection of excess particles. All the adaptations of the mantle cavity are for a shallow-burrowing, suspension-feeding existence. The extremely large and powerful foot is capable of rapid burrowing, a necessity if animals are to rebury between successive wave surges. In general, donacid stomach anatomy is like that already described for the superfamily and for the Psammobiidae in particular, but the major typhlosole and intestinal groove fail to penetrate the right caecum in a few species – a simplified condition Purchon (1987a) interpreted as evidence of reversion to an ancestral state. The heart's auricles and pericardial gland are poorly differentiated. Mouëza & Frenkiel-Renault (1973) investigated reproduction, and Webb (1986) described post-larval development in overseas species of *Donax*.

Donax (Plebidonax) deltoides (Pl. 15.1) is popularly called the eugarie in southern Queensland, pipi in New South Wales and Victoria, and Goolwa cockle in South Australia. According to Dakin (1980), this species is the most common large bivalve inhabiting the surf zone of ocean beaches in New South Wales. Maximum abundance is attained just below low tide level. Juveniles live at higher levels; they must remain closer to the surface because of their proportionately smaller siphons, consequently they suffer higher mortality through dislodgment by surges. The following information on *Donax deltoides* is taken from King's (1985) investigations in South Australian waters. Sexual maturity is attained at a shell length of 36 mm which corresponds approximately with 13 months of age. Spawning starts in spring and continues all through summer. Fertilisation is external and the larvae spend 6–8 weeks in the plankton. Although *D. deltoides* can tolerate a salinity range from 20–45‰ (Nell & Gibbs 1986), it withdraws its siphons and foot wherever salinity is less than 25‰. Therefore at times when salinities are depressed for extended periods, such as when the Murray River is in flood, mass mortality occurs through starvation. Large natural fluctuations like this seem to be a feature of donacid populations worldwide.

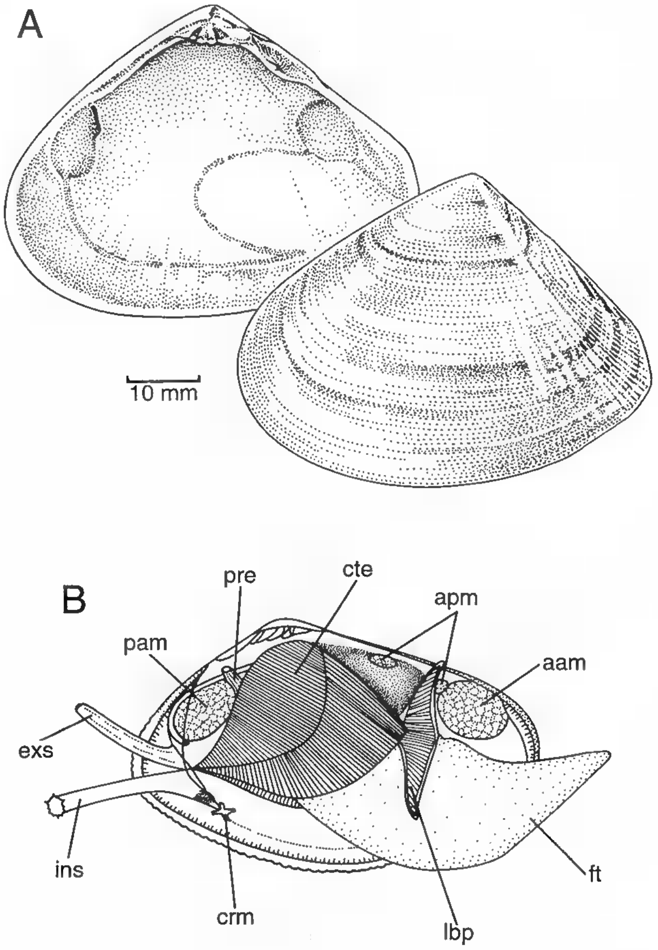


Figure 8.32 Family Donacidae. **A**, *Donax (Plebidonax) deltoides*, shell valves, right valve in internal view, left valve in external view. **B**, *Donax vittatus*, internal anatomy, right view, palps exposed and siphons extended. **aam**, anterior adductor muscle; **apm**, anterior pedal muscles; **crm**, cruciform muscle; **cte**, ctenidium; **exs**, exhalant siphon; **ft**, foot; **ins**, inhalant siphon; **lbp**, labial palp; **pam**, posterior adductor muscle; **pre**, posterior retractor muscle. (B, after Yonge & Thompson 1976) [A, R. Plant; B, C. Eadie]

The presence of *Donax deltoides* in coastal middens throughout south-eastern Australia attests to this bivalve's importance, in the past, in the diet of Aborigines. Nowadays quantities are regularly gathered for fishing bait and, to a lesser extent, for food.

Four of the six Australian donacid species have temperate distributions, with one, *Donax columbella*, endemic to Western Australia and the other three – *Donax deltoides*, *Deltachion brazieri*, *Tentidonax veruinus* – ranging widely around the continent's southern half. Of the tropical species, *Donax cuneata* lives in northern Australia and the southern Pacific, and *Donax faba* occurs commonly through the Indo-Pacific Ocean (Cernohorsky 1978). D.A.S. Smith (1975) investigated polymorphism in this species in eastern Africa. Australian *Donax* species have been described briefly and illustrated by Lamprell & Whitehead (1992).

In view of its potential for aquaculture, *Donax (Plebidonax) deltoides* is likely to be the subject of further ecological investigations. These studies will be hindered by the species' requirement for open beaches where sampling is notoriously difficult and distributions are naturally patchy. In the long term, cultivation may be compromised by population fluctuations and the extended larval life.

Superfamily ARCTICOIDEA

The commonly accepted definition of this superfamily relies principally on shell characters appropriate for its predominantly fossil component. The heterodont hinge structure of the aragonitic shell is important, with the two or three cardinals in each valve tending to radiate from the beak. Well-developed lateral teeth are present in most forms. External sculpture may be lacking but, if present, is predominantly commarginal. Internally the shell lips (that is, the inner margins of the shell) may be smooth or slightly crenulate. The ligament may range between being external but anchored to nymphs in well-incised insertion grooves to being internal. The shell is inequilateral with the outline varying from almost circular to elongate. The position, prominence and degree of spiral twisting of the prosogyrous beaks vary with the shell shape.

The degree of similarity of the adductor muscle scars again varies with the shell shape, being less isomyarian in elongate forms with anterior beaks. In such forms the diameter of the anterior adductor and the anterior pedal retractor muscles, and so that of their scars, is reduced in size. The pallial line is usually thick. Its sinus, if present, is wide and very shallow, although in living forms the very short siphons may be deeply withdrawn.

The eulamellibranchiate gills of living arcticoideans consist of unequal, usually plicate demibranchs with ciliation that conforms to Atkins' (1937a) Type C(1) in which the only distal food groove is located only on the free edge of the inner demibranch. Sieved particles are passed forward and sorted by the generally short labial palps. Those selected are ingested and passed to the stomach which is of Purchon's (1960a) Type V.

There is no single distinct difference by which members of this superfamily, with few Recent species worldwide, can be separated from those of the superficially similar Veneroida comprising some hundreds of living species. Shell features which, taken together, distinguish arcticoideans, involve the generally subdued nature of the shell sculpture, the non-sinuate pallial line, and the hinge teeth consisting of three or fewer cardinals and, generally, posterior laterals. Some helpful anatomical characters include the presence of a byssus in mature animals of some species and the small size or lack of inhalant and exhalant siphons.

Arcticoideans are shallow burrowers in soft substrata or nestlers within crevices, abandoned burrows in coral rock, *etc.* Some maintain position using byssal threads. All contact with the water column is through the posteriorly placed pallial apertures except in kelliellids which have an anterior inhalant area.

The evidence that this superfamily originated during the Palaeozoic Era depends on the inclusion of the family Mecynodontidae which appears to have arisen and died out during the Middle Devonian of Europe and North America (La Rocque 1969). Most other arcticoidean families, including the brackish and freshwater Neomiodontidae represented in the Upper Cretaceous of New South Wales (Etheridge 1902), arose in the Mesozoic (Casey 1969). Apart from the Arcticidae and the Trapeziidae, which survive to the present, all of these families with Mesozoic origins died out during the Cretaceous Period. Other extant arcticoidean families are the Kelliellidae and the Vesicomyidae which arose in the Cainozoic and which some workers regard as non-arcticoideans (see below), and the Bernadinidae which consists of a few species of very small arcticoideans limited to the Recent fauna of the Americas (Keen 1969g; Keen & Casey 1969a; Coan 1984).

The Arcticidae, which arose in the Upper Triassic and diversified greatly in the Cretaceous (Nicol 1986) and again in the Tertiary (see Keen & Casey 1969a), are recorded from Middle Jurassic deposits in Antarctica (Quilty 1983) and in Lower Cretaceous deposits in the Northern Territory (Skwarko 1966) and the Carnarvon and Canning Basins of Western Australia (Cox 1961b; Skwarko 1970). The genus *Fissilunula* of the Lower Cretaceous of South Australia and Queensland, referred to Arcticidae by Ludbrook (1966), was later identified as an isocardiid (= glossid) in those and in other deposits in the Northern Territory, New South Wales and the north of Western Australia by Skwarko (1967). Fossil arcticids have also been found in Europe, the Americas, southern and south-western Asia and in Africa. The family may be represented today by perhaps only the North Atlantic and European species *Arctica islandica*, although the Japanese genus *Akebiconcha* has been placed in this family by some authors (Franc 1960; Okutani 1962, 1966).

The distribution of the Bernadinidae, a family of small to minute arcticoideans, appears limited to the Recent of the Americas (Keen 1969g; Coan 1984). Its few species are distinguished from other arcticoideans not only by their size, but by the ligament which is partly or entirely internal, attaching to the walls of a more or less sunken pit behind the two or three cardinal hinge teeth. The posterior margin of one valve fits into a groove in the other, so reinforcing the function of the lateral teeth.

The family Trapeziidae and, perhaps, the Kelliellidae are represented in the extant Australian fauna. No vesicomyids have yet been recorded from Australian waters, although some have been collected in nearby waters off both Indonesia and New Zealand.

Family Trapeziidae

Of relatively recent origin in the Cretaceous, this family appears to have maintained its level of diversity up to the present, with genera that arose in the Cainozoic replacing those that had died out earlier (see Keen 1969g). The present marine distribution of this family is predominantly tropical and subtropical in the Indo-West Pacific region (including northern Australia) and in the waters off southern United States of America, the Caribbean, the eastern Atlantic and the Mediterranean, as detailed in the review of the family by Solem (1954). The geographic range has seemingly contracted away from the now cooler waters of South America and Europe as well as from warmer waters of south-western Asia and Africa. The genus *Glossocardia*, with species in the Philippines and New Caledonia and the tropical western Atlantic, was reviewed by Matsukuma & Habe (1995).

The names Cypricardiidae, Lithophagellidae and Libitinidae have also been used for this family, the last most recently by Thiele (1929–1935).

Trapeziid shells are generally of medium size, with those of *Trapezium* species reaching a length of about 70 mm. They are, in general, elongate and inequilateral with the beaks nearer to the anterior end (Fig. 8.33A–C)). As they grow, the shells of most *Trapezium* species become solid and relatively more convex, and many become deformed because of their nestling habit. However, *Coralliophaga* species, inhabiting burrows abandoned by other organisms, generally maintain the regular cylindrical shape of their thin and almost transparent shells. Similarly, the thin-shelled byssally attached *Fluviolanatus* species generally retain their roundly rectangular shape throughout life.

The outermost layer of the shell is a thin periostracum which. in some species of *Trapezium*, is extended beyond the ventral shell (lips) margins as a strong membrane. Internal to the periostracum of *Trapezium* are two layers of aragonite of differing crossed-lamellar structure separated by a thin pallial myostracum left behind by the ventral advance of the pallial line. This line is indented to form a shallow sinus in some species. The outer aragonitic layer forms the hinge (Taylor *et al.* 1973).

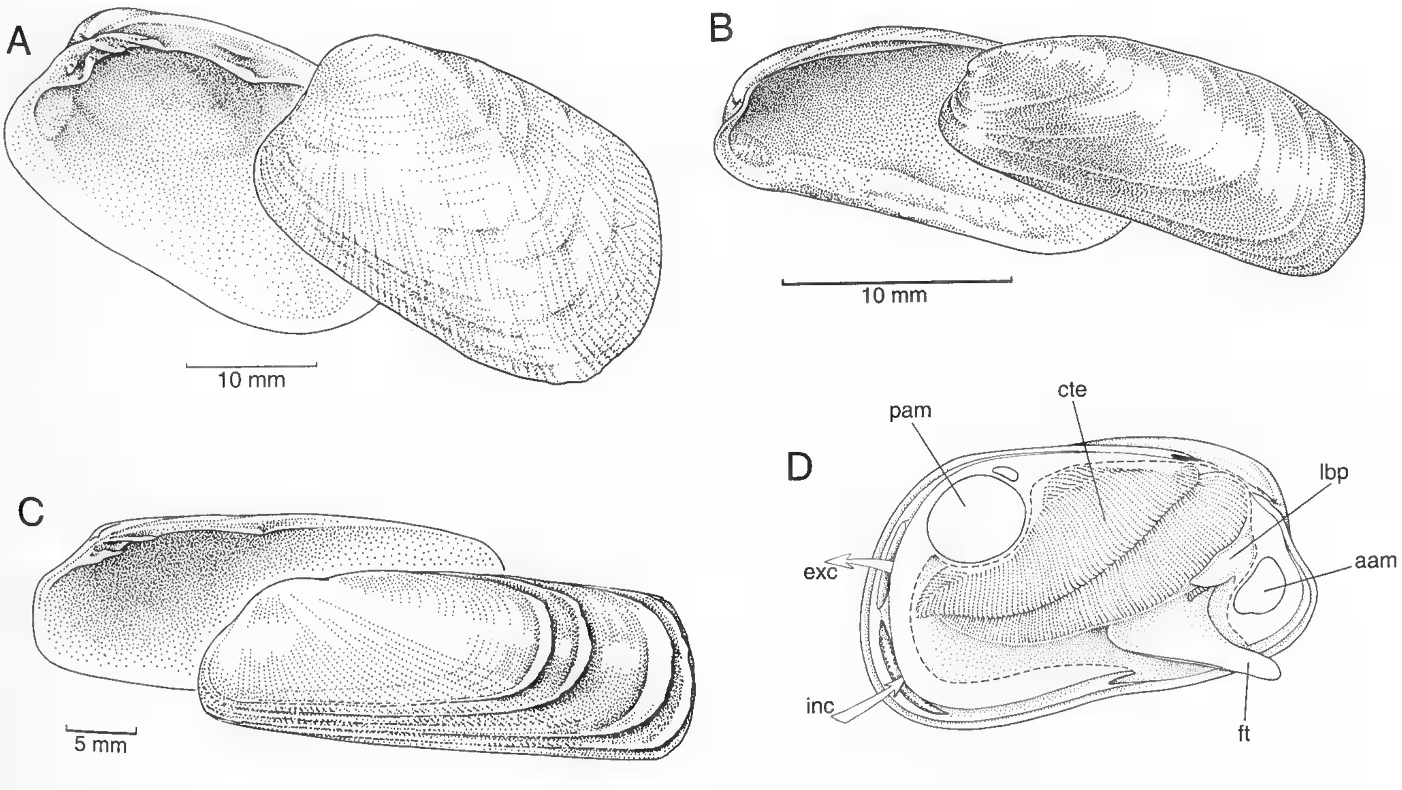


Figure 8.33 Family Trapeziidae. **A–C**, shell valves, right valve in internal view, left valve in external view: **A**, *Trapezium oblongum*; **B**, *Fluviolanatus subtorta*; **C**, *Coralliophaga coralliophaga*. **D**, *Trapezium oblongum*, pallial cavity, from right, right shell valve and pallial lobe removed. **aam**, anterior adductor muscle; **cte**, ctenidium; **exc**, exhalant current; **ft**, foot; **inc**, inhalant current; **lbp**, labial palp; **pam**, posterior adductor muscle. [R. Plant]

The hinge is basically heterodont with a flat, straight and narrow hinge plate supporting two or three divergent cardinals in each valve. Anterior and posterior laterals are usually present, their relative lengths depending upon the shape of the shell and the position of the beaks. However, hinge teeth are much reduced in *Coralliophaga* and absent in the Australian *Fluviolanatus*. In both these genera the shells have a slight posterior gape. Most if not all trapeziid species are byssiferous to some extent. However, the shells of even those species of *Trapezium* which have a stout byssus do not have a ventral byssal gape.

As is appropriate in inequilateral bivalves, the adductor and pedal retractor muscles and their scars are unequal with the anterior set being much smaller in those species with more anteriorly placed beaks.

The pallial folds are papillate, and inhalant and exhalant siphons are formed by fusion of the inner folds except in species of *Coralliophaga* in which the middle folds are also involved (Morton, B. 1980b). These siphons are relatively short and deeply retractable into the large space between the pallial line and the posterior shell margins (lips). The aperture of the inhalant siphon is guarded by a complex series of tentacles. Anterior to the siphons is a short pedal aperture through which the small compressed foot can be protruded for locomotion and for byssal attachment.

Lateral to the foot within the pallial cavity hang the eulamellibranchiate gills. These have ciliation of Atkins' (1937a) Type C1 with a distal food groove on the inner demibranch only. The gills are plicate except in *Fluviolanatus* species in which the non-plicate gills are unusually large. The deeper internal demibranchs extend anterior to the external demibranchs to lie between the labial palps (Fig. 8.33D). These palps are moderately large and fleshy in most forms, though quite small in *Fluviolanatus*. In some forms, both sets of demibranchs are expanded postero-ventrally to project into the inhalant siphon. The ascending lamellae of the inner demibranchs are joined by tissue fusion to the visceral mass, and those of the outer demibranchs to the intersiphonal area, completely separating the inhalant and exhalant pallial chambers.

The trapeziid stomach corresponds to Purchon's (1960a) Type V, with a large gastric shield and sorting areas. This seems to indicate a high rate of food consumption even in *Fluviolanatus* in which the expanded pallial folds house what appear to be algal cells. B. Morton (1982b) postulated that these may be zooxanthellae with a role in nutrition and respiration. Among the trapeziids, the structure of the midgut varies, being extensively joined to the style-sac except in *Fluviolanatus*. The rectum passes through the ventricle of the heart which is located behind the beaks.

Trapeziid species are shallow coral reef nestlers that live in crevices, under coral boulders and in coarse sand and rubble. Marine trapeziids are commonly preyed upon by fish and octopus. The Australian trapeziid fauna includes the Indo-West Pacific marine genera *Trapezium* and *Coralliophaga*, and the endemic lagoonal/estuarine genus *Fluviolanatus*.

The shells of *Trapezium* species tend to be oblong to quadrate, generally with a marked increase in thickness and in convexity at maturity (Fig. 8.33A). The three extant Australian species belong to the fauna of the Indo-West Pacific region and occur only in tropical to subtropical northern waters. Perhaps the most commonly occurring is the nestling species, *T. (T.) bicarinatum* which is typically found on coral reefs. *Trapezium (Neotrapezium) sublaevigatum*, by contrast, is limited to waters along the coasts of continents and large islands (Morton, B. 1979c), inhabiting a wide range of sheltered habitats. These include the sometimes turbid waters of mangals with freshwater input and oyster reefs. The third Australian species, *T. (Glossocardia) obesa*, is the least common, though apparently occurring over much the same latitudinal range as the other two. It is atypical of the family in inhabiting deep as well as shallow waters, and is recorded from a number of widely separated localities in the Indo-West Pacific region including the northern parts of the Great Barrier Reef and south to North West Cape on the west coast.

The elongate fragile-shelled *Coralliophaga coralliophaga* is, apparently, the only one of the two extant Indo-West Pacific species of this genus to occur in Australian waters, having been recorded as far south as the Houtman Abrolhos off Western

Australia. This same species has also been reported to occur in the Caribbean area. It typically lives in burrows in dead coral which have been excavated and then vacated by other animals such as lithophagid mussels (Morton, B. 1980b). The sculpture of commarginal lamellae on its thin, translucent shell and its byssal attachment both help prevent dislodgment.

Fluviolanatus is a monotypic Australian genus that was placed in the family Mytilidae until B. Morton (1982b) determined its real affinities. The fragile brown-rayed shell of *F. subtorta*, which attains a maximum length of about 15 mm, is inequivalve with the larger right valve overlapping the left. It attaches to logs, reeds, *etc.*, with a fine byssus. This species (recorded as a species of *Anticorbula* by Kendrick 1976) has an apparently disjunct distribution; it has been recorded from estuaries and coastal lagoons along the entire east coast from Victoria to the Northern Territory and in sheltered embayments and estuaries in south-western Western Australia. It appears to have moved upstream recently in some Western Australian estuaries (Kendrick 1976), possibly in response to the increasing salination of rivers and streams which drain cleared catchment areas.

Family Kelliellidae

Kelliellids are small to minute, shallow to deep-water marine bivalves. Their aragonitic shells are equivalve, oval to round in outline and inflated (almost orbicular) in shape. The valve margins are smooth internally and the pallial line is generally simple. The beak is slightly closer to the anterior end with a distinct lunule in front of it in some species. Behind the beak is the ligament which is not strong. In some species it is external whereas in others it is internal and anchored to a fossette under the beak. The interpretation of the kelliellid hinge structure is not clear, with a lack of agreement among workers not only on the origins of the teeth, but even of their number (see Studencka 1987).

This family has been placed by Keen (1969g) and Vokes (1980) in the superfamily Arcticoidea. However, Newell (1965) considered that it belongs within the Glossoidea. Some of its members have even been considered to be neotenous venerids (Boss 1969c). In her revision of the family, Studencka (1987) followed Scarlato & Starobogatov (1979), placing the Kelliellidae in the superfamily Kellielloidea.

The entire development of the family appears to have occurred within the Cainozoic and the known fossil record derives only from the Northern Hemisphere. Only the genus *Kelliella* has persisted throughout this period and is now represented by species in the Mediterranean and Atlantic (Clausen 1958) and in the Pacific south to the Indonesian Archipelago, New Caledonia and the Kermadec Trench (Filatova 1969). Two other genera *Pauliella* and *Warrana* have only Recent Southern Hemisphere records (Munier-Chalmas 1895; Laseron 1953).

The mantle folds of kelliellids are fused in one place only to form an exhalant orifice, which may be extended as an exhalant siphon in some. However, the inhalant aperture is not separated from the pedal gape (Fischer 1880–1887). Indeed, the inhalant flow is anterior, a seemingly primitive condition in heterodonts (Allen 1985). Around this inhalant area the mantle folds are fringed with tentacular processes.

Within the mantle cavity are unequal demibranchs hanging on each side of the strong, cylindrical and sometimes bent foot. The gills terminate anteriorly at the palps which in *Kelliella* are small. In general, the anatomy is very similar to that of some vesicomyids.

Although little is known about the habitat or biology of these small, shallow to very deep-water species, they seem to be epifaunal or shallowly burrowing suspension-feeders (Allen 1983). They move sluggishly and, at least in some species, attach by fine byssal threads to particles in the muddy sand substratum (Clausen 1958). In some areas kelliellids are very abundant and are preyed upon by boring gastropods. A number of species of *Kelliella* are known to be lecithotrophic with a very short pelagic larval life (Knudsen 1979).

The genus *Kelliella* is now almost entirely limited to the abyssal and hadal zones, with only one North Atlantic species, *K. miliaris* ranging into the deep sublittoral zone. However, Late Eocene to Miocene records are from shallow-water deposits (Studencka 1987).

Specimens tentatively placed in this family have been taken off south-eastern Australia. Some, of undetermined generic placement, have been dredged at about 2000 m, but minute specimens of the genus *Warrana* have been taken in shallower waters and beach drift (Laseron 1953). Nothing is known of the anatomy or biology of these Australian species.

Family Vesicomyidae

No vesicomyids have been recorded from Australian waters, but species of *Vesicomya sensu stricto* inhabit nearby Indonesian waters at depths of from 750 to over 1000 m, and the Antarctic Ocean at shallower depths (see Odhner 1960). The family comprises the genera *Vesicomya* and *Calyptogena.*

The superfamilial placement of this family is problematic. Although Newell (1965), Keen (1969h) and Vokes (1980) placed it in the Glossoidea, the work on its shell microstructure by Taylor *et al.* (1973) indicates a closer relationship with the Arcticoidea. Scarlato & Starobogatov (1979) placed it in the superfamily Veneroidea. The family has also been known under the name Vesicomyacidae.

Most vesicomyids inhabit deep waters from the outer zone of the continental shelf to the abyssal plain. Locally dense populations of some species of *Calyptogena* have recently been found around hydrothermal vents along the deep-sea rifts (Boss 1969c; Boss & Turner 1980; Laubier, Ohta & Sibuet 1986). Vesicomyids are known to occur through the East and West Atlantic, the North, East and South Pacific, the North Indian Ocean and from the Philippines and Indonesian deeps, as well as off South Africa and in other parts of the Southern Ocean. The present geographic range of this family is apparently more extensive than that known from the past, though this may be due to the relative paucity of deep-water facies in the fossil record.

Shells of vesicomyid species, which have in the past been placed in the families Arcticidae and Carditidae, range in size from small to more than 180 mm in length, though some of the smaller forms may prove to belong to the family Kelliellidae. Vesicomyids show a close similarity in form. In general, they are oval to narrowly elongate and laterally compressed. The shell is aragonitic and ranges from thin and pearly to heavy and chalky in texture (Boss 1969c; Roux, Rio, Fatton, Marien & Pachiaudi 1983). Most are covered by a thick periostracum which is ornamented by processes in some forms and which may flake off from dead shells as they dry. Most vesicomyids have an obvious prosogyrate beak, an antero-ventral pedal gape, a more or less well-defined escutcheon and a lunule demarcated by a groove. The opisthodetic ligament may be deeply sunken into the escutcheon. Shell sculpture lacks any radial elements and consists at the most of commarginal growth lines.

Internally, the hinge is heterodont and very similar to that of some venerids. It consists of three, or sometimes two, cardinal teeth which are long, simple and almost parallel. In some species these cardinals are not clearly differentiated from the lateral teeth where these latter are present. The laterals and even the cardinals may tend to obsolescence during the growth of some forms.

The pallial line, which is sometimes only faintly marked, may be entire or only slightly indented posteriorly to accommodate the small posteriorly located inhalant and exhalant apertures. These may protrude on very short siphons in some taxa. These apertures are associated with marked thickenings of the pallial muscles around the areas of pallial fusion. Anterior to these is a long pedal aperture through which the large, compressed and pointed foot protrudes.

The anatomy of only a few species has been examined. B. Morton (1986b) found that the gills of *Calyptogena magnifica* are thick, fleshy, eulamellibranch and non-plicate with ciliation as in Atkins (1937a) Type C(1). The inner demibranch is larger than the outer, has a very narrow marginal food groove, and only its anteriormost filaments enter the proximal oral groove as in Stasek's (1963a) Type 3. The palps are small and lack ciliated sorting ridges. The digestive system is of the normal type for a bivalve, except that the crystalline style sac is reduced. The blood contains intracellular haemoglobin.

Following the report by Boss & Turner (1980) of the presence of symbiotic organisms in the gills of their new species from the Galapagos Rift, *C. magnifica*, a number of workers have investigated chemoautotrophic activity in these animals (see Grassle 1985). However, B. Morton (1986b) maintained that evidence of intracellular bacteria has not been demonstrated conclusively, that the anatomy of *C. magnifica* is that of a filter-feeder which collects and processes a diet of bacteria, and that the high chemoautotrophic activity levels found in the gills by some workers may merely reflect the entrapment of free-living bacteria filtered from the vent water.

Investigators have produced varying estimates of growth rate and so of life span in *C. magnifica* (Turekian, Cochran & Nozaki 1979; Rhoads, Lutz, Revelas & Cerrato 1981; Roux *et al.* 1983; Turekian, Cochran & Bennett 1983; Turner & Lutz 1984), which may reflect variations in growth rate, perhaps related directly or indirectly to variations in the degree of activity of the vents (Grassle 1986). Metabolic rates more closely resemble those of shallower water species than those of abyssal bivalves living away from the warm waters near the vents.

Grassle (1986) considered that sexual maturity is first attained by *C. magnifica* at some time between the ages of one and four years, though full sexual maturity may not occur till much later. He postulated that larvae, which develop from large yolky eggs (Berg & Turner 1980), may be dispersed over large distances by bottom currents.

Most vesicomyids are at least partly infaunal in muddy substrata. However, *C. magnifica*, seen to be nestling without byssal attachment in rock crevices and between mussels when viewed and photographed using submersible craft, is unusual in being epifaunal.

The fossil history of this family is apparently confined to the Cainozoic with the oldest fossils dating from the Oligocene. However, extant taxa exhibit the greatest diversity so far attained by this family (see Keen 1969h).

Superfamily GLOSSOIDEA

Living glossoideans all belong to the family Glossidae. Their shells are, in general, equivalve and inequilateral and each valve has a prominent, spirally coiled and enrolled beak situated in a more or less anterior position. The smooth, commarginally folded or ribbed shells do not gape, despite the presence of a fine byssus in some extant glossids. Internally the pallial line of the aragonitic shell is usually entire, although slightly sinuate in some species. The lateral hinge teeth are aligned parallel to the dorsal margins of each valve. In some species, the two or three cardinal teeth below the beaks and the external ligament are similarly aligned.

Glossoideans are eulamellibranchs with gill ciliation of Atkins (1937a) Type C1. The ventral tips of the more anterior filaments of the inner demibranchs are inserted into and fused with the distal oral grooves, thus fitting Stasek's (1963a) Type 2. Their stomachs are of Purchon's (1960a) Type 5 (Newell 1965).

This superfamily, comprising two Mesozoic and two or three Cainozoic families, has never achieved great diversity of form. The extinct family Dicerocardiidae arose in the Upper Triassic and co-existed through the Middle and Upper Jurassic with the Ceratomyopsidae which it survived. Dicerocardiids appear to have died out in the Upper Cretaceous (Cox 1969c 1969d). The apparently small gap in time before the appearance of the Glossidae in the Palaeocene gains greater significance if Cox's proposal of a diphyletic nature of this superfamily is considered. He maintained that the similarity between the shells of the Glossidae and Dicerocardiidae is due to convergence. The families Vesicomyidae and Kelliellidae have been included separately or together in the Glossoidea by some authors (Newell 1965; Keen & Casey 1969b; Boss 1982; Sorensen 1984). However, in this work the Kelliellidae is included in the Arcticoidea, following Keen (1969i). Also included in that superfamily, although more tentatively, is the Vesicomyidae, this decision being based upon the work if Taylor *et al.* (1973) on the structure of the shell.

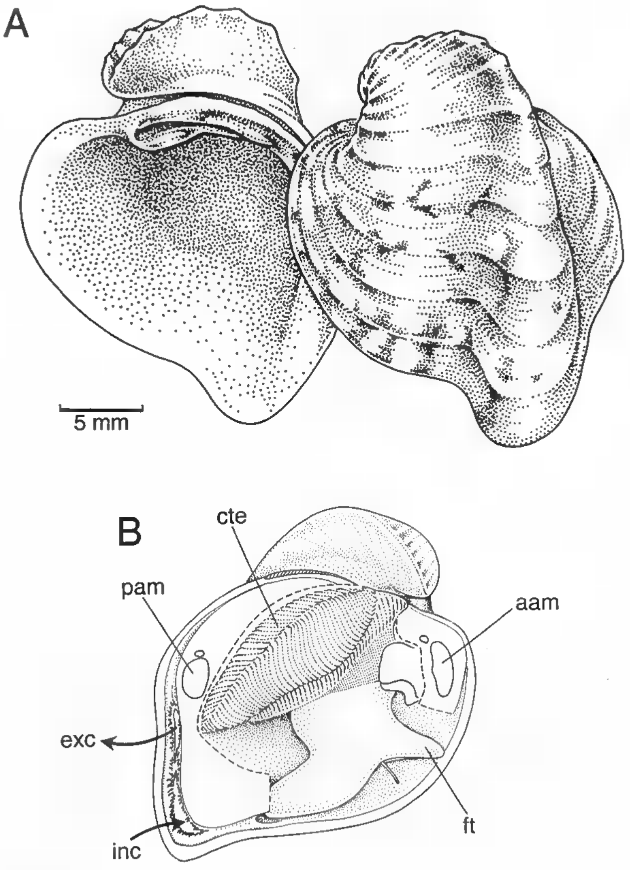


Figure 8.34 Family Glossidae. *Glossus (Meiocardia) sanguineomaculata*: A, shell valves, right valve in internal view, left valve in external view; B, internal organs, right view, right shell valve and pallial lobe removed. **aam**, anterior adductor muscle **cte**, ctenidium; **exc**, exhalant current; **ft**, foot; **inc**, inhalant current; **pam**, posterior adductor muscle. [R. Plant]

Family Glossidae

Arising early in the Cainozoic, this family achieved its greatest diversity in the Lower to Middle Tertiary, thereafter contracting into a much less diverse group which survived into the Quaternary and present. Extant species are, however, distributed widely in the Indo-West Pacific region and the tropical to temperate Atlantic Ocean (Keen & Casey 1969b).

Glossids are small to medium-sized extant species, with distinctive shells of lengths up to about 90 mm. The shells are generally equivalve and ventricose, ovate to globose, with a keel to the postero-ventral corner (Fig. 8.34). The valves of all species are, to some extent, planispiral with a large tangential growth component. Their most distinctive features are the large beaks, inclined forward (prosogyrate), but well separated due to continual growth on the dorsal shell margin. This growth pattern is reflected in the form of the ligament which is narrow, external, opisthodetic and anchored to nymphs. As the shell grows the ligament also grows posteriorly at a fusion layer and splits apart at its anterior end.

The aragonitic porcellaneous shells of glossids are smooth or commarginally ribbed, polished or covered with a fibrous periostracum and lightweight, but moderately strong. They are composed of two main shelly layers, the inner being of complex crossed-lamellar structure separated by a thin, prismatic, pallial myostracum from the outer more or less homogeneous or crossed-lamellar layer (Taylor *et al.* 1973).

The hinge is heterodont with two long cardinals in each valve and two long posterior lateral teeth tending to be parallel to the dorsal valve margins. The anterior lateral teeth of some species tend to become weak or absent. This situation may then be reflected externally in the incomplete lunule.

Internally the valves are smooth-edged with an entire and simple pallial line and approximately equal adductor muscle scars. However, the anterior scar may be smaller and more deeply incised into the internal shell surface than is the posterior. The adductor muscles have a very distinct line marking the junction of their quick and catch sections.

The anterior part of the laterally compressed, hatchet-shaped foot (Fig. 8.34B) has a deep byssal groove which runs forward from the byssal gland. The byssus, however, may consist of only a few threads and may be present only in the young (Owen 1953a). The inner pallial folds are fused, separating the long ventral pedal aperture and the posterior inhalant and exhalant apertures. The latter apertures are not produced into siphons and are controlled by strong pallial muscles. Either only the inhalant aperture or, in some species, both apertures are surrounded by papillae or by tentacles.

The eulamellibranchiate gills are large and the demibranchs are nearly equal, although the inner is slightly larger and has a deep food groove along its distal edge. These large gills appear to be well adapted to filtering large volumes of clear water as Owen (1953a) described in the European species *Isocardia* (= *Glossus*) *humanus*. The gills are deeply plicate except at their anterior ends, and the ascending limbs of the inner demibranchs are fused medially to one another and/or to the visceral mass except around its posterior edge. The labial palps are large and contractile and the intestine is long and very convoluted. The morphology and functioning of the stomach of *Glossus humanus* was described in detail by Owen (1953a).

The ventricle of the heart is traversed by the rectum. The auricles of the Indo-West Pacific *Glossus (Meiocardia) lamarckii* are separate from one another (Pelseneer 1911), though those of the European species (*G. humanus*) are interconnected ventral to the ventricle. The posterior aortic bulb is outside the pericardium (Franc 1960).

Owen (1953a) reported that *Glossus humanus* is dioecious. However, no data are available on the reproductive system of Indo-West Pacific species.

All extant species in this family are generally regarded as belonging to the genus *Glossus*, and located in the subgenera *Glossus sensu stricto* and *Meiocardia* (Keen & Casey 1969b). Some authors, however, elevate *Meiocardia* from subgeneric to generic rank (see study by Matsukuma & Habe 1995).

The glossid species, *Glossus (Meiocardia) sanguineomaculata*, *G. (M.) vulgaris*, *G. (M.) lamarckii*, and *G. (M.) moltkiana*, recognised in the Australian fauna, are all of tropical affinity with a wide Indo-West Pacific distribution (Matsukuma & Habe 1995). No living southern Australian representatives are known.

Glossids typically live in sheltered situations and in shallow waters to depths of about 400 m. They are relatively inactive, and are shallow burrowers that lie embedded and almost motionless in the surface layer of soft mud (Owen 1953a; Purchon 1968) or rubble (Melvill 1909) with only the exhalant and inhalant orifices exposed.

Palaeocene fossils of an unidentified glossid have been found in the Cardabia Group of the Giralia Range in the region of Exmouth, Western Australia (G.W. Kendrick personal communication). A species of *Glossus (Miocardiopsis)* has been found in Late Eocene Pallinup Siltstone of south-western Australia (Darragh & Kendrick 1980). This subgenus is otherwise known only from the Eocene of Europe.

Superfamily CORBICULOIDEA

Members of the superfamily Corbiculoidea are minute to medium-sized (2–100 mm), freshwater to estuarine, bivalve molluscs. The aragonitic shell is oval to subtrigonal in shape and has a crossed-lamellar inner layer (Prime 1865; Prashad 1920; Benthem Jutting 1953; Tan Tiu & Prezant 1989b). Shell sculpture is not elaborate, the surface being smooth or having low, narrow, commarginal ridges. Both the inner and outer surfaces of the shell valves may be brightly adorned with pink to red, yellow or purple colouration.

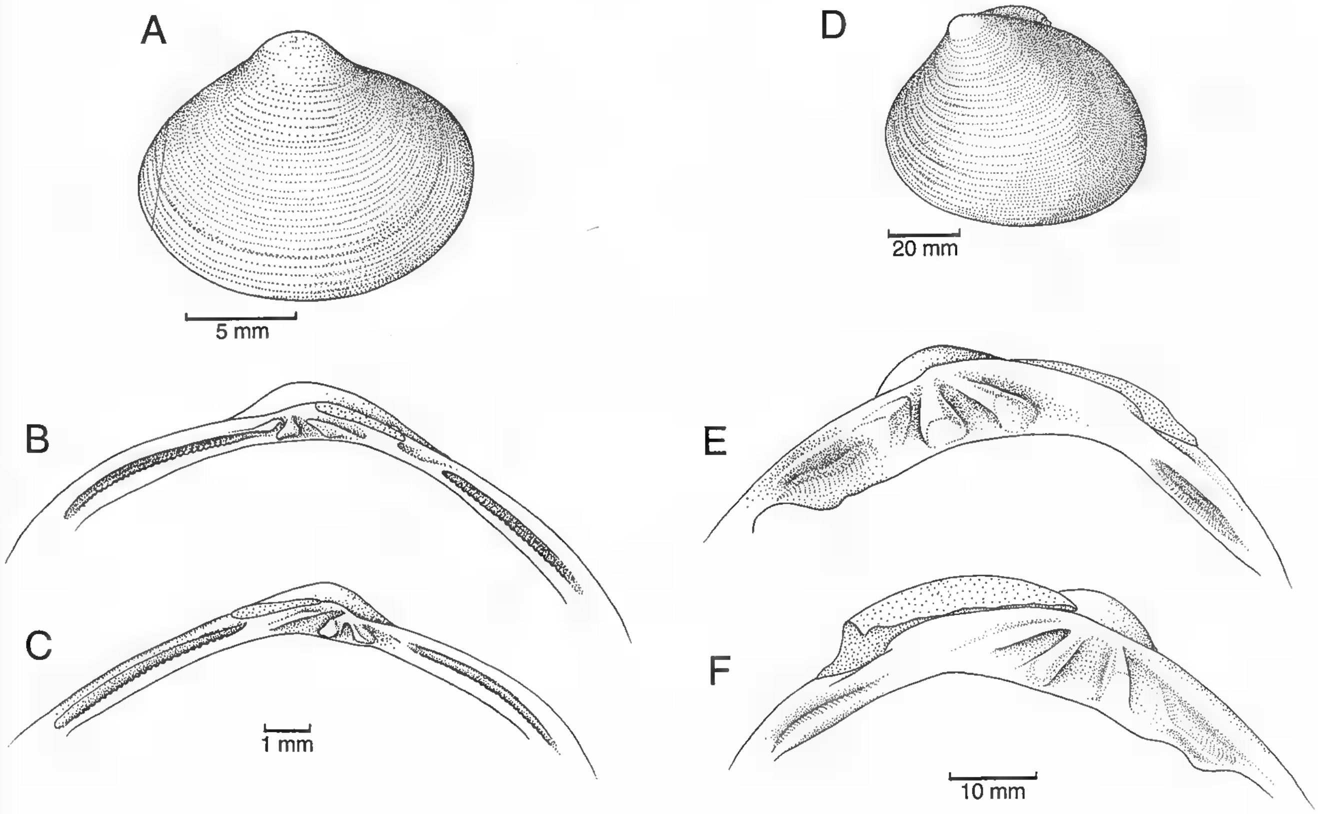
The higher classification of the Corbiculoidea, like that of most groups, is unresolved with some debate on the number of families which should be included (for example, Boss 1982). This account recognises two families, Corbiculidae and Sphaeriidae (= Pisidiidae) (after Clarke 1970; Kuiper 1981, 1983; Spangler 1981; ICZN Opinion 1331, 1985).

Representatives of the Corbiculoidea occur globally in many different brackish and freshwater habitats, from temporary ponds in arid regions to high Arctic environments (Prashad 1928, 1929, 1930; Benthem Jutting 1953; Herrington 1962; McKee & Mackie 1980; Smith, B.J. & Kershaw 1981; Kuiper 1983; Morton, B. 1983c; Kuiper, Okland, Knudsen, Koli, von Proschwitz & Valvorita 1989). The Corbiculoidea are considered to be recent colonisers of fresh waters, derived from a marine veneroid ancestor (Keen & Casey 1969c; Morton, B. 1985b, 1989). On the basis of their osmotic and ionic analyses, Raj & Fergusson (1980) also discussed the evolutionary history of corbiculoid colonisation of freshwater environments from brackish waters.

The first European collection, from Australia, of a corbiculoid was probably made by Cook's party in the vicinity of the Daintree River, north of Cairns (Iredale 1943). Monographs by E.A. Smith (1882) and Benthem Jutting (1953) contain minor treatments of Australian corbiculoid bivalves. May (1932), Cotton & Godfrey (1938) and Gabriel (1939) described and figured a few species. Iredale (1943) listed a large number of generic and specific names based on small shell differences, but many of these names are probably synonyms of a few variable and widespread species (McMichael 1967; Smith, B.J. & Kershaw 1979; Morton, B. 1980c, 1982c; Kuiper 1983). Kuiper (1983) reviewed the Australian Sphaeriidae.

The morphology and physiology of Australian corbiculoids have not been studied. However, the biology and life history of some extralimital species has received considerable attention and this work forms the basis of the present account. The valves are thick and heavy in the large estuarine clams (for example, *Polymesoda*, *Batissa*), but thin and translucent in the freshwater 'fingernail shells' (*Pisidium*) and the 'pea shells' (*Sphaerium*). Up to three cardinal teeth occur on the hinge of each valve and there are two, usually lamellar, lateral teeth anteriorly and posteriorly. The ligament is opisthodetic and parvincular. Corbiculoids are (primitively) dimyarian and the anterior and posterior adductor muscles are subequal (Boss 1982; Britton & Morton 1982). The pallial line is simple and, if present, the sinus is shallow and indistinct. The mantle is usually unfused. Siphons are short and not well developed into tubes except in *Sphaerium* species (Britton & Morton 1982; Kuiper 1983; Morton, B. 1989).

The majority of members are filter-feeders either living infaunally (Corbiculidae) or amongst macrophytes (Sphaeriidae). The feeding biology is mirrored by modifications of the alimentary system, particularly the stomach. Posterior to the foot, two pairs of synaptorhabdic gills unite with each other (Britton & Morton 1982). The gills have interlamellar septa of variable morphology. The foot is byssate only in the young, and generally wedge-shaped and strong in adults, for burrowing and ploughing (Benthem Jutting 1953; Yonge 1962; Clarke 1973; Britton & Morton 1982).



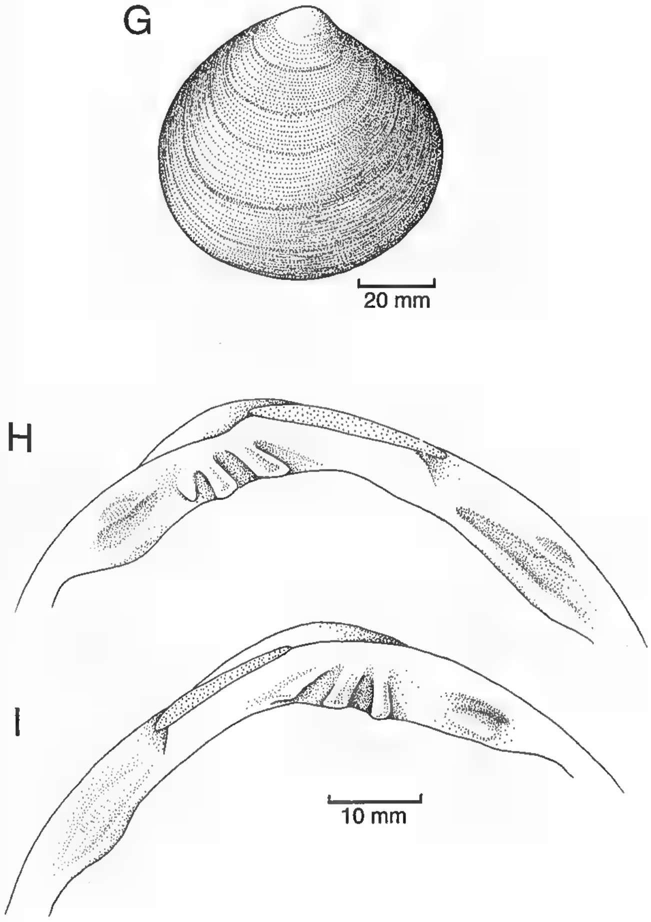


Figure 8.35 Family Corbiculidae. A–C, *Corbicula* sp.: A, left shell valve, external view; B, right valve hinge; C, left valve hinge. D–F, *Batissa* sp.: D, left shell valve, external view; E, right valve hinge; F, left valve hinge. G–I, *Polydesma* sp.: G, left shell valve, external view; H, right valve hinge; I, left valve hinge. [S. Weidland]

The rectum passes through the ventricle and the pericardial gland is auricular (Boss 1982). The gonads lie ventrally. Corbiculoids may be dioecious or hermaphroditic, or may vary reproductive strategies with environmental changes (Morton, B. 1982c, 1983c, 1985b, 1985c, 1986c).

Very little is known of the life history and ecology of Australian corbiculoid species. However, there is a growing literature on Asian corbiculids (see Britton & Morton 1980c, 1982b, 1986 and references therein; Morton, B. 1984b). Some species thrive in fast flowing steams and have become pests, in the economic sense, because they interfere with water reticulation systems (Smith, B.J. & Kershaw 1979; Morton, B. 1982c, 1983c).

The fossil history of corbiculoids from the Australian continent is largely unknown. *Corbicula* has been recorded from Tertiary deposits in South-East Asia (van de Vlerk 1931; Oostingh 1935; Benthem Jutting 1953). An extinct fossil corbiculid, *Surbula* (Upper Cretaceous), has been reported from Seymour Island, Antarctic Peninsula (Zinmeister & Macellari 1988). *Sphaerium* is known from Pliocene and Pleistocene beds in central North America (Herrington & Taylor 1958).

It is manifest, both in an Australian context and in a global context, that the corbiculoid classification requires a detailed re-assessment based on modern taxonomic methods (Britton & Morton 1980; Morton, B. 1982c). Individual variation observed among and between isolated populations suggests that a combined approach incorporating shell morphology, comparative and functional anatomy, and electrophoretic methods (for example, Günther & Hinz 1986) would be appropriate.

Family Corbiculidae

Members of the family Corbiculidae have triangular (with rounded edges) to oval, robust, commarginally ridged shells with a small umbo (Fig. 8.35A, D, G). Externally, the shell may be covered with a greenish to black, fibrous periostracum. They range in size from small (for example, *Corbicula* species, up to 30 mm in length) to moderately large (for example, *Polymesoda* and *Batissa*, about 100 mm in length). Each hinge has three cardinal teeth with the pivotal cardinal in the right valve, and one or two lateral teeth on each side of the umbo (Fig. 8.35B, C, E, F, H, I). In *Batissa*, *Corbicula* and *Corbiculina* the lateral teeth are transversely serrated, in *Polymesoda* they are smooth (Prime 1865; Benthem Jutting 1953; McMichael 1967; Smith, B.J. & Kershaw 1979).

Australian representatives include the predominantly brackish water genera, *Polymesoda* (= *Geloina*) and *Batissa*. A third genus *Corbiculina* includes freshwater species and is possibly endemic to Australia (see Iredale 1943; McMichael 1967). The number of species that occur in Australasia is unresolved, but is almost certainly fewer than the number of available names (Morton, B. 1977, 1982c; Smith, B.J. & Kershaw 1979).

The first species described from Australia was *Corbiculina australis*. It lives in the sandy beds of shallow, running streams and has an attractive shell that reaches 25 mm in length (Smith, B.J. & Kershaw 1979; Williams 1980). E.A. Smith (1882) provided the first list of Australian species. Iredale (1943) recognised sixteen species of *Corbiculina*, but Smith, B.J. & Kershaw (1979) have since pointed out that these may represent only one biological species. It is likely that a few endemic species exist in isolated localities in Australia. Corbiculids appear to be widely distributed throughout most parts of Australia except for the far south-west and Tasmania (McMichael & Iredale 1959; Smith, B.J. & Kershaw 1979).

The functional anatomy of corbiculids, particularly Australian species, is not well known. Recently, *Corbicula fluminea* has received considerable attention (see Britton & Morton 1982, 1986), and the functional morphology of *Batissa violacea* was described by B. Morton (1989). Tan Tiu & Prezant (1989b) have demonstrated seasonal variations in the crossed-lamellar microstructure of the shell of *Corbicula* species. They have also shown that these shells contain numerous microtubules, whereas the shells of *Polymesoda* species lack tubules (Prezant & Tan Tiu 1986; Tan Tiu & Prezant 1989a). Some aspects of the environmental physiology of Asian corbiculids are known. Osmolality and the effects of desiccation have been studied by Raj & Fergusson (1980), Byrne, McMahon & Dietz (1989) and B. Morton (1989).

Most species are infaunal filter-feeders. *Batissa* and *Polymesoda* exhibit pedal gape feeding (Morton, B. 1989). Corbiculids have a Type V stomach with two internal caeca but lack an appendix posteriorly. A long typhlosole enters the right caecum, passes across to the left caecum, and terminates anterior to the left pouch. The digestive diverticula also open into the caeca (Prashad 1920; Dudgeon 1980; Boss 1982; Britton & Morton 1982).

The reproduction and life history of Australian representatives is unknown. B. Morton has studied the reproduction of Asian *Corbicula* species (see Morton, B. 1982c, 1983c, 1986c and references therein). In general, corbiculids are dioecious with a single period of reproduction during summer, and produce veliger larvae without incubation (for example, *Polymesoda erosa*; Morton, B. 1985b). The two Asian species of *Corbicula* display quite different and variable reproductive strategies. *Corbicula fluminalis*, a winter breeder, is dioecious with a trend to protogynous, consecutive hermaphroditism, a strategy that is adaptive for the variable, lentic estuarine environment. No incubation occurs in *C. fluminalis*. *Corbicula fluminea* prefers freshwater lotic environments and is a protandric hermaphrodite that breeds in spring and autumn. It broods fertilised eggs in an inner gill pouch, to a pediveliger larval stage (200–240 μm) (Morton, B. 1977, 1982c, 1983c, 1986c; Britton & Morton 1982, 1986). In rapidly flowing water, brooding is a strategy that increases larval survival as the pediveliger is adapted for crawling. Subsequently, juvenile byssal attachment may be maintained for up to one year (Britton & Morton 1982). Throughout its natural and introduced distribution (North America), *C. fluminea* appears to be an opportunistic *r*-strategist with a range of temperature tolerance, shell plasticity, high fecundity and variable life history strategies (Britton & Morton 1982, 1986; Morton, B. this volume).

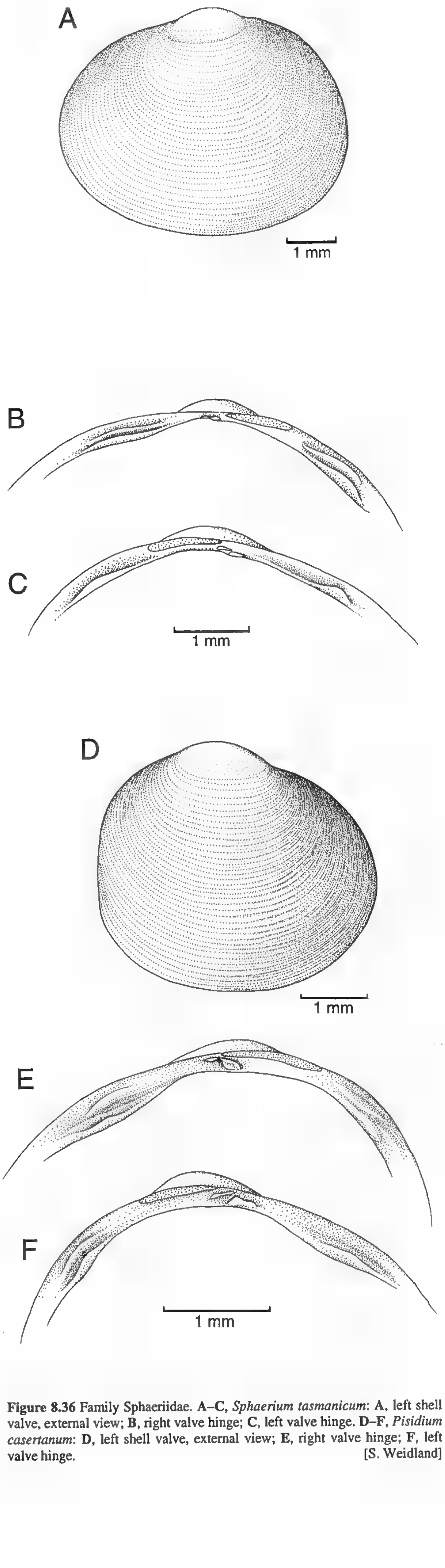


Figure 8.36 Family Sphaeriidae. **A–C**, *Sphaerium tasmanicum*: **A**, left shell valve, external view; **B**, right valve hinge; **C**, left valve hinge. **D–F**, *Pisidium casertanum*: **D**, left shell valve, external view; **E**, right valve hinge; **F**, left valve hinge. [S. Weidland]

Paralytic shellfish toxins have been reported from Asian *Corbicula*, but these were not associated with dinoflagellates (Ogata, Sato & Kodama 1989). The affinity of some corbiculids for fast-flowing water has made them pests, in the economic sense, because they block agricultural irrigation systems (Smith, B.J. & Kershaw 1979) and the cooling systems of nuclear power plants in North America (Boozer & Mirkes 1979; Kraemer & Galloway 1986). Flushing of systems with copper solutions can reduce corbiculid numbers, but is environmentally dangerous (Suresh & Mohandras 1990). In Asia and the Indian subcontinent, corbiculids are used as food for humans and poultry, and may carry trematode parasites (Prashad 1928, 1929; Benthem Jutting 1953). There appear not to be any published accounts of the use of corbiculids by Australian Aboriginals. However, staff at the Australian Museum, Sydney, have identified *Polymesoda* and *Batissa* from some Aboriginal middens in northern Australia and New Guinea.

Family Sphaeriidae

Sphaeriids have a minute to small shell (commonly 2–5 mm to a maximum of 15 mm). The equivalve shell is ovate to subovate in shape, thin and usually translucent (Fig. 8.36A, D; Smith, B.J. & Kershaw 1979, 1981; Williams 1980; Kuiper 1983). The valves have fine pores (punctae) with epithelial filaments (Robertson & Covey 1979). The narrow, curved hinge lacks a hinge plate (Fig. 8.36B, C, E, F). The left valve has two cardinal teeth and a single long marginal tooth on each side of the umbo. The right valve has one cardinal and two long marginal, lateral teeth. The very fine cardinal teeth lie almost parallel to the hinge margin. The ligament is short and weak. The mantle edges are unfused ventrally and smooth (*cf.* papillate). The pallial line is indistinct. In the genus *Sphaerium*, the two siphons are fairly well developed but short and smooth. The siphons are reduced in other genera (Benthem Jutting 1953; Cotton 1961; Herrington 1962; Keen & Casey 1969c; Clarke 1973).

Confusion over the family name for this group (homonymy with Sphaeriidae Erichson, 1845 for *Sphaerius* Waltl, 1838; Insecta) has recently been resolved and the use of Sphaeriidae Jeffreys, 1862 (1820) for *Sphaerium* Scopoli, 1777, was confirmed in ICZN Opinion 1331 (1985). For the history of this case, see Clarke (1970, 1973), Kuiper (1981), Spangler (1981) and Starobogatov (1981).

The first Australian sphaeriid to be described was *Sphaerium egregium* in 1846, from the Hunter River Valley (Kuiper 1983). Tenison Woods (1876) contributed three new species from Tasmania. Further species descriptions were provided by E.A. Smith (1882), Cotton & Godfrey (1938), Gabriel (1939) and Cotton (1953, 1961). Iredale (1943) introduced three new genera, *Sphaerinova, Australpera, Glacipisum*, for Australian forms and a further seven species. Iredale introduced these taxa with barely any description or differentiation and therefore, they are not recognised by current workers (see Smith, B.J. & Kershaw 1979; 1981; Kuiper 1983). Kuiper (1983) recognised twelve Australian species (including four new species) which he placed in either *Sphaerium* or *Pisidium*.

Very little is known of the anatomy of Australian sphaeriids. The most recent, detailed anatomical treatments of extralimital species are those of Herrington (1962) and Heard (1965). In sphaeriids, the gills are fused together behind the foot. The outer demibranch is much smaller and shorter than the inner one which has the function of brooding the young. The labial palps are generally small (Drew 1896; Herrington 1962). The narrow foot is grooved and has a small gland which produces a few, fine byssal threads in juveniles (Yonge 1962). Cotton (1961) reported some Australian representatives to be very active, utilising their mobile foot for movement. Sphaeriids are phytophagous filter-feeders. They have a Type IV stomach with a large hooked typhlosole and several groups of digestive diverticula (Drew 1896; Herrington 1962; Heard 1965; Keen & Casey 1969c).

The reproduction and life history traits of extralimital species have received considerable attention (see citations in Mackie 1979; Morton, B. 1985c, 1986c), but again, information on Australian species is lacking. In the taxa studied in the Northern Hemisphere reproduction takes place two or three times a year. Since the life cycle takes approximately one year, successive generations overlap (Hornbach, Wissing & Burky 1982; Morton, B. 1985c, 1986c). Sphaeriids are protandric simultaneous hermaphrodites (Morton, B. 1985c) and the eggs undergo direct development in anterior, inner gill pouches (Heard 1965, 1977; Zumoff 1973; Mackie 1979; Holopainen & Jónâsson 1989). Heard (1977) reported three developmental stages (embryos, foetal larvae & prodissoconch larvae) that occur in primary, secondary and tertiary sacs respectively. Before release the 'extra-marsupial' larvae may be either free in the interlamellar space or are byssally attached to the demibranch (Heard 1977).

Most species display mixed or variable life history tactics, or switching of strategies, for survival in ephemeral habitats or under highly variable environmental regimes (Mackie 1979; McKee & Mackie 1981; Mackie & Flippance 1983; Morton, B. 1985c). In general, sphaeriids living in ephemeral habitats show characteristics of *r*-strategists whereas those in perennial conditions tend to be *K*-strategists (Heard 1977; Morton, B. 1985c, 1986c). Hornbach *et al.* (1982) suggested that a 'bet-hedging' tactic best explains the life history characteristics of a population of a *Sphaerium* species that they studied. They discussed the life strategies of freshwater molluscs and concluded that sphaeriid bivalves show adaptive plasticity (see also Heard 1965). In addition to life history strategies that allow sphaeriids to live in variable environmental regimes, some species also show burrowing and aestivating behaviour which protects them from desiccation (Gale 1976; McKee & Mackie 1980). It is likely that Australian sphaeriid species are similarly equipped to survive seasonal drought.

McMichael (1967) and B.J. Smith & Kershaw (1979) suggested that these tiny bivalves could be dispersed by insects, birds or windstorms. However, until recently none of these mechanisms was observed. Entomologists (Soldan, Campbell & Papácek 1989) collecting insects in the *Eucalyptus* forests of Victoria observed *Sphaerium tasmanicum* attached to the middle legs of a water-boatman, *Sigara* species (Heteroptera: Corixidae). Only immature bivalves in a narrow size range (1.7–1.9 mm maximum length) were found attached to the insect. Apparently, the bivalves clamp their valves onto a claw of the middle leg of the insect and they were not found attached to the other legs. As corixids have fixed migratory habits and remain close to water, Soldan *et al.* (1989) considered the association to be a sphaeriid dispersal adaptation.

Further research is required on the taxonomy (including anatomical studies) and ecology of Australian sphaeriid species and will, no doubt, prove very rewarding. Distributional studies of populations will probably indicate that these, along with other freshwater molluscs, are important environmental indicators.

Superfamily VENEROIDEA

Veneroideans are shallow, burrowing, marine and estuarine bivalves that are infaunal filter-feeders. They are dimyarian, having a pair of adductor muscles and pedal retractor muscles. Each pair is subequal, with an anterior and posterior component. Veneroideans can be distinguished from other bivalves within the Heterodonta by shells that usually have prosogyrous umbos, three cardinal teeth in each valve, and a pallial sinus. Anterior lateral teeth sometimes occur; posterior ones are not present, although the inner edge of a shallow trough often occurring on the dorsal posterior margin of the right valves of venerids is sometimes mistaken for one. This trough allows for a slight insertion of the left valve into the right (for example, in species of *Pitar*, *Antigona* and *Globivenus*). The ligament is wholly posterior to the umbo and longitudinally elongate, comparable to a cylinder split on one side with the severed edges inserted in each valve at the nymph, an often raised area of the hinge plate (Fig. 8.37A, C). The ligament is often set in a grooved escutcheon between the valves.

One large family, Veneridae, and four small families, Petricolidae, Glauconomidae, Cooperellidae and Turtoniidae, compose this group, according to Boss (1982). Keen (1969j) included Rzehakiidae as well. Only the first three families occur in Australia. The Cooperellidae are represented solely by the American marine genus *Cooperella*, which has three species. Rzehakiidae is represented solely by the fossil European genus *Rzehakia*. The family Turtoniidae is represented by the sole, extant member, *Turtonia minuta*, which is marine, circumboreal and matures at about 1.5 mm in length (Ockelmann 1964).

The following anatomical description of Veneroidea derives from Boss (1982), or as noted (see also Figs 8.37–8.40). The mantle consists of two simple folds and an inner duplex fold, and opens broadly into an anterior ventral pedal gape. The inner mantle folds fuse posteriorly, usually to form two siphons, inhalant and exhalant, which can be separate or partly to fully fused, and terminally papillate. There are two synaptorhabdic gills, one on each side of the body. Each gill consists of an inner and an outer sheet of connected lamellae. These are folded back on themselves to form the inner and outer demibranchs. The lamellae are plicate, each lamella having several vertical folds. The lamellar surface is embedded with small rod-like units, the filaments, on which are cilia that create the currents for directing trapped food. The filaments are heterorhabdic, that is, of two types: larger ones at the inner base of the folds, and smaller ones elsewhere. The outer, usually smaller demibranch has a supra-axial extension, and the gills are usually united behind to form a separate suprabranchial chamber.

Most, but not all adult veneroideans are non-byssate (unattached) with an active, powerful and compressed foot. They have a globose, Type V stomach (Purchon 1960a, 1985) in which the style and midgut are united, and a ridge, the major typhlosole, which enters the right then the left caecum (tube-like extensions). A left pouch adjoins the left caecum, and the openings of the digestive diverticula open from both caeca and the pouch. The heart generally has a bulbous posterior aorta. Further description of the structure and function of veneroidean viscera can be found in the works of Purchon (1955b), Owen (1959), Ansell (1961), C.C. Jones (1979) and Boss (1982). Most members are dioecious and larviparous, and sometimes protandrous and incubatory. They are marine, sometimes brackish, shallow, burrowing, infaunal filter-feeders.

Family Veneridae

Veneridae is a circumglobal family of marine, occasionally brackish water bivalves with over 500 species. Venerids have three simple or bifid cardinal teeth in each valve (Fig. 8.37A, C). A lunule and an escutcheon (Fig. 8.37C) are usually present, and anterior lateral teeth are sometimes present, traits that are absent in Petricolidae and Glauconomyidae. Internal marginal structures include crenulations (Venerinae, Chioninae and Sunettinae), oblique striations (*Transennella*), or a commarginal groove (*Lioconcha*). The cardinal teeth can be pustuled (*Placamen*); the nymph can be rugose (*Mercenaria*, *Chione (Lirophora)*, *Anomalocardia*, and *Amiantis*), striated (*Meretrix*), or subdivided and sculptured into pseudocardinals (*Tivela*).

The shells range in size from 4 mm to over 100 mm, and vary in shape from circular, ovate, subquadrate or trigonal to elongate; they usually have a pallial sinus (Fig. 8.38). The aragonitic shell structure is arranged in two layers of crossed-lamellar or homogenous crystals or in three layers: a composite prismatic layer outside, a middle crossed-lamellar or homogeneous layer, and a complex crossed-lamellar inner one (Shimamoto 1986). The umbo usually occurs near or at the middle of the dorsal margin. The posterior adductor muscle is usually greater than or sometimes equal in size to the anterior one. A grooved escutcheon often surrounds the ligament, which is inserted in the nymph. The lunule can be incised, and impressed, flat or protrusive. Shells are smooth or strongly sculptured; the sculpture is mainly commarginal, but can be cancellate, or with radial or divaricate ribbing, commarginal lamellae and, in some rare cases, posterior spines. The periostracum varies from being generally absent to occasionally thin and glossy, or thick and sculptured with cemented sand (*Samarangia*, *Granicorium*). Few adult venerids retain a functional byssal gland (some species of *Venerupis*, *Transennella*, *Chione*) (Jones, C.C. 1979).

The description of venerid anatomy presented here is derived from the works by Ansell (1961), Boss (1982), and C.C. Jones (1979); the latter having many extensive, detailed anatomical illustrations. The large, wedge-shaped, compressed, heeled foot is not grooved and is used mainly for burrowing. Papillae or sometimes arborescent tentacles occur along the mantle margins. The posterior inhalant siphon might be partly or wholly fused with the exhalant siphon. The terminally papillose siphons are only rarely covered with a protective organic matrix when extended from the shell. The inner lobes of the two bilobed gills are twice as thick as the outer ones. The labial palps are small to moderate in size. Water passes over the gills, where oxygen is extracted and food particles are trapped and collected along a ventral groove between and on each lobe. The food rope moves anteriorly to the palps and then to the mouth at the anterior dorsal edge of the foot. Food then passes posteriorly through a short oesophagus, to the stomach, midgut and intestine. Faecal pellets are expelled through the anus near the exhalant siphon.

Most venerids are bisexual, although some (*Mercenaria*, *Venus*) are protandrous (Jones, C.C. 1979; Boss 1982). The gonads surround the digestive system. Ova and spermatozoa are released into the mantle cavity, and then usually broadcast via the exhalant siphon. Some genera with minute shells brood young (for example, *Gemma*, *Parastarte*, *Psephidia*, and *Transennella*), and *Liocyma* species have direct development (Sellmer 1967; Boss 1982). The fertilised gametes develop into planktonic trochophore larvae, then soon after form a straight hinge, two valves and a velum during the planktotrophic veliger stage (Prodissoconch I stage). Umbones and species-specific traits form during the subsequent umboned stage (Prodissoconch II). At this stage the larvae settle down to become byssally attached juveniles (Goodsell, Fuller, Eversole, Castagna & Lutz 1992). Venerids can be sexually mature within one year (Sellmer 1967), with individuals living more than 40 years (Peterson 1986).

The classification of Veneridae began with a scattered group of genera proposed during the first half of the 19th Century. These were eventually grouped into four subdivisions: Dosiniana, Meretriciana, Venusiana and Tapesiana (Deshayes 1853). By 1936, 11 venerid groups were recognised by Frizzell (1936), who raised these groups to familial rank, and raised Veneridae to the rank of superfamily. His groups included Veneridae, Gemmidae, Circidae, Sunettidae, Meretricidae, Pitaridae, Dosiniidae, Cyclinidae, and Tapetidae, as well as two further families he created, Clementiidae and Chionidae. Although Iredale & McMichael (1962) retained some of Frizzell's groups as families, Frizzell's rankings were rejected by most later workers (Keen 1969j, 1971; Fischer-Piette & Testud 1970; Fischer-Piette & Metivier 1971; Fischer-Piette & Vukadinovic 1972, 1975, 1977; Fischer-Piette 1975; Habe 1977), who continued to view Veneridae as a large, heterogeneous family comprising several subfamilies.

Adding one more group to Frizzell's (1936) list, Keen (1969j) recognised 12 subfamilies (also recognised by Vaught 1989): Venerinae, Chioninae, Dosiniinae, Pitarinae, Tapetinae, Circinae (since renamed Gafrariinae), Sunettinae, Clementiinae, Samarangiinae, Gemminae, Meretricinae, and Cyclininae. She recognised 51 extant genera and an additional 70 *non sensu stricto* extant subgenera. The first nine subfamilies listed occur in Australia, and include 26 genera and an additional 15 *non sensu stricto* subgenera. Venerinae (50+ species), Chioninae (100+ species), Dosiniinae (100+ species), Pitarinae (100+ species) and Tapetinae (50+ species) are large subfamilies with several genera and/or subgenera. Except for Pitarinae, Sunettinae and Meretricinae, relatively recent revisions are available for all subfamilies (Fischer-Piette 1968, 1969, 1975; Fischer-Piette & Metivier 1971; Fischer-Piette & Vukadinovic 1972, 1975, 1977).

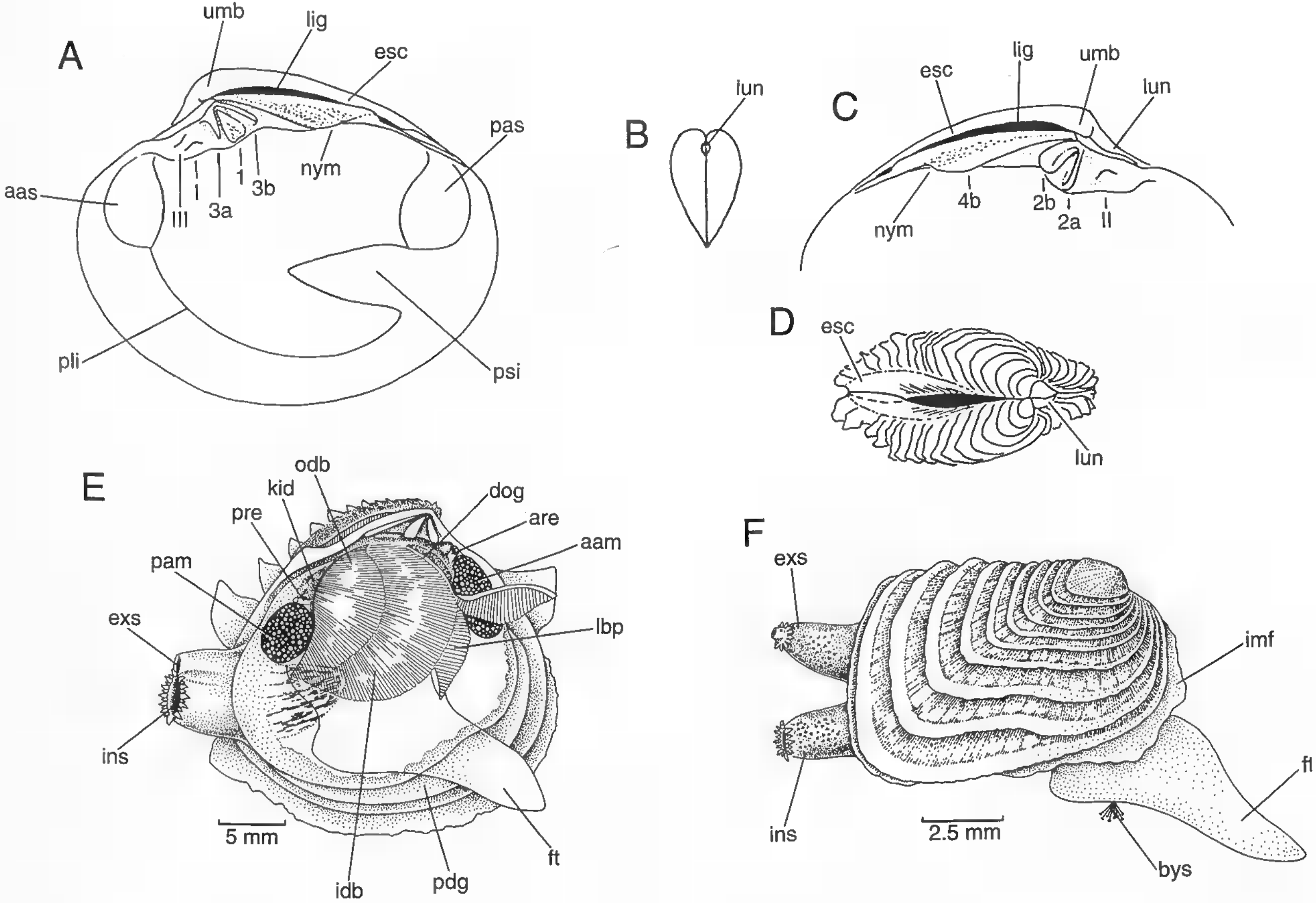


Figure 8.37 Family Veneridae. **A–C**, *Amiantis callosa*, shell and hinge features (cardinal teeth – 1, 2a, 2b, 3a, 3b, 4b; lateral teeth – I, II, III): **A**, right shell valve, internal view; **B**, anterior profile; **C**, hinge of left shell valve, cardinal teeth, anterior lateral teeth and a developed nymph are present. **D**, *Circomphalus foliaceolamellosa*, dorsal view. **E**, anatomy of *Placamen callophylla*, showing organs and ciliary currents (arrows). **F**, *Irus irus*, right valve, with siphons and foot extended. **aam**, anterior adductor muscle; **aas**, anterior adductor muscle scar; **are**, anterior retractor muscle; **bys**, byssus; **dog**, distal oral groove; **esc**, escutcheon; **exs**, exhalant siphon; **ft**, foot; **idb**, inner demibranch; **imf**, inner mantle fold; **ins**, inhalant siphon; **kid**, kidney; **lbp**, labial palp; **lig**, ligament; **lun**, lunule; **nym**, nymph; **odb**, outer demibranch; **pam**, posterior adductor muscle; **pas**, posterior adductor muscle scar; **pdg**, pedal gape; **pli**, pallial line; **pre**, posterior retractor muscle; **psi**, pallial sinus; **umb**, umbo. (D, after Cox 1969a; E, F, after Morton, B. 1985d) [A–D, M. Harte; E, F, R. Plant]

Earlier revisions of *Sunetta*, *Meretrix*, and *Tivela* are also available (Fischer & Fischer-Piette 1938; Fischer-Piette & Fischer 1939, 1941, 1942). The controversial taxonomy of Veneridae has led some to suggest that the family might be polyphyletic (Keen 1969j; Boss 1982). Insufficient research on extant genera still hinders adequate taxonomic treatment.

The family can be divided into two sections, roughly, but not exclusively characterised as follows: those clams with generally weak surface ornamentation, smooth margins, well-developed pallial sinuses, and well-developed anterior lateral teeth (Pitarinae, Dosiniinae, Meretricinae, Sunettinae, Clementiinae, some gafrariinines, some tapetines); and those clams with pronounced surface ornamentation, crenulate margins, little or no pallial sinus, and little or no anterior lateral teeth (Venerinae, Chioninae, Gemminae, Samarangiinae).

The family Veneridae is one of the largest bivalve groups in Australia, with more than 150 species in the fauna. Lamprell & Whitehead (1992) documented and illustrated 148 of these species; other workers have documented solely southern representatives (Cotton & Godfrey 1938; Cotton 1961; Macpherson & Gabriel 1962; Ludbrook 1984; Ludbrook & Gowlett-Holmes 1989). Previous documentation of northern representatives has been incomplete and often based on obsolete taxonomy (Allan 1959; Rippingale & McMichael 1961).

Of the 26 genera found in Australian waters, two, *Granicorium* (one species, *G. indutum*) and *Katelysia* (three species), are endemic, as are the subgenera *Bassina sensu stricto* (two species, *B. (Bassina) pachyphylla* and *B. (B.) jacksoni*), *Gouldia (Gouldiopa)* (one species, *G. (Gouldiopa) australis*), and *Circe (Redicirce)* (two Australian species, *C. (Redicirce) mistura* and *C. (R.) consola*). Most species of *Tawera* (eight Australian species), *Dosinia (Austrodosinia)* (nine Australian species, according to Fischer-Piette & Delmas 1967; for example, *D. juvenilis*), *Notocallista* (two Australian species, *N. disrupta* and *N. kingii*) are restricted to Australia. All three *Katelysia* species (*K. scalarina*, *K. rhytiphora* and *K. peronii*) intergrade morphologically (Roberts 1984a), but have distinct tidal ranges or breeding seasons; they are often predominant in the shallow estuarine and marine embayments of southern Australia (Nielsen 1964; Roberts 1984a).

In addition to these endemic taxa, a rough perusal of the literature indicates that there are several venerid species of more widely dispersed taxa that have been found only in Australia, to date. The total number of species, derived from the list provided by Lamprell & Whitehead (1992) with the addition of the endemic (or mostly endemic) taxa mentioned above (taking into account some overlap), indicates that 64 species, or roughly 43% of all known Australian venerids are endemic.

Venerids usually burrow in muddy or sandy habitats but vary considerably in lifestyles, occurring in coral reefs and lagoons, mangroves, intertidal flats, bays, estuaries, estuarine lagoons, surf zones, offshore and in the deep sea. Most burrow to shallow or medium depths in soft intertidal or subtidal substrata. Once buried, some envelop themselves in coats of fine sediments (for example, species of *Compsomyax*, *Liocyma*, *Callocardia*; P. Scott personal communication), some of which contain broods (*Liocyma*); others create siphonal coats (*Pitar subpellucidus*; M. Harte personal observation). Some nestle among rocks and clumps of byssally attached bivalves, or bore into stiff clay.

Venerids may occur in dense, large beds or sparsely and singly. For many species, food uptake ceases with exposure at low tide, and data suggest that digestion is tidally cyclic (Jones, C.C. 1979; Peterson 1991). Many subtropical and tropical intertidal venerids and other bivalves have been observed to 'pop' from their substratum positions and lie flat on the surface just as low tide turns and the first flows of high tide return (M. Harte personal observation; K. Lamprell personal communication). Venerids are eaten by a host of carnivorous gastropods, especially muricids and naticids, that bore through the shell. Starfish, crustaceans, fish and waterfowl also take their toll, especially on juveniles, and fish are known to nip at extended feeding siphons (Carter, R.M. 1968). Most animals are restricted to burrowing deeper and/or rapidly to escape predation, but at least one bivalve, a species of *Glycydonta*, is known to hop away from predators (Kilburn & Rippey 1982; B. Collins personal communication).

Venerids form the basis of minor fisheries worldwide, and are cultured as well. They can be seasonally toxic from the ingestion of certain phytoplankton, or contain toxins from local coastal pollution (for example, Shumway 1990; Sadiq & McCain 1993; Bebianno, Serafim & Rita 1994). Some bivalves (for example, species of *Saxidomus*) sequester toxins from ingested phytoplankton in their siphons, deterring predation (Kvitek & Beitler 1991).

In subtropical and tropical Australia, combinations of species of *Antigona*, *Anomalodiscus*, *Placamen*, *Tawera*, *Timoclea*, *Circe*, *Gafrarium*, *Pitar*, *Callista*, *Costacallista*, *Tapes*, *Marcia*, sometimes *Paphia* and *Sunetta*, and the rare *Clementia* occur in tidal flats and seagrass beds of mud and sand (Peterson & Black 1987; Peterson 1991; Lamprell & Whitehead 1992). In northern coral lagoons and reefs, some species of *Periglypta* burrow as deep as 200 mm at the base of coral heads, and *Lioconcha*, *Globivenus* and certain species of *Tawera*, *Timoclea*, *Glycydonta*, *Circe*, *Callista*, *Costacallista*, *Pitar*, and *Tapes* burrow in coral lagoons. These are mostly common Indo-Pacific tropical genera. *Bassina* occurs in tropical and temperate sandy mud banks. *Dosinia* occurs in these and shallower and/or more sheltered zones all around Australia. *Irus* nestles in sheltered crevices, or under coral and rock. *Callocardia* and *Granicorium* are relatively deep-water genera, known only from off the east coast in depths of 70–120+ m. In the temperate south, *Irus* and *Venerupis* species nestle in mussel clumps, gravelly sand or mud in sheltered crevices, or in littoral seagrass root mats, *Eumarcia* lives in beds in the sand and mud of estuaries or tidal inlets, *Katelysia* ranges from the sandy shores of lower littoral zones (*K. scalarina* and *K. rhytiphora*) to the sandy mud of estuarine midlittoral zones (*K. peronii*), *Notocallista* species often associate with those of *Tawera* in clean sand with high current flow in subtidal depths of 10–40 m. *Circe* occurs commonly in good current flow areas of fine sand and silt in gulfs. *Placamen* occurs in high current flow sand-areas, 10–40 m deep, often with *Circe*. *Dosinia* occurs in good current flow areas of sand and silt from 5–20 m deep, sometimes in association with the seagrass *Posidonia*. *Bassina* lives sublittorally (for example, 30 m) in sand, usually associated with *Posidonia*. *Tawera* is abundant in sand areas of good current flow on medium to high energy coasts from 5–30 m deep (Ludbrook & Gowlett-Holmes 1989). *Sunetta* lives in littoral and sublittoral sand, sometimes to 90 m (Lamprell & Whitehead 1992), and *Gomphina* species occupy littoral and sublittoral surf zones (Lamprell & Whitehead 1992; M. Harte personal observation). In addition, the effects of competition and tidal elevation on Australian venerids have been studied extensively (Peterson & Black 1987, 1988, 1991; Peterson 1991).

Venerines and chionines are mostly shallow, intertidal burrowers, characterised by strongly ornamented shells of lamellate or cancellate sculpture, short triangular pallial sinuses, and crenulate and often partially overlapping margins. Hinge teeth are solid and often flexed. Venerines (*Venus*, *Antigona*, *Circomphalus*, *Chamelea*, *Clausinella*, *Globivenus*) have pustular lateral teeth; the subfamily occurs globally, ranging from temperate to tropical climes. Conchological data indicate that *Periglypta* is a subgenus of *Antigona* and that *Ventricolaria* is synonymous with *Globivenus*, conventions used by Lamprell & Whitehead (1992). In Australia, there are 12 venerine species: nine species of *Antigona* and three species of *Globivenus*.

Chionines (*Chione*, *Anomalocardia*, *Austrovenus*, *Anomalodiscus*, *Bassina*, *Eurhomalea*, *Humilaria*, *Irusella*, *Mercenaria*, *Placamen*, *Protothaca*, *Tawera*, and *Timoclea*) have no lateral teeth. The subfamily occurs globally, from Arctic and subpolar to tropical climes. Although considered a subgenus of *Anomalocardia* (Keen 1969j; Vaught 1989), subtle conchological differences (radial sculpture, smooth nymphs; Harte 1992) indicate that *Anomalodiscus* is probably a distinct genus (perhaps more closely allied with *Timoclea*) with a convergent profile. Fischer-Piette & Vukadinovic (1977) reclassified *Eurhomalea* as a chionine, not a tapetine, as assigned by Keen (1969j). Similarly, preliminary biomolecular data indicate that the American genus *Irusella* is a modified chionine allied with *Humilaria* and *Protothaca*, not a tapetine (M. Harte personal observation) and that *Austrovenus* is a distinct genus from *Chione* (Harte 1992). Although *Placamen* and *Bassina* are often confused (for example, Oliver 1992), the two genera are quite distinct (Matsukuma & Yoosukh 1988). In Australia, chionine species include three species of *Bassina*, one species of *Anomalodiscus*, seven species of *Placamen*, some five or more species of *Timoclea* and eight species of *Tawera*.

Sunettines have smooth, usually laterally compressed oval to elongate shells with crenulated margins, a small to medium pallial sinus, and a ligament deeply sunk into a narrow, sharply defined escutcheon. These traits indicate that they are shallow to moderately deep, fast burrowers. Hinge teeth are relatively blunt and straight, with fairly well-separated, well-developed lateral teeth. The few subgenera (Keen 1969j) of the sole extant genus *Sunetta* are often raised to generic level by Pacific workers (for example, Kira 1962; Habe 1977). The genus is primarily tropical and subtropical, ranging from the west Pacific to the west Indian Oceans and contains roughly two dozen species. In Australia there are four species of *Sunetta* (for example, *Sunetta vaginalis*).

Gafrariines have little or no pallial sinus, indicative of a very shallow existence. The internal shell margins can be smooth (most *Circe*) or crenulate (most *Gafrarium*). The shells are moderately to strongly ornamented, usually with divaricating sculpture that aids burrowing (Seilacher 1984), and are either relatively large and compressed, as in *Circe*, or smaller and more obese (*Gafrarium*). Several *Circe* subgenera of minute size (*Laevicirce*, *Microcirce*, *Privigna*) occur in the mid to western Pacific. The Australian taxon, *Circe (Fluctiger)*, is based on a small, very worn specimen (Lamprell & Whitehead 1992), and thus, is of dubious status. The African genus *Comus* has characteristics of both *Gafrarium* and *Circe*. The minute American genus *Gouldia* lacks divaricating sculpture. Hinge teeth are straight, blunt and radiating, with well-developed lateral teeth. In Australia, a rare subgenus, *Circe (Redicirce)*, shows some dosiniine affinities. The subfamily occurs globally, primarily in tropical Indo-Pacific zones but ranging into temperate ones. Subgenera (Keen 1969j) are often raised to generic level in the literature. In Australia, there are eight species of *Gafrarium*, nine species of *Circe sensu stricto*, and two species of *C. (Redicirce)*.

Dosiniines are fast, deep burrowers, widely rocking as they burrow vertically (Stanley 1970). The shells have smooth margins and are externally white, often compressed, sometimes with faint radial striations or marked with brown patches; the pallial sinus is large, acutely angular, and often directed dorsally. Lateral teeth range from virtually absent to quite well developed. The escutcheon ranges from nearly absent to bevelled and deeply excavated. The subfamily occurs globally, primarily in tropical Indo-Pacific zones but ranging into temperate ones. Keen (1969j) recognised a single genus, *Dosinia*, with several subgenera – *Asa*, *Austrodosinia*, *Dosinella*, *Dosinisca*, *Dosinorbis*, *Kereia*, *Pectunculus* and *Phacosoma*. Some Pacific workers have raised the subgenera to generic level (for example, Kira 1962; Habe 1977), whereas others have eliminated

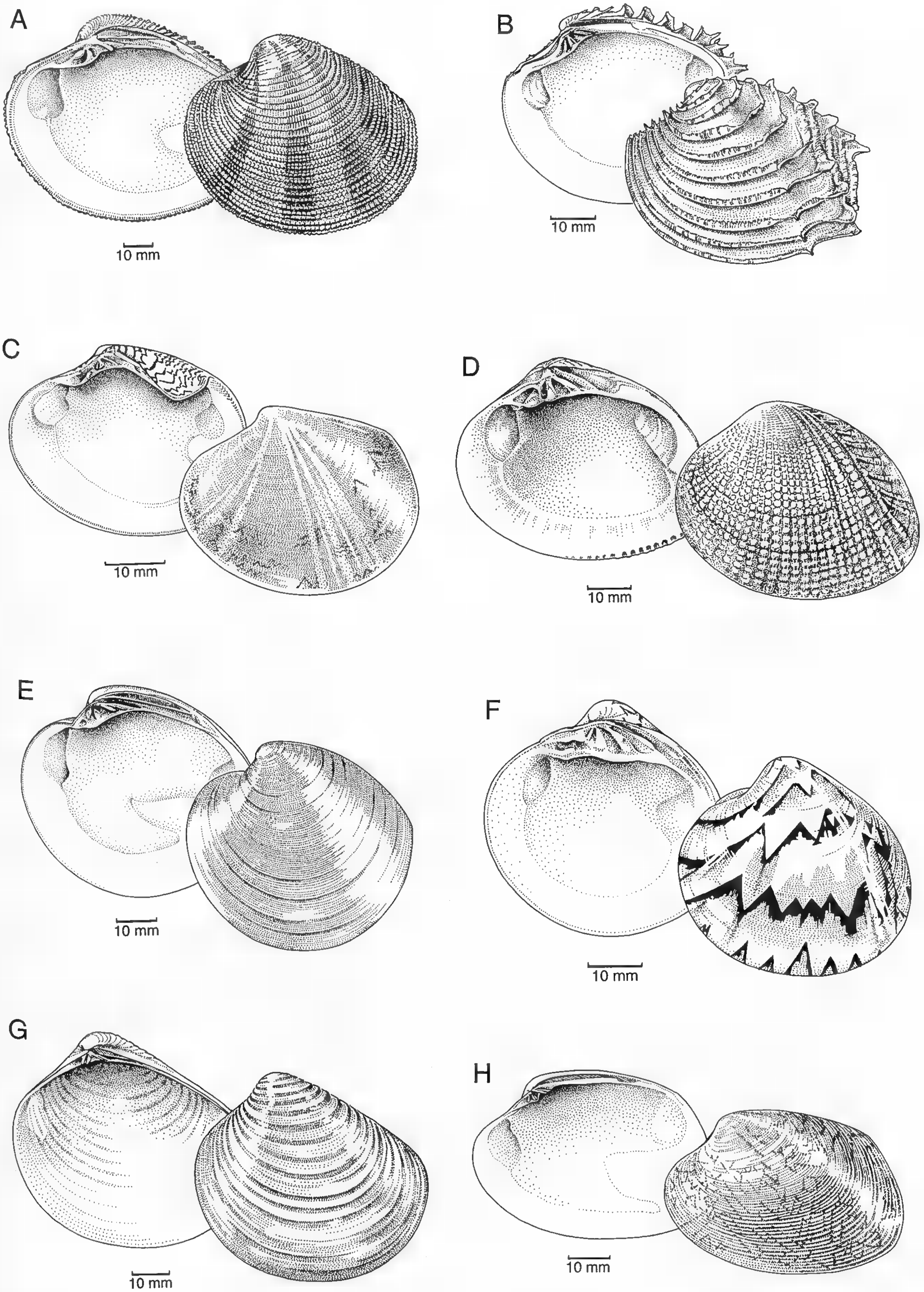


Figure 8.38 Family Veneridae. Shell valves, right valve in internal view, left valve in external view: **A**, *Antigona (Antigona) chemnitzii* (Venerinae); **B**, *Bassina (Callanaitis) disjecta* (Chioninae); **C**, *Sunetta perexcavata* (Sunettinae); **D**, *Gafrarium tumidum* (Gafrariinae); **E**, *Dosinia caerulea* (Dosiniinae); **F**, *Lioconcha castrensis* (Pitarinae); **G**, *Clementia papyracea* (Clementiinae); **H**, *Tapes dorsatus* (Tapetinae). [R. Plant]

them, considering their definitions too ambiguous (Lamprell & Whitehead 1992). There are 30 or more Australian species, most of which are tropical. Iredale (1929b, 1930b) proposed several dosiniine genera (*Bonartemis*, *Pardosinia*, *Fallartemis*, *Meridosinia*, *Semelartemis*) that were suppressed as synonyms by later workers (Fischer-Piette & Delmas 1967; Keen 1969j).

Pitarines (*Pitar*, *Agriopoma*, *Amiantis*, *Callista*, *Callocardia*, *Lepidocardia*, *Lioconcha*, *Macrocallista*, *Megapitaria*, *Notocallista*, *Saxidomus*, *Transennella*, *Transenpitar*) are shallow to moderately deep burrowers ranging from mostly littoral and sublittoral to offshore depths. The subfamily occurs globally, primarily in tropical zones (all genera) but ranging into temperate zones (*Saxidomus*, some *Callista*, *Pitar*, *Transennella*). *Pitar* occurs globally; *Callista* occurs tropically; *Lioconcha* and *Callocardia* occur in the tropical Indo-Pacific; *Lepidocardia* is a small African genus; *Notocallista* is restricted to Australasia; the rest of the genera occur in the Americas. Pitarines are characterised by having a smooth or finely commarginally sculptured shell, well-developed lateral teeth that are relatively closely associated with the cardinal teeth, and usually smooth margins. The 3a and 1 cardinal teeth are closely parallel to each other. The shell may be quite colourful and the periostracum quite prominent and glossy, as in *Callista* and allied genera (*Macrocallista*, *Megapitaria*, *Notocallista* and *Lepidocardia*). Habe (1977) proposed dividing the subfamily, placing *Callista* and *Lioconcha* with their respective allied genera into their own subfamilies. Keen (1969j) considered *Notocallista* a genus, but its callistine affinities have led other workers to accord it subgeneric status in *Callista* (Lamprell & Whitehead 1992). In Australia, pitarine species include 20+ species of *Pitar*, nine species of *Callista*, one species of *Callocardia*, and five species of *Lioconcha*.

Clementiines are assigned to two genera and five or six species. They have very thin shells, smooth margins and no lateral teeth. The surface sculpture is finely commarginal, and may be overlain with undulating waves that affect the shell's interior. The hinge teeth resemble those of *Pitar*, but are thin and fragile. The subfamily is represented by two small, extant intertidal genera. *Clementia* occurs in the tropical Indo-Pacific and contains three or four species; the American genus *Compsomyax* consists of one temperate offshore species. The clementiine form suggests that they are moderately deep, fast burrowers. In Australia, one species, *Clementia papyracea*, is rarely found.

Tapetines (*Tapes*, *Eumarcia*, *Irus*, *Liocyma*, *Marcia*, *Paphia*, *Psephidia*, *Venerupis*) occupy several different habitats and niches: some are intertidal rock nestlers and estuarine and inlet inhabitants, others live on tidal flats, and in subtidal and surf zones. They are characterised by shells with smooth margins, and without lateral teeth, often with elongate posterior ends and ellipsoidal profiles. Hinge teeth are usually straight, relatively narrow and compressed, and often overhang a narrow hinge plate, the area on which the hinge teeth are based. The intertidal, mostly tropical genera, *Tapes*, *Paphia*, *Eumarcia*, *Katelysia*, *Marcia*, and the subtidal, temperate genera, *Liocyma* and *Psephidia*, have smooth to commarginal sculptured shells, sometimes with radial elements (some *Tapes*). The smooth, triangular *Gomphina* resembles other bivalve surf inhabitants. The nestling *Venerupis* and *Irus* tend to be cylindrical and have prominent commarginal sculpture, and sometimes radial sculpture (*Venerupis*). *Psephidia* is a western North American genus of small bivalves (from less than 10–20 mm). The subfamily occurs globally, primarily in tropical Indo-Pacific zones (*Eumarcia*, *Marcia*, *Paphia*, *Tapes*, *Venerupis* and *Irus*), but ranging into temperate (*Psephidia*, some *Tapes*, *Irus*, *Venerupis* and *Paphia*) and Arctic (*Liocyma*) zones. In Australia, tapetine species include eight species of *Tapes*, three species of *Gomphina*, five species of *Irus*, three species of *Katelysia* (see above), two species of *Marcia*, four species of *Paphia*, and five species of *Venerupis*.

Samarangiines are rare and little known, consisting of two tropical, generally deep-water genera, each represented by a single rare species occurring in deep channels off eastern Australia (*Granicorium indutum*) or in the Indo-Pacific (*Samarangia quadrangularis*); the latter has pustular lateral teeth whereas the former has none. They have no pallial sinus and solid, smooth shells covered by a thick sculptured periostracum of cemented sand, all indicating that samarangiines are slow, shallow burrowers. *Samarangia* has been found singly in inclusions along the edges of outer Pacific silt-free reefs (P. Clarkson personal communication) or in coral rubble from 3–30 m (Loch 1989; Lamprell & Whitehead 1992), and under rocks in volcanic black sand sediments in the western Indian Ocean (J. Drivas personal communication). Keen (1969j) places *Granicorium* within Tapetinae, but its lack of a pallial sinus, its *Samarangia*-like solid, flexed hinge teeth and sand-covered periostracum all indicate it belongs in the Samarangiinae.

Gemminae are a small, American, temperate to subtropical subfamily of minute, incubatory venerids, with crenulate margins, smooth shells, and no lateral teeth. The two genera, *Gemma* and *Parastarte*, are represented by three or four species.

Meretricinae (*Meretrix*, *Tivela*) are a subtropical to tropical subfamily occurring in Asia, Africa and the Americas. The subfamily is characterised by well-developed lateral teeth, smooth margins, a smooth surface and well-developed, sculptured nymphs. *Meretrix* is prosogyrous and has a striated nymph; it occurs in tidal flats and estuaries. *Tivela* is orthogyrous, and has nymphs that have developed into pseudocardinal teeth; it occurs in surf and subtidal zones, and off sand bars.

Cyclininae superficially resemble Dosiniinae, with their circularly shaped, relatively smooth shells. It is a small subfamily of two genera and roughly eight species that occur in tropical America (subtidal *Cyclinella*, roughly seven species) and on the tidal flats of tropical north-western Asia (one species). *Cyclina* has crenulate margins, is tinged purple and is more obese than a typical *Dosinia*. *Cyclinella* has smooth margins, is white and compressed, but with no distinct lunule.

Fossils indicate that Veneridae originated in the Cretaceous, beginning with the pitarines and branching into similar subfamilies, then blooming into the Middle and Late Tertiary. The family underwent a significant change about 38 million years ago, when the subfamilies Venerinae and Chioninae began to evolve in the Oligocene (Palmer 1927); these subfamilies constitute about one third of all extant venerid species. There are at least 40 extinct venerid genera (Keen 1969j). In Australia, extinct taxa include *Callistina* (Pitarinae), *Proxichione* (Chioninae) and *Dosinia (Dosinobia)*. Table 8.2, derived from Darragh (1965b, 1994, in preparation) presents a summary of the fossil record for venerid genera and subgenera in Australia.

The general shell morphology of basal subfamilies (for example, Tapetinae, Pitarinae and Dosiniinae) suggests the early evolution of a strategy that emphasised avoidance of exposure and predation mainly through fast and/or deep burrowing. Such venerids are

Table 8.2 The earliest known Australian fossil records for venerid taxa. Extinct taxa are indicated by an asterisk.

Late Palaeocene (63.6 mya): _Dosinobia_*, _Callistina_*

Late Eocene (40 mya): _Dosina, Dosinia_, _Fossacallista_*

Late Oligocene (30 mya): _Callanaitis, Kereia_, _Proxichione_*, _Striacallista, Tawera_

Miocene (23.7 mya)

Early: _Hina_*

Middle: *Katelysia*

Late: *Bassina, Placamen*

Pliocene (5.3 mya): *Gomphina, Notocallista, Phacosoma, Timoclea*

Early: *Gafrarium, Sunetta*

Late: *Chioneryx, Venerupis*

Quaternary (1.6 mya): *Irus*

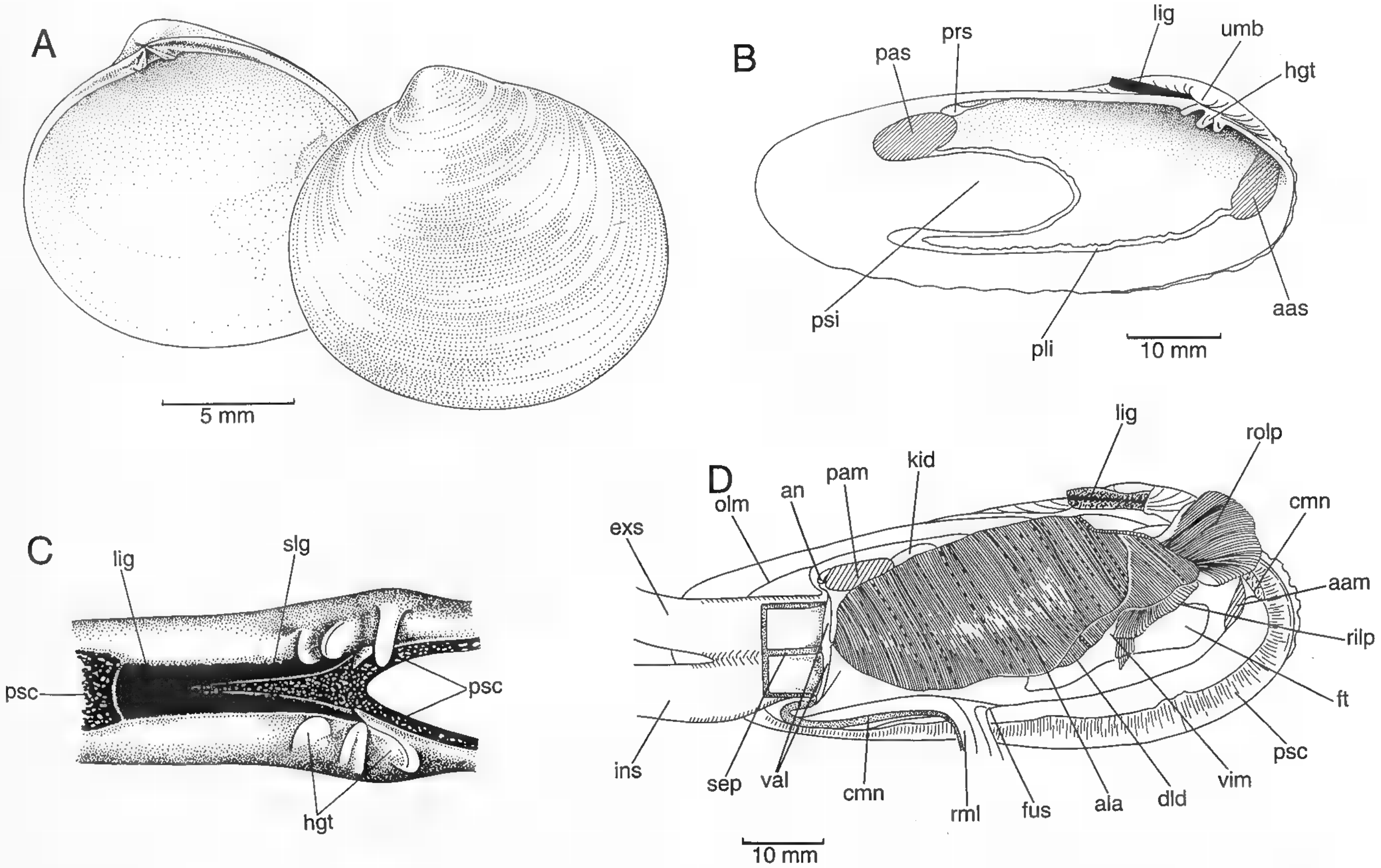


Figure 8.39 Family Petricolidae. **A**, *Mysia pellucida*, shell valves, right valve in internal view, left valve in external view. **B–D**, *Petricola pholadiformis*: **B**, left shell valve, internal view; **C**, hinge plate, ventral view with anterior end to the right, note valves are widely parted; **D**, internal organs, right shell valve and most of the right mantle lobe removed. **aam**, anterior adductor muscle; **aas**, anterior adductor muscle scar; **ala**, ascending lamella of the outer demibranch; **an**, anus; **cmn**, cut surface of the mantle; **dld**, descending lamella of the inner demibranch; **exs**, exhalant siphon; **ft**, foot; **fus**, anterior limit to the fusion of the mantle lobes; **hgt**, hinge teeth; **ins**, inhalant siphon; **kid**, kidney; **lig**, ligament; **mn**, mantle; **olm**, outer and middle lobes of the mantle edge; **pam**, posterior adductor muscle; **pas**, posterior adductor muscle scar; **pli**, pallial line; **prs**, posterior retractor muscle scar; **psc**, periostracum; **psi**, pallial sinus; **rilp**, right inner labial palp; **rml**, portion of right mantle lobe turned downwards; **rolp**, right outer labial palp; **sep**, septum in the siphonal process; **slg**, split in ligament; **umb**, umbo; **val**, valves in the base of the exhalant and inhalant siphons; **vim**, visceral mass. (B–D, after Purchon 1955b) [R. Plant]

characterised by their smooth shells or weak ornamentation and well-developed pallial sinuses, which are indicative of well-developed siphons, and hence, a relatively deep infaunal existence. This initial trend was followed by the development of a second strategy, as represented by the later evolution of Venerinae, Chioninae, Sunettinae, and certain genera of other subfamilies, emphasising anti-predatory defences and/or anchorage. This subsequent development was a response to the post-Mesozoic radiation of important intertidal predators, such as teleost fish, crabs, and carnivorous gastropods (Stanley 1977), and allowed fuller exploitation of the shallower depths. These more recent venerids are characterised by marginal crenulations and overlapping margins that deter predatory intrusions, and usually have shells with anchoring ornamentation such as commarginal lamellae.

Family Petricolidae

Petricolids are shallow, marine bivalves that nestle or bore into rock, mud and coral. The shell is usually oval to elongate (Fig. 8.39A, B). The valves have an anterior umbo, a short, rather stout ligament and a well-developed pallial sinus. The posterior adductor muscle is slightly larger than the anterior one. There are two cardinal teeth on the right valve (1 and 3b) and three on the left, with 2b bifid (Fig. 8.39C). The narrow hinge plate, with small, overhanging, radiating teeth is reminiscent of tapetine venerids. Sculpture is radial, cancellate and/or divaricate.

Although anatomically very similar to Veneridae, petricolids differ in having smooth mantle margins which open into a long pedal gape, extending along half the shell's length. The plough-shaped foot is byssally grooved, but not byssate in adults (Fig. 8.39D). The half-fused siphons are terminally fringed with irregular pinnate papillae at the inhalant orifice and conical papillae at the exhalant orifice. The outer gill lamellae are slightly smaller than the inner ones; the labial palps are large and muscular. As in most venerids, gametes are broadcast, and fertilisation is external, with the eggs developing into planktonic larvae.

The family comprises about 30 extant species classified into two genera, *Petricola* (containing eight subgenera) and *Mysia*, according to Keen (1969j) and Boss (1982). *Petricola (Claudiconcha)*, *P. (Velargilla)*, *Petricola sensu stricto*, and *Mysia* occur in Australia. *Petricola sensu stricto* is characterised by having oval to elongate shells, often distorted by nestling, with a shell sculpture of fine radial, divaricate or zigzag riblets (Keen 1969j). *Petricola (Claudiconcha)* is characterised by cancellate shell sculpture that is lamellose posteriorly, not unlike certain venerid species of *Irus* or *Venerupis*. *Petricola (Velargilla)* is similar to *Petricola sensu stricto*, but the shell is much thinner. Lamprell & Whitehead (1992) list two species, *P. (P.) divergens*, which nestles in littoral crevices from Queensland to southern Australia, and *P. (V.) rubiginosa*, which burrows in oozy muds in southern Australia; they indicates that a third species, *P. (V.) parvita* of South Australia, might be a smaller, more brightly coloured form of *rubiginosa*. A species of *Mysia* occurs in southern and eastern Australia (Macpherson & Gabriel 1962). This genus is characterised by having an orbicular profile, and smooth sculpture (Keen 1969j). The classification of *Mysia* is controversial. Keen (1969j), noting that *Mysia* resembles *Cyclinella* (Veneridae: Cyclininae), placed it in Petricolidae and this was recognised by later workers (Boss 1982; Vaught 1989). Cotton & Godfrey (1938) and Macpherson & Gabriel (1962) classified it in the Lucinoidea. The most recent taxonomic treatment of *Petricola* is by Lamy (1922b).

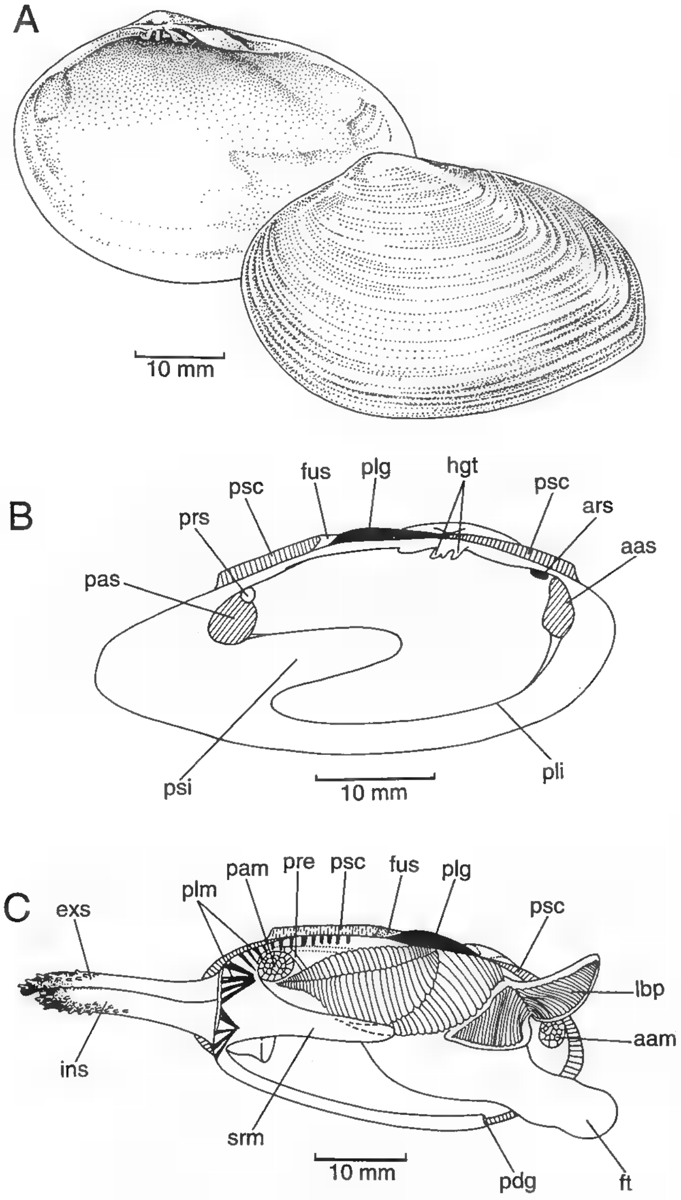


Figure 8.40 Family Glauconomidae. **A**, *Glauconome chinensis*, shell valves, right valve in internal view, left valve in external view. **B, C**, *Glauconome rugosa*: **B**, left shell valve, internal view; **C**, internal anatomy, right valve and mantle lobe removed. **aam**, anterior adductor muscle; **aas**, anterior adductor muscle scar; **ars**, anterior retractor muscle scar; **exs**, exhalant siphon; **ft**, foot; **fus**, fusion layer; **hgt**, hinge teeth; **ins**, inhalant siphon; **lbp**, labial palp; **pam**, posterior adductor muscle; **pas**, posterior adductor muscle scar; **pdg**, pedal gape; **plg**, primary ligament; **pli**, pallial line; **plm**, pallial retractor muscle; **pre**, posterior retractor muscle; **prs**, posterior retractor muscle scar; **psc**, periostracum; **psi**, pallial sinus; **srm**, siphonal retractor muscle. (B, C, after Owen 1959) [R. Plant]

Family Glauconomidae

Members of this small, Indo-Pacific tropical family live generally permanently embedded in the substrata of marine to brackish habitats in estuaries and mudflats in east and South-East Asia and Australia (Brandt 1974; Boss 1982). The shells are usually less than 50 mm long, and are elongate to elliptical, equivalve, thin, fragile, slightly inequilateral with elongate posteriors and rounded, angular or subquadrate extremities (Fig. 8.40A, B). The pallial sinus is long, horizontal, and finger-like. The posterior adductor muscle is somewhat rounded and the anterior one is narrow. The ligament has a posterior outer extension and attaches to the nymphs. Three separate cardinal teeth extend out from a narrow hinge plate in each valve; anterior lateral teeth, lunule and escutcheon are absent. The fine, slightly uneven, commarginally sculptured surface is covered by a strong, smooth or slightly wrinkled, green to yellowish-brown periostracum dorsally united between the valves.

According to Boss (1982), the mantle is fused ventrally except for a small, antero-ventral pedal gape and posterior elongate inhalant and exhalant siphons, which are almost totally fused together. These siphons are covered with papillae that are differentiated on the inhalant siphon into long and short tentacles. The labial palps are more or less broad and large. The foot is somewhat reduced, thick, linguiform, directed anteriorly, and non-byssate. In other respects, the anatomy (Fig. 8.40C) is generally similar to that of Veneridae. Owen (1959) described the anatomy in further detail.

According to Keen (1969j) and Boss (1982), members of the family (= Glaucomyidae, Glauconomyidae and Glauconomeidae) are represented by the sole genus *Glauconome*, of which there are 10 species or less (Boss 1982). According to K. Lamprell (personal communication) four species occur in Australia: *Glauconome plankta* occurs in brackish water in New South Wales; *Glauconome virens* occurs in the mud and sand of mainland estuaries in Queensland; *Glauconome rugosa* is found in the same habitat as *G. virens* and might be conspecific with it, occurring from Queensland to the Northern Territory; *Glauconome cerea* also occurs in the same habitat, ranging from Queensland to western Northern Territory. *Glauconome virens* and *G. rugosa* are the largest of the Australian species, reaching 80 mm in length.

Order MYOIDA

The myoids were relative late-comers in the history of bivalve evolution. They are burrowers, borers or nestlers, some of them lining burrows with calcareous secretions or building adventitious tubes. The fossil record of the order is fragmentary, perhaps because they occupy these niches, and the relationships and origins of the families remain obscure.

Myoid shells are relatively fragile, typically widely gaping ventrally, and are either homomyarian or heteromyarian. Most are edentulous though some have reduced hinge teeth, with at most one cardinal tooth in each valve. A chondrophore is developed in some families for ligament attachment. In the Pholadoidea, there is also a structure called the apophysis, a curved arm of shell emerging from beneath each umbo to which the pedal muscles attach, allowing the foot to be pulled directly fore and aft. The Pholadidae are unique in the Bivalvia in having secondary dorsal shell plates. The shells of most myoids are inequilateral and equivalve. The Corbulidae are exceptional in that their shells are mostly strongly inequivalve, the left valve being smaller and less convex than the right valve. The ligament may be massive in burrowing species or reduced or lacking in boring species.

Myoids have eulamellibranch ctenidia and most are suspension-feeders. A remarkable exception is seen in the wood-boring Teredinidae which, apart from the genus *Kuphus* (Kuphinae), have a wood-storing caecum and at least supplement their planktonic food resources by digesting the wood shavings produced from the deepening of their burrows. Equally remarkable is the extreme worm-like elongation of the body in the Teredinidae, in which the major organs are located behind the posterior adductor muscle.

The majority of myoids are gonochoristic spawners, as far as is known. However, pholads and teredines are oviparous or larviparous. Protandry is known to occur in some teredines.

Most myoids have long siphons which are usually combined. In deep-burrowing myoideans and hiatellids the siphons have a periostracal sheath and are so large that they cannot be withdrawn completely into the shell. Strong siphonal retractor and pallial muscles and a correspondingly deep pallial sinus are associated with the large siphons. There is extensive ventral fusion of the mantle lobes. Contractions of the muscular mantle creates powerful hydrostatic pressures within the mantle cavity associated with respiratory, feeding and burrowing activities. A unique siphonal feature seen in the Teredinidae is the presence of pallets. These are a pair of stemmed periostracal structures, usually impregnated with calcareous particles, which serve to block the entrance of the burrow when the animal retracts its siphons.

The four myoid superfamilies exhibit an array of habits including shallow and deep burrowing in soft or compacted sediments, nestling and shallow boring by mechanical means in rocks, boring by mechanical means in wood, and boring by chemical means in calcareous rocks. There are two possible evolutionary routes by which boring in hard substrata may have been achieved. Nestling and byssal attachment in rock crevices may have led to rock-boring; both byssal nestling and boring occur in the genus *Hiatella*. Alternatively, burrowing in soft sediments may have led to burrowing into compacted sediments by means of mechanical abrasion, and thence to mechanical boring in rocks. Deep-burrowing species are characterised by a powerful ligament that helps to contain the hydrostatic pressures developed within the mantle cavity, and by weak hinge dentition that allows the valves to be rocked around the dorso-ventral axis, so assisting the burrowing action. Dorso-ventral rocking of serrated shell valves against the burrow walls is the means of boring in compacted sediments. In the endolithic borers in which the shells are supported by the walls of the burrow, the function of the ligament is reduced and in these myoids the ligament is small or lacking. There is also a trend towards shortening of the shell and further reduction in hinge dentition to the extent that some forms have become edentulous. Evolution of rock and wood-boring in the Pholadoidea, in which the shells and musculature are highly specialised for mechanical boring, appears to have followed this route. Perhaps the most specialised mechanical boring is seen in those pholads and teredines that bore in wood. The endolithic gastrochaenids have developed boring, at least in part, by chemical means. As well as boring in calcareous rocks these animals secrete a calcareous lining around the walls of the burrow so that deposition and dissolution of shelly material both occur as the animal grows. The gastrochaenid *Eufistulana* retains, or has reverted to, an infaunal habit in soft sediments, building an adventitious calcareous tube (Morton, B. 1985a).

The Hiatelloidea is the oldest superfamily in the order, first appearing in the Permian. There are some doubtful records of pholads and teredines from the Carboniferous, but the first certain records of those families are from the Jurassic (Turner 1966; Hoagland & Turner 1981). All four families were well established by the Upper Jurassic although the relationships among them are not known. The most dramatic radiation occurred in the Pholadoidea when wood-boring adaptations arose, allowing that group to diversify in a previously unoccupied marine habitat.

Superfamily MYOIDEA

Myoideans are shallow to deep-burrowing heterodont bivalves, living in sand or mud substrata primarily in marine and estuarine habitats, but also occasionally in freshwater. The superfamily consists of four families: Myidae (cosmopolitan), Erodonidae (south-eastern Atlantic and Indo-Pacific), Spheniopsidae (eastern Pacific and New Zealand; Coan 1990) and Corbulidae (cosmopolitan) among which only the Myidae and Corbulidae occur in Australian waters. Boss (1982) estimates that the number of extant species in the Myoidea is approximately 150 or less, the majority of which belong to the extremely successful Corbulidae ('basket clams').

The four myoidean families differ considerably in shell morphology, ranging from the thin, posteriorly gaping, moderately large shells of the Myidae to the thick, non-gaping, small shells of the Corbulidae. Unquestionably these differences between families reflect strongly dissimilar lifestyles and shell requirements. Valves may be equivalve or slightly inequivalve (Spheniopsidae, Myidae) to moderately or strongly inequivalve (Corbulidae, Erodonidae). Sculpture consists primarily of commarginal ridges in the Corbulidae and Spheniopsidae (combined with traces of fine radial striae in some species). Radial ribs occur in the genus *Cryptomya* (Myidae) but in other myid genera and the Erodonidae sculpture is essentially lacking. Shells of myoideans are composed of aragonite arranged in three layers: an outer prismatic layer (homogeneous in Myidae); a crossed-lamellar middle layer and a crossed-lamellar inner layer (homogeneous in Myidae) (Boss 1982). The pallial line usually exhibits a sinus, although in many species this may be weak. The hinge line exhibits a well-developed chondrophore which supports the internal ligament (resilium). In addition the hinge shows a greatly simplified dentition, typically having one prominent cardinal tooth on the right valve and only occasional traces of any lateral teeth or, as in the Myidae, no hinge teeth at all. The periostracum is well developed, although often abraded through valve erosion.

Myoideans have anterior and posterior adductor muscles (the dimyarian condition, muscles equal or subequal in size) and a mantle fused along its ventral margin, with the exception of a small pedal gape anteriorly. As is typical of most eulamellibranchs, mantle eyes are not developed in the Myoidea, although some taxa (for example, *Mya* species) have pigmented, light sensitive areas on the siphon (Morton, J.E. 1967). The foot is well developed, especially in the deep-burrowing Myidae, and is equipped with a byssal gland for production of an anchoring byssus in the Corbulidae. Inhalant and exhalant siphons are joined along their length and are retractile, but vary in length depending on the family and genus. Projecting processes around the lip of each siphon aid in the filtration of large, particles of extraneous matter from water drawn into the branchial chamber. The ctenidia have both outer and inner demibranchs, the outer ones being the smaller. The stomach is of Type V (of Purchon's 1960a scheme) and is associated with a style sac and gastric shield. The circulatory system features a heart consisting of an elongate, quadrangular to rectangular ventricle penetrated by the rectum, a posterior aortic bulb and two sac-like auricles. Two sac-like kidneys are present. Members of the Myidae and Corbulidae are generally gonochoristic, but hermaphroditic individuals are sometimes detected (for example, in *Mya* species; Coe & Turner 1938). Spawning is external and the spermatozoa are of the aquatic type with a short head (= acrosome plus nucleus), short midpiece and a single flagellum (Franzén 1955; Popham 1979). The larvae are pelagic, and in *Mya* species, remain in the plankton for about two weeks (Coe & Turner 1938). Little is known of reproduction in the other families.

There have been no recent revisions of the Myidae, Corbulidae, Erodonidae, or Spheniopsidae (see Coan 1990). Several small papers were published by Lamy on the Myidae (1924, 1926, 1927) and Corbulidae (1941). Lamy (1926) also provided good illustrations of hinge features in the genera *Tugonia*, *Mya*, *Cryptomya* and *Sphenia*. The classification of Recent and fossil Corbulidae was last revised by Vokes (1945) and this work was basically adopted for use in the *Treatise on Invertebrate Paleontology* (see Keen 1969k).

A notable, though not ubiquitous, trend in the superfamily has been in the direction of morphological and behavioural modification for burrowing. This is particularly obvious in the Myidae, in which mobility has been sacrificed for a deep and permanent burrowing capability. In these myoideans, the shell valves tend to gape, and in many species the shell cannot contain the siphons, which may be very large. The shell is often fragile, and the hinge weak, with the teeth either poorly developed or entirely lacking, but with a well-developed chondrophore in the left valve.

The best known myoidean is the edible soft-shelled bivalve, *Mya arenaria*, which may attain a length of 150 mm. Originally confined to the Atlantic, it was deliberately introduced to the Pacific coast of the United States of America, and penetrates to upper estuarine regions. As a readily available and substantial mollusc, it has been a frequent subject for study. In this regard, *Mya* provides a useful exemplar of myoidean biology, although extrapolation from these researches to other myoidean families should be approached with caution, since *Mya arenaria* is a deep-burrowing species and is thus at one end of the adaptive spectrum of the superfamily.

The deep-burrowing myoideans maintain contact with the water by means of a single stout siphonal process, formed by the union of the inhalant and exhalant siphons. These are partitioned internally, and open as discrete inhalant and exhalant apertures. The siphonal process is relatively stiff and inflexible, and is generally protected against abrasion by a stout leathery sheath of periostracum. The structure is too large to be withdrawn wholly between the shell valves. Myoideans are essentially immobile, their only movement being to push slowly further downwards into the substratum as they grow. Young of *Mya* species are byssally attached, with an active foot. As development proceeds, the shell becomes more vertical. The foot assumes less importance as the animal grows, to the extent that semi-mature and mature individuals cannot rebury themselves after being excavated. As a general rule, the loss of the byssus in the Myoidea appears to be correlated with siphonal enlargement (Allen 1985).

Closure of the pedal gape and the two siphonal orifices, allows hydraulic pressure in the mantle cavity of *Mya* species to be raised sufficiently to force the valves apart against the resistance of the surrounding substratum (Trueman 1954) which apparently enlarges the chamber slightly to permit growth of the shell. *Mya* species normally occur in rather plastic substrata that will not collapse against the shell valves when they are adducted. Deep-burrowing myoideans also exhibit a tendency towards cross-fusion of the mantle and augmentation of pallial musculature. In these bivalves, the mantle cavity has assumed a tubular form, somewhat similar to that of the Scaphopoda. This arrangement permits the generation of considerable hydrostatic pressures within the mantle cavity, necessary in the deeper-burrowing species, particularly where substrata such as stiff muds offer significant resistance. In *Mya* and *Platyodon* species, the adductor muscles can be contracted either alternately or independently. The siphonal process of *Mya* is extended in a staged sequence in which the siphonal apertures are closed and more water is progressively injected by adduction into the lumina of the process from the mantle cavity. In alternation with this, further water is drawn into the mantle cavity through opened siphons when the shell valves are parted. This use of water in the mantle cavity for hydraulic purposes is only made possible by the nature of the very extensive ventral fusion of left and right mantle lobes with consequent reduction of the pedal aperture, and also by the valvular nature of the pedal aperture itself. This contrasts with many other bivalves, in which the siphons are extended through haemocoelic pressure. The hinge ligament is also modified, permitting the shell valves to move about a dorso-ventral axis, as well as normal opening/closing. With the enclosure of the mantle cavity, this dorso-ventral motion allows the siphonal process to be withdrawn. The posterior ends of the shell valves can be separated in order to accommodate the base of the contracted siphonal process (Chapman & Newell 1956; Purchon 1977). *Platyodon* species (Myidae) have taken the further step of developing a capacity to penetrate soft rocks, such as mudstones. In this genus, the tip of the siphonal process is further strengthened by four scales, which may assist in smoothing the inner wall of the burrow, but the shell valves provide the main mechanical abrasion. These are forced apart by hydraulic pressure and then the posterior adductor muscle is contracted, forcing the anterior part of each valve to scrape against the walls of the burrow (Yonge 1951b).

The Myoidea are eulamellibranchiate, with homorhabdic ctenidia that have their food selection function restricted almost entirely to the labial palps. The oesophagus is long and leads to a stomach which is of Type V and incorporates a style sac and a gastric shield (Purchon 1960a). A major typhlosole enters the right caecum and terminates within the left caecum; each caecum also features a direct connection to the digestive gland (Boss 1982). As in most bivalves, the myoidean stomach has elaborate internal structures necessary for the handling of particulate food materials. The mechanisms of digestion are imperfectly known, except in a few studied species. Extracellular digestion appears to be more important than intracellular, at least in *Mya* species. Preliminary extracellular digestion in the stomach involves the crystalline style as the principal source of digestive enzymes. Examples of enzymes detected in *Mya* include amylase, glycogenase and cellulase (Yonge 1923, 1926; Lavine 1946).

Family Myidae

The Myidae are best represented in the Northern Hemisphere, both in terms of species and genera. Only three small species in two genera occur in the Australian fauna – *Cryptomya (Venatomya) elliptica* (Fig. 8.41A–D), an undescribed species in this same subgenus (Fig. 8.41G–I), and *Tugonia (Distugonia) inopinata* (all under 26 mm; Lamprell & Stanisic in press).

The shells are usually thin, weakly sculptured (often with a smooth but chalk-like surface) and gape, at least partially, at the posterior extremity. A pallial sinus is present and typically is strongly developed. Hinge teeth are absent, but a chondrophore of varying strength is present and supports the resilium. Myids are usually found in soft subtidal sandy mud, are deep burrowing and typically have a single long fused siphon. However, in *Cryptomya californica* the siphons are very short – undoubtedly because this species (and presumably other congeners) makes contact with the surface through crustacean burrows (Yonge 1951a).

Mya arenicola is a facultative anaerobe, and can survive eight days without oxygen, during which time glycogen levels in the tissues decline (Ricketts & Calvin 1948). This may be a specific adaptation to an intertidal situation, but it is perhaps significant that some members of the Corbulidae are also known to exhibit great tolerance to oxygen depletion (Weigelt & Rumohr 1986). This occurs in several littoral species which have developed great tolerance to prolonged exposure to fresh water such as occurs during floods.

Myid internal anatomy is illustrated in Figure 8.41J. The digestive system is as described above for the superfamily except that the style sac is not united to the midgut (Boss 1982). Circulatory system, reproductive biology and renal organs are as described for the superfamily.

Commensalism in the superfamily is exhibited by *Cryptomya californica* which lives within the burrows of thalassinid Crustacea, or of the echiuroid, *Urechis caupo*. *Cryptomya* occurs at a depth of up to 500 mm, but since it taps the host's burrow for its water supply, it requires only a short siphonal process and has no pallial sinus (Yonge 1951a). Presumably Australian species of *Cryptomya* show similar interesting interrelationships with crustaceans.

Just how many names have been proposed for the Recent Myidae is uncertain, however Habe (1977) has recorded 10 Recent species from Japan, Oliver (1992) four from the Red Sea, Abbott (1974) fourteen from America, and Lamprell & Stanisic (in press) three from Australia.

These species are referred to six genera: *Mya* which has an elongate, chalky shell with a wide posterior gape and a large chondrophore in the left valve; *Cryptomya* which is more compressed and smoother than *Mya*, which has a narrow posterior gape, and has the chondrophore in the right valve appressed under the umbo; *Paramya* which has a small, quadrate, smooth shell with a chondrophore in each valve; *Platyodon* with a smaller chondrophore than *Mya*, a large, deep pallial sinus and sculpture of raised growth striae; *Sphenia* which includes small to very small species that are quadrate, often distorted and have a small to large pallial sinus; *Tugonia* in which the shell is anteriorly inflated and constricted and attenuate posteriorly, is usually widely gaping, has subequal chondrophores, and a usually shallow pallial sinus. *Mya* comprises two subgenera, *Cryptomya* two, *Platyodon* two, and *Tugonia*, which is the largest genus, has five subgenera (Keen 1969k). Two of the Australian species are in included in *Cryptomya* and one in *Tugonia* (Lamprell & Stanisic in press).

There appear to be no records of fossil myids from Australia. According to Keen (1969k), the family dates from the Cretaceous.

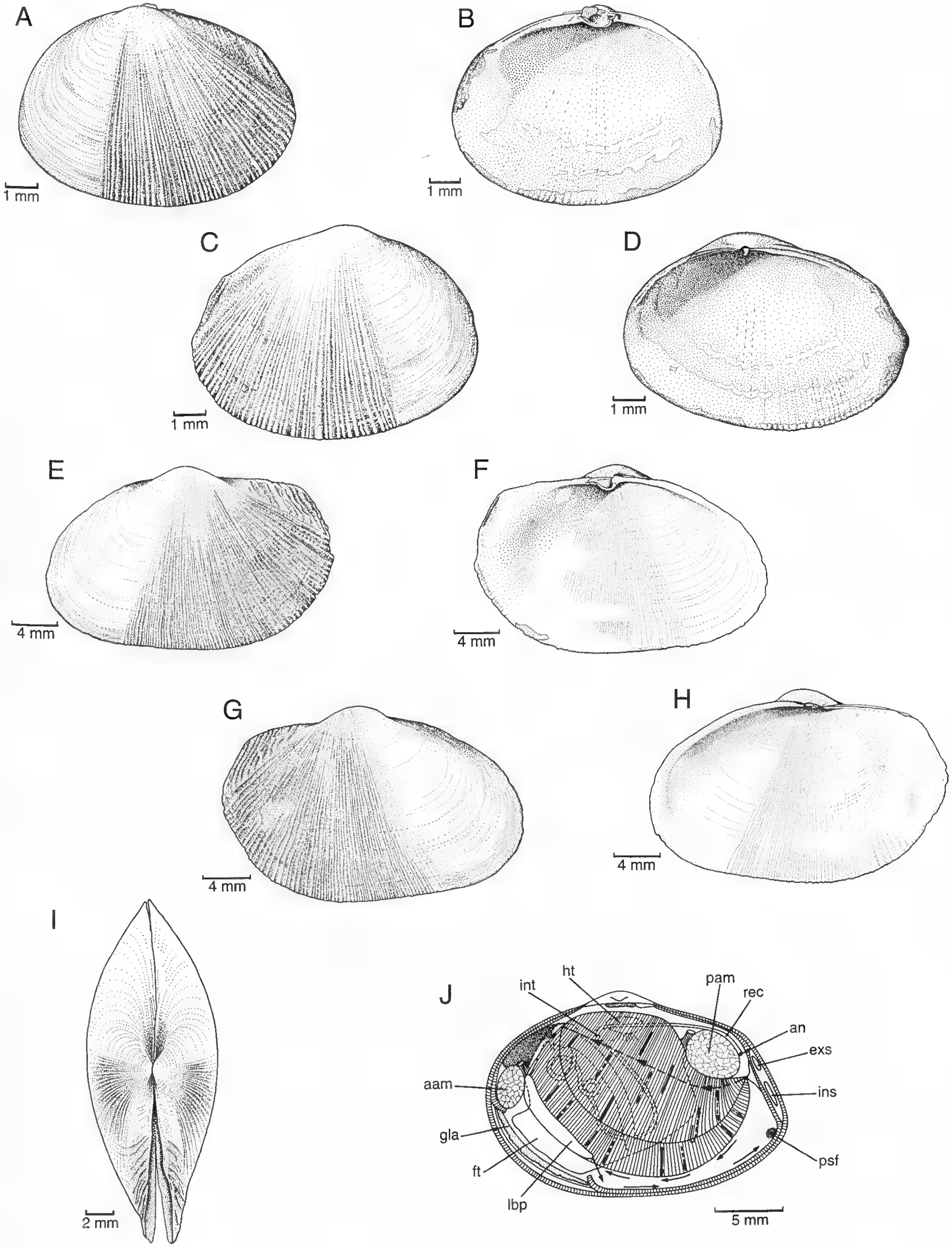


Figure 8.41 Family Myidae. A–H, shell valves, internal and external view. A–D, *Cryptomya elliptica*: **A**, **B**, left valve; **C**, **D**, right valve. **E–H**, *Cryptomya (Venatomya)* sp.: **E**, **F**, left valve; **G**, **H**, right valve. **I**, *Cryptomya (Venatomya)* sp., paired shell valves, dorsal view, showing gape through which the siphons project. **J**, *Cryptomya californica*, organs in the mantle cavity, internal anatomy, left shell valve and mantle lobe removed. Unbroken arrows indicate ciliary currents on exposed surfaces and broken arrows on inner surfaces of demibranchs; feathered arrows indicate rejection currents from tip of palps and along midventral line where mantle edges are fused. **aam**, anterior adductor muscle; **an**, anus; **exs**, exhalant siphon; **ft**, foot; **gla**, glandular area bounding inner margin of pedal gape; **ht**, heart; **ins**, inhalant siphon; **int**, intestine; **lbp**, labial palp; **pam**, posterior adductor muscle; **psf**, accumulated pseudofaeces; **rec**, rectum. (J, after Yonge 1951a) [A–I, A.J. Hill; J, C. Eadie]

Family Corbulidae

The Corbulidae are the largest family of the Myoidea and are cosmopolitan in distribution. Corbulids are readily recognised by their unusual shape, differing from other members of the Myoidea in being inequivalve and having the two valves not meeting at their ventral margins (Fig. 8.42D). Most species are small and usually less than 20 mm in length. Some authors recognise up to six subfamilies (Vokes 1945), but only two, the Corbulinae and Lentidiinae, are recognised among the extant fauna (see Boss 1982). Corbulid affinities were discussed by B. Morton (1990). All Australian species are referred to the subfamily Corbulinae.

The shell is usually small and inequilateral (8.42A–D). It is strongly to moderately inequivalve, the left valve being usually less convex and smaller than the right (Fig. 8.42A, B) and subtrigonal or elongate-trigonal, with commarginal sculpture; some species have strong radial ridges on the left valve. The hinge teeth are either weakly developed, or characterised by one, or at most, two, subumbonal teeth. A spatulate cartilaginous process or chondrophore serves as the ligament attachment in the left valve, and this is received in a corresponding right valve socket discrete from the margin. Living specimens lie buried in muddy gravel, sand, or mud (Fig. 8.42F), with a small byssus attached to a piece of gravel or shell (Yonge 1946; Boss 1982). Corbulids have an unusual arrangement of conchiolin layers embedded within the shell that is thought to be a deterrent to shell-drilling naticid gastropods (Kelley 1988). Incompletely drilled corbulids are often encountered in collections.

With the exception of a small pedal gape and the siphonal apertures (incurrent postero-ventral; exhalant postero-anterior), the mantle edge of corbulids is closed ventrally. The foot is compressed (Fig. 8.42E) and grooved and may be associated with a byssal gland which produces threads to anchor the animal to small rocks or other hard surfaces within the substratum (Boss 1982).

Corbulids are shallow burrowers in sandy, sand-mud or muddy substrata in subtidal situations, usually at depths greater than 4 m. They are occasionally dredged from the continental shelf to depths in excess of 350 m (Lamprell & Healy in preparation). Corbulids are a reasonably common component of eastern Australian estuaries and embayments and can occur in large numbers in their preferred habitat. Rainer (1982), for example, found that *Notocorbula vicaria* (= *Corbula tunicata*) contributes significantly to the biomass and net production of the macrobenthos community in Gunnamatta Bay, Port Hacking. *Notocorbula stolata* is also known to be gregarious. Stephenson *et al.* (1974) reported that *Notocorbula hydropica* ranks among the more commonly encountered subtidal benthic species in parts of Moreton Bay, south-eastern Queensland. The minute species *Corbula monilis* and *Corbula rotalis* both occur in coarse coral sand in depths to 350 m along the Great Barrier Reef from central to northern Queensland (K. Lamprell & J.M. Healy personal communication).

All corbulids are ciliary suspension-feeders. The siphons are short, fused, naked and wholly retractile (Fig. 8.42E, F). The palps and gills are, at least in some species, involved in rejection of large particles (Yonge 1946). According to Yonge (1946), the discarding of large quantities of pseudofaeces by *Varicorbula gibba* (as *Aloidis gibba*) is facilitated by the presence of adductors containing a large proportion of 'quick'-contracting muscle, an inequivalve shell which favours the rapid collapse of the inhalant chamber upon adductor contraction, and some interplay between the foot and ctenidia. The digestive system is as described above for the superfamily except that the style sac is united to the midgut (Boss 1982). Yonge (1946) notes that the crystalline style of *V. gibba* is dissolved except when in use.

The circulatory system, reproductive biology and renal organs are as described for the superfamily.

Nothing is known of the physiology of Australian corbulids, but studies on Atlantic species (especially *Varicorbula gibba*) suggest a high degree of tolerance by members of the family to environmental deterioration or degradation. Corbulids were among the few survivors of a catastrophic oxygen depletion in Kiel Bay, Germany in 1981, that killed most of the benthic fauna (Weigelt & Rumohr 1986). Some species have also been recorded in large numbers in polluted areas (for example, *Varicorbula gibba* in the northern Adriatic Sea; Hrs-Brenko 1981) and other species are known to occur in areas of widely fluctuating salinity. It has been proposed that the inequivalve morphology, which enables corbulids to close their valves tightly, may assist in their ability to withstand certain unfavourable environmental conditions (Lewy & Samtleben 1979).

In excess of ninety names have been proposed for the Recent Corbulidae of which approximately fifty are considered valid (Vokes 1945). *Corbula* is by far the largest genus and was previously subdivided into twelve subgenera (Keen 1969k), several of which are rather poorly defined and in need of revision. According to P. Maxwell (personal communication), the type species of *Corbula*, *C. sulcata*, differs from species in *Varicorbula*, *Notocorbula*, *Anisocorbula* and *Serracorbula* in lacking a projecting chondrophore in the left valve, and therefore is unlikely to be related. Thus eight genera, *Corbula*, *Varicorbula*, *Notocorbula*, *Anisocorbula*, *Serracorbula*, *Panamicorbula*, *Physoida* and *Potamocorbula*, are recognised.

The name Aloididae was often used for the family. However, with re-acceptance of the generic name *Corbula*, the family name has now reverted to Corbulidae. The Corbulidae have not been revised for almost fifty years (since the work of Lamy 1941 and Vokes 1945) and have, until very recently, been imperfectly known from Australian waters (K. Lamprell & J.M. Healy personal communication). Sampling in the years leading up to and just after the turn of the last century in the southern states, provided reasonably adequate quantities of material for State museum collections, some of which subsequently became well documented (Cotton 1930; Macpherson & Gabriel 1962).

Corbulids are especially well represented in Australian waters with a total of fifteen Recent species. Two of these species are placed in the genus *Anisocorbula*, which has an elongate shell with a sharp umbonal ridge, a sinuous ventral margin, lacks a pallial sinus, and has strong commarginal ridges and fine radial striae in the interstices. Six species are referred to *Notocorbula*, characterised by a large shell, the right valve strongly encompassing the left, a bipartite chondrophore and large adductor scars. Five species are placed in *Serracorbula* (one an undescribed species), which can be recognised as being almost equivalve, with the left valve only slightly smaller than the right, and in having the ventral margin evenly serrate. Finally two species are be placed in *Varicorbula*, one of which is an introduced Atlantic-Mediterranean species, *Varicorbula gibba* (Healy & Lamprell in press). Species of *Varicorbula* are small, with commarginal sculpture and well-defined radial ridges on the left valve.

Iredale (1930a) believed that the genus *Corbula* was invalid and proposed dividing the Australian species between two new genera: a southern group, *Notocorbula* (type, *Corbula vicaria* = *tunicata*) and the tropical *Anisocorbula* (type, *Corbula macgillivrayi*) on the basis of conchological features and with the understanding that *Corbula* was invalid. The availability of *Corbula* was subsequently upheld by the International Commission on Zoological Nomenclature, but *Notocorbula* and *Anisocorbula* have been retained (Vokes 1945).

The Corbulidae first appeared in the Upper Jurassic, and the genus *Corbula* dates from the Cretaceous. Australian fossil corbulids and fossils of extant species are known from the Tertiary and/or the Holocene of South Australia (*C. adelaidensis*, *C. verconis*) and Victoria (*C. ephamilla*) (Cotton 1961; Ludbrook 1984).

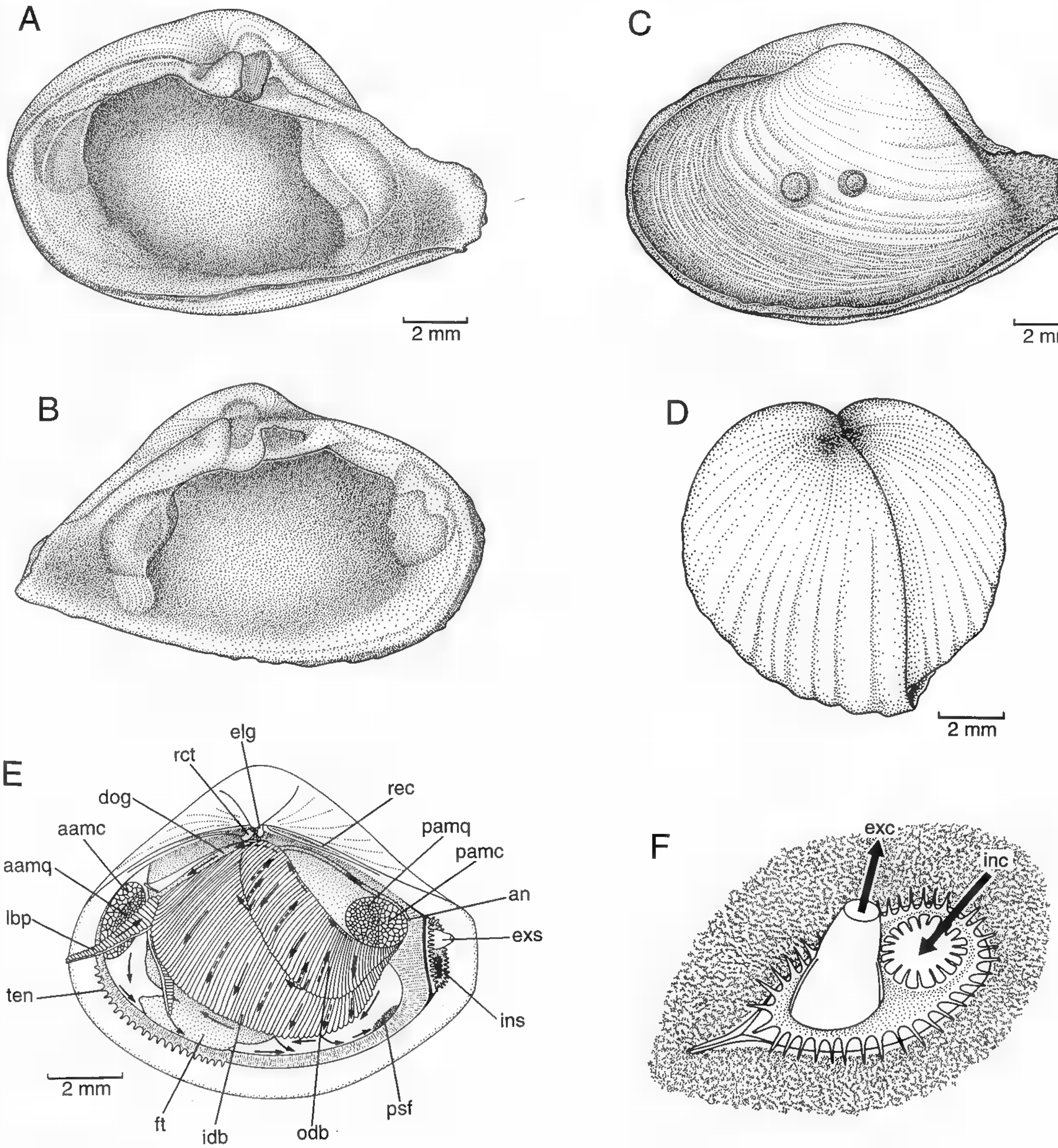


Figure 8.42 Family Corbulidae. **A–D**, *Notocorbula coxi*, shell valves: **A**, right valve, internal view; **B**, left valve, internal view; **C**, paired shell valves, lateral view; **D**, paired shell valves, anterior view, showing the right valve encompassing the left valve. **E**, **F**, *Varicorbula gibba*: **E**, internal anatomy, left shell valve and mantle lobe removed – small unbroken arrows indicate ciliary currents on exposed surfaces and broken arrows on inner surfaces of demibranchs and feathered arrows indicate rejection currents; **F**, siphons fully open after the animal has burrowed in the substratum. **aamc**, anterior adductor muscle, 'catch' component; **aamq**, anterior adductor muscle, 'quick' component; **an**, anus; **dog**, distal oral groove; **elg**, external ligament; **exc**, exhalant current; **exs**, exhalant siphon; **ft**, foot; **idb**, inner demibranch; **inc**, inhalant current; **ins**, inhalant siphon; **lbp**, labial palp; **odb**, outer demibranch; **pamc**, posterior adductor muscle, 'catch' component; **pamq**, posterior adductor muscle, 'quick' component; **psf**, pseudofaeces; **rct**, right cardinal tooth; **rec**, rectum; **ten**, tentacles on the right mantle lobe lining pedal gape. (E, F, after Yonge 1946)
[C. Eadie]

Superfamily GASTROCHAENOIDEA

The gastrochaenoideans are endolithic or infaunal tube building marine bivalves of tropical and temperate waters. The superfamily is represented by one family, the Gastrochaenidae. The following family description therefore applies equally at superfamily level.

Family Gastrochaenidae

Gastrochaenids have shells that are small (usually less than 30 mm, but may be up to 50 mm), edentulous, thin, more or less elongate, equivalve and widely gaping antero-ventrally (hence the origin of the name) (Fig. 8.43). The ligament is external, opisthodetic, and based in an elongate groove in each valve. The shell valves lie free within the bore hole or tube (Fig. 8.43B, D, F, I, J; Pl. 16.1). Gastrochaenids are heteromyarian or isomyarian. The mantle lobes are fused ventrally (middle and inner folds) except at the pedal aperture. The siphons are greatly elongated, are either fused or separate, and are not protected by a periostracal sheath. There is a very deep pallial sinus. The foot is small, columnar and suctorial, and a byssus is lacking.

Pennant, in 1777, was the first to describe a member of this family under the name *Mya dubia*, and shortly after, in 1783, Spengler erected the genus *Gastrochaena*. Early Australian records of Gastrochaenidae can be found in the works of E.A. Smith (1885), Tenison Woods (1877), Tate (1887b, 1887c, 1889), Jack & Etheridge (1892), Adcock (1893), Melvill & Standen (1899), Tate & May (1901), Verco (1908) and Cotton (1934).

The generic subdivision of the family is variously treated by different authors (for example, Lamy 1925; Carter, J.G. 1978; Keen 1969l; Freneix & Roman 1979; Savazzi 1982; Morton, B. 1983a, 1985a; Pisera 1987). Three living genera are recognised (K. Kleemann personal data) within the family: *Gastrochaena* (including the subgenus *Cucurbitula*), *Spengleria*, and *Eufistulana*; and the Eocene genus *Kummelia*, in North America. *Spengleria* is treated as a subgenus of *Gastrochaena* by some authors (for example, Lamy 1923, 1938), but there are significant differences in musculature, siphon structure and shell sculpture so that it is given generic rank here.

The gastrochaenids have received scant attention in Australia. There are several Indo-West Pacific species in the tropical north. Two temperate Australian species have been described: *Gastrochaena tasmanica* by Tenison Woods (1877) from south-eastern Australia, and *G. frondosa* (= *G. gigantea*) by Cotton (1934) from South Australia. There are two fossil species in eastern Australia: *Eufistulana australis* and *G. (?) terra-reginae*. Otter (1937) described the bore holes of two tropical species of *Gastrochaena* at Low Isles, Queensland.

The anatomies of three Indo-West Pacific species, all of which occur in northern Australia, have been described in detail from non-Australian localities: *Gastrochaena cuneiformis* (non Spengler 1783, = *G. gigantea* Deshayes 1832) by Purchon (1954); G. (Cucurbitula) cymbium by B. Morton (1982a); and *Eufistulana mumia* by B. Morton (1983d). J.G. Carter (1978) published a detailed account of the morphology, manner of boring, and evolution of two Atlantic species of *Gastrochaena* and one of *Spengleria*.

Gastrochaena and *Spengleria* species are borers in calcareous rocks or shells (Pl. 16.1). They line the bore holes with a calcareous secretion, but the shell valves remain free in the tubular cavity. *Eufistulana* species are infaunal burrowers, usually in muddy sediments. They secrete an adventitious calcareous tube which provides protection and support for the body. The periostracum is thin and inconspicuous in most species, and in *Spengleria* contains numerous aragonitic denticles (Carter, J.G. & Aller 1975).

The shell valves of *Gastrochaena* are elongate, equivalve and widely gaping antero-ventrally so that the suctorial foot can be used as an anchor as there is no byssus. In some species a pair of calcareous projections, the myophores, extend laterally and ventrally from the dorsal margins. These serve as sites for the attachment of the anterior pedal retractor muscles. Unlike the shells of pholads, gastrochaenid shells are relatively smooth anteriorly except for commarginal ridges, but the anterior margins are thickened. The valves of *Spengleria* have an elevated area, acute-angulated at the umbo and posteriorly truncated between two furrows, the oblique medial one being prominent. In *Eufistulana* species the valves are elongately quadrate with a deep ventral indentation and an angulate umbonal ridge. They are tumid below the umbones, but compressed and truncate posteriorly. The anterior ends are strongly radially ribbed.

Gastrochaena and *Spengleria* species are heteromyarian with the anterior adductors greatly reduced, in keeping with the reduction of the anterior end of the shell. In both genera there are anterior and posterior pedal retractor muscles of almost equal size and a pair of anterior pedal protractor muscles. The anterior protractors in *Gastrochaena* are single muscle bands that attach behind and above the anterior adductor. The protractors in *Spengleria* are bifurcate and larger than in *Gastrochaena*, and they attach ventral to and slightly lateral to the anterior adductor. *Spengleria*, in keeping with a trunk-shaped foot, also differs in having prominent pedal elevator muscles as well (Carter, J.G. 1978). In *Eufistulana*, the anterior and posterior adductors and the anterior and posterior retractors are of roughly equal size. The pallial muscles are grouped in small bundles so that the pallial line is discontinuous. A feature of all gastrochaenids is the very long siphonal retractor muscles and correspondingly deep pallial sinus. The foot is columnar with an approximately circular terminal pedal disc which is suctorial and functions to secure the animal at the end of the bore hole or tube. A small anterior papilla known as the pedal organ, is believed to produce probing tubules to direct boring (Carter, J.G. 1978). A small byssal gland and a byssal groove are present although byssal threads are lacking.

The mantle lobes of gastrochaenids are unusual. In *Eufistulana* reflected inner and middle lobes cover much of the shell valves. The left and right inner lobes are fused ventrally except at the pedal gape. In front of the gape the middle lobes are greatly enlarged and reflected over the anterior part of the shell. Beside the pedal gape the middle and outer lobes are reduced, but the inner lobes are greatly enlarged and reflected over the edges of the valves. Posterior to the gape the inner lobes are muscular and fused, and the middle lobes are enormously enlarged and reflected over the sides of the valves. The inner and middle lobes are both glandular and the various glands serve different functions in boring, shell formation and secretion of the bore hole lining (Morton, B. 1983d).

In all the living genera the siphons may be retracted within the shell. In *Gastrochaena* the long siphons (Fig. 8.43D) are fused to their tips by the middle and inner lobes. The siphons of *Eufistulana* (Fig. 8.43J) are also fused to their tips but only by the inner lobes. In the latter genus the inhalant siphon is larger than the exhalant one and is fringed by tiny papillae. *Spengleria* has completely separate siphons (Fig. 8.43B; Carter, J.G. 1978).

All gastrochaenids are filter-feeders. The ctenidia are long and either flat or plicate. They become concertina-like when the siphons are retracted. The demibranchs are subequal, but the outer one is shorter anteriorly and does not project between the labial palps; its terminus instead opening into the distal oral groove of the inner demibranch. Only the inner demibranch has a ventral food groove. The labial palps are small and triangular and the junction of the palps and ctenidia is grade 2 of Stasek (1963a). B. Morton (1983d) has described the alimentary canal of *Eufistulana*. The heart consists of a small rectangular ventricle and two large lobulate auricles. There is a pericardial gland and a wide posterior aortic bulb. The rectum enters the ventricle ventrally near the reno-pericardial aperture (White 1942; Morton, B. 1983d). The stomach is Type 4 of Purchon (1958). There is no published information on reproduction, development and life history of gastrochaenids. However, sperm and eggs are released after the warm season, and the duration of the veliger stage is estimated to last up to some weeks before settlement on dead substrata and metamorphosis has to take place (K. Kleemann personal observation).

Features of particular interest in gastrochaenids are the mode of boring, and the bore hole and tube formation. Purchon (1954) and Yonge (1963) believed that the bore holes of *Gastrochaena* are formed by abrasion effected by the opening and closure of the shell valves and contractions of the pedal retractors. J.G. Carter (1978) noted that the primary abrasion surface is the latest-formed, projecting commarginal shell ridge. Tiny aragonitic spines in the periostracum may assist the process (Carter, J.G. & Aller 1975; Carter, J.G. 1978). The commarginal anterior ridges on the anterior parts of the shell in *Spengleria* may serve the same function. However, the mantle lobes are reflected over the shells (Sluiter 1891) and there seems little doubt that chemical secretions contribute significantly to the boring process (Carter, J.G. 1978; Morton, B. 1982a; Savazzi 1982; Kleemann 1990, 1996) although which of the glandular areas in the mantle lobes are responsible is not yet known. In the case of the outer, siphonal part of the bore holes the chemicals aiding boring must be produced in the tissues of the siphons. This is most evident in *Spengleria* in which the divergent exhalant and inhalant siphons have separate tubes that must be repeatedly dissolved and reformed as the animal grows.

As well as boring, gastrochaenids line the sides of their dwellings with aragonitic deposits. These secretions are also produced from the mantle lobes. Particularly in *Eufistulana* and *Spengleria* species, the bore holes have two parts, an inner shell chamber and an outer siphonal part. The latter is usually thickly lined and may have commarginal thickenings or baffles (in *Gastrochaena*).

There is a partial partition separating the two chambers (Bromley 1978; Carter, J.G. 1978; Morton, B. 1983d). The animals are capable of repairing the tube linings when they are damaged and also of extending them upwards if there is a threat of being overgrown. Individually twisted dwellings, under crowded conditions, demonstrate the ability to change boring direction (Kleemann 1974).

A special type of bore hole lining is seen in *Gastrochaena (Cucurbitula)* species which bore into the shells of larger bivalves (Morton, B. 1982a; Savazzi 1982). This has been observed in *G. (G.) dubia* from muddy bottoms in the northern Adriatic of the Mediterranean. The larvae settle on the outer side of the bivalve shell, usually near the umbo, and bore through to the inner surface. There they form a calcareous capsule or 'igloo' that acts as the shell chamber. The capsule must be partially dissolved and remade, probably yearly, as long as the animal grows. The shell-boring species *G. tasmanica*, in south-eastern Australia, is described as having a flask-like capsule formed of fragments of shell cemented together (Cotton 1961, fig. 336; Macpherson & Gabriel 1962, fig. 448). If this is correct, the process must be different from that described by B. Morton (1982a) for the subgenus *Gastrochaena (Cucurbitula)* and the taxonomic relationships of this species will need to be reconsidered.

Eufistulana species are not rock borers, but live in soft sediments. They protect themselves and provide support for their long siphons by building a long, straight, tapered, calcareous tube up to 150 mm long (Morton, B. 1983d). The tube stands vertically in the sediment and has a cap at the inflated bottom end which is equivalent to the shell chamber of *Gastrochaena*, and there is an annular partition separating the lower shell chamber. When the animal enters a period of growth the end cap is dissolved so that the tube can be lengthened.

As bore hole or tube dwellers, gastrochaenids are sedentary bivalves. The animals do not rotate within the shell chamber, and are prevented from moving along the long axis of the bore hole by the partition separating the shell and siphonal chambers. The suctorial foot attaches ventrally near the deep end of the bore hole or tube, forming an anchor and allowing contraction of the siphonal muscles (Sluiter 1891). It often leaves a scar on the wall (Fischer 1866; Soliman 1973; Morton, B. 1983d). According to J.G. Carter (1978), in *Gastrochaena* spasmodic contraction of the muscular, fused, inner mantle lobes creates a pumping action which drives eroded particles at the bottom of the bore hole through the mantle cavity and out the inhalant siphon.

Gastrochaenids are not fished or eaten by humans, but the boring species contribute to the breakdown of coralline limestone, and empty chambers may function as domiciles and hatching place for various invertebrates and even small fish (gobies).

Gastrochaena and *Spengleria* are circumtropical genera, the former extending into temperate waters. Species of *Gastrochaena sensu stricto* are found across northern Australia and as far south as central New South Wales in the east and around the south-western corner of Western Australia and as far east as South Australia. The Indo-West Pacific shell-boring subgenus *Cucurbitula* is common across northern Australia from Carnarvon to Moreton Bay. The taxonomic status of the shell-boring *G. tasmanica* from south-eastern Australia is uncertain. There are unidentified museum specimens of the Indo-West Pacific genus *Eufistulana* from

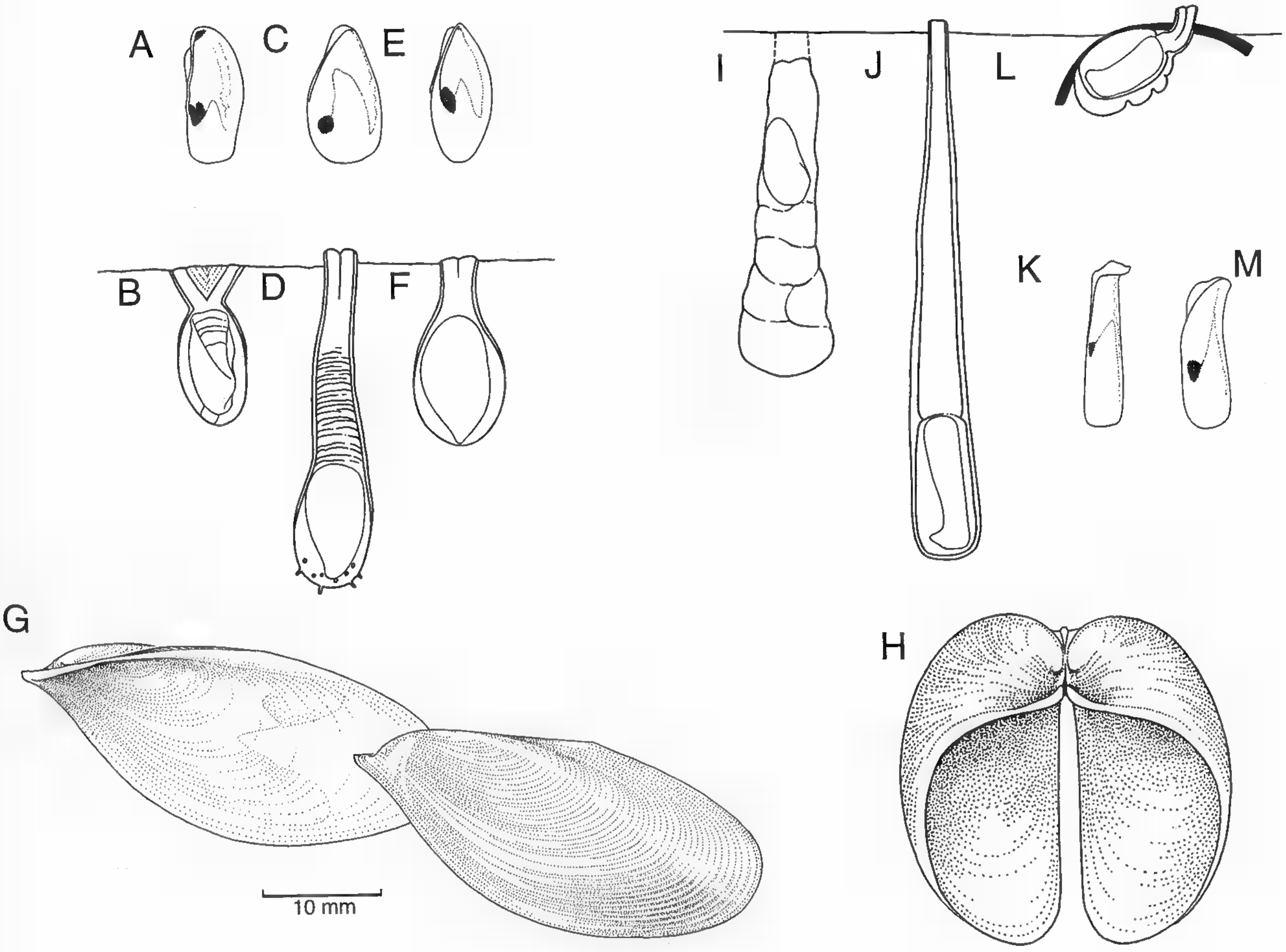


Figure 8.43 Family Gastrochaenidae. **A, B,** *Spengleria* sp.; **C, D,** *Gastrochaena cuneiformis*; **E–H,** *Gastrochaena gigantea*; **I,** *Kummelia* sp.; **J, K,** *Eufistulana mumia*; **L, M,** *Gastrochaena (Cucurbitula) cymbium*. **A, C, E, K, M,** left valve, internal view, showing the pallial sinus and muscle scars. **B, D, F, I, J, L,** animals in their bore holes, siphons extended. **G, H,** shell valves: **G,** right valve in internal view, left valve in external view; **H,** paired valves, ventral view.

[A–F, I–M, N. Froteler; G, H, R. Plant]

northern localities between Point Cloates and Hervey Bay. Representatives of the genus *Spengleria* have been collected off Queensland (Kleemann 1990).

Gastrochaena and *Spengleria* have a range from the (Upper) Jurassic to the Recent. The subgenus *Cucurbitula* is recorded only from the Recent. *Eufistulana* is known since the Cretaceous. The fossil *E. australis* from the Rolling Downs Formation in Queensland appears to be a tube of this genus. *Kummelia* appeared only in the Eocene. The evolutionary origin of the Gastrochaenoidea remains uncertain. Purchon (1954) and J.G. Carter (1978) discussed the similarities between them and living Pholadoidea and Hiatelloidea but concluded that neither group is a likely ancestor for the Gastrochaenidae. J.G. Carter (1978) also discussed the possibility of evolution of the group from the extinct Permophoridae (Heterodonta) and Grammysiidae (Anomalodesmata) but again reached no conclusion. Boss (1967) considered the evolution of *Spengleria*. B. Morton (1985a) discussed the evolution and radiation of the superfamily.

Superfamily HIATELLOIDEA

Representatives of the superfamily Hiatelloidea are burrowing, nestling or boring marine bivalves. The generally equivalve shell is posteriorly elongate and quadrate to trapezoidal in shape, but is often irregular because of physical constraints of habitat (Hunter 1949; Yonge 1971; Narchi 1973; Ludbrook 1984). Shells can be very large with a shell length up to 300 mm or more in the North American 'geoduck' clam, *Panopea generosa*, but are typically 60–100 mm in length (Yonge 1971; Bernard, F.R. 1979; Angioy, K. & Angioy, M. 1983). *Panopea* is the largest of the deep-burrowing bivalves and its siphons can attain an extended length of two or three times the shell length (Yonge 1971).

The superfamily Hiatelloidea includes the more primitive members of the Myoida, for example, *Saxicavella* (Keen 1969m; Allen 1985). The byssally attached, epifaunal genus *Saxicavella* is slightly heteromyarian (other genera are isomyarian). In this genus, mantle fusion may be regarded as Type B rather than Type C as occurs in all other hiatelloideans (Yonge 1971; Narchi 1973).

Shell gape is pronounced in hiatelloideans because of the large, well-developed siphons that are covered with periostracum. Associated with this feature is the almost entire fusion of the mantle margin and considerable enlargement of the pallial musculature (Yonge 1971, 1982b). There is a massive, external opisthodetic ligament and the hinge teeth are reduced or lost in adults (Yonge 1971; Narchi 1973). Functionally, all these morphological developments allow tremendous hydrostatic pressures to be generated within the mantle cavity. This is considered a necessary adaptation for deep burrowing in sediments (for example, species in *Panomya*, *Panopea*) and is probably an important pre-adaptation for crevice nestling or boring (for example, *Hiatella* species) (Hunter 1949; Yonge 1971, 1982b; Allen 1985).

Hiatellids were first recognised and described in the mid-eighteenth Century. *Hiatella arctica* (as *Mya arctica* Linné) was the first described species.

The Hiatelloidea are well represented in the cold temperate waters of the Northern Hemisphere. *Hiatella arctica* is said to occur globally in warm temperate to cold waters, including Subantarctic waters, but is replaced by the larger species, *H. australis*, in southern Australia (Beu 1971b). The affinities of Australian hiatellids with widespread representatives of the superfamily (*i.e. H. arctica*) are unclear (see Beu 1971b).

At least three Cainozoic species of *Panopea*, *P. agnewi*, *P. kalimnensis* and *P. ralphi*, and several Late Cretaceous species, are recorded from Australia (Darragh & Kendrick 1991). Species of *Hiatella* have been recorded from the Lower Eocene of New Zealand (Fleming 1966; Beu 1971b; Beu & Maxwell 1990). Fossilised shells of hiatelloideans are known from Europe, North America and Asia from as far back as the Permian (Keen 1969m). Representatives of *Panopea* have been reported from glaciomarine deposits (Tertiary) at King George Island (Pugaczewska 1984), and from Cainozoic strata on Seymour Island (Antarctic Peninsula; Zinsmeister & Macellari 1988). Strauch (1968) surmised that the shell lengths of fossil hiatelloids could be used to estimate palaeotemperatures. However, Rowland & Hopkins (1971) discounted such a relationship pointing out that for Recent Pacific populations, shell length is influenced chiefly by substratum and habitat.

The only family in the superfamily, the Hiatellidae, comprises five extant genera: *Cyrtodaria*; *Hiatella* (= *Saxicava*); *Panomya*; *Panopea* (conserved over *Panope*, see Dall 1912; Melville 1983; ICZN Opinion 1414 1986); and *Saxicavella*. One species in each of two genera, *Hiatella* and *Panopea*, occurs in shallow, subtidal waters of southern Australia (Beu 1971b; Noonan 1981; Ludbrook 1984; Ludbrook & Gowlett-Holmes 1989).

Family Hiatellidae

Members of the Hiatellidae generally have an equivalve shell (for example, *Panopea*), although large specimens of *Hiatella* tend to be slightly inequivalve (Lucas 1975, 1976; Angioy, K. & Angioy, M. 1983). The aragonitic shell is robust with a thick periostracum, the surface being smooth or having irregular commarginal striae. The pale shells are usually posteriorly elongate due to changes in growth gradients around the mantle edge (Fig. 8.44A, D; Yonge 1971; Narchi 1973). The form of the hinge is illustrated in Figure 8.44B, C, E, F. Yonge (1971) regarded hiatellids as isomyarian with a simple hinge having a considerably reduced heterodont dentition. There are no lateral teeth and the single cardinal of each valve is reduced or lost in adults. The large, external opisthodetic ligament is probably the result of reduction in hinge dentition (Yonge 1971; Le Pennec 1980). The anterior and posterior pedal retractor muscles insert dorsally to each adductor. The mantle (Type C) is largely fused, apart from an opening for the small digitate foot, and expands into large siphons which are also covered with periostracum (Yonge 1971; Narchi 1973; Bernard, F.R. 1979). There is a distinct pallial sinus. The siphons are united for most of their length, diverging just prior to the openings which generally have short papillae around the perimeter (Hunter 1949; Yonge 1971, 1982b; Narchi 1973; Lucas 1975, 1976).

There has been no complete synthesis of Australian representatives. *Hiatella australis* was recognised from southern Australian waters including Sydney Harbour (as Port Jackson; Smith, E.A. 1885). *Hiatella angasi* is considered indistinguishable from the former species (Beu 1971b; Noonan 1981). *Hiatella subalta*, also from southern Australia, is a sportellid, rather than a hyatellid (Ponder 1971a; Noonan 1981). Tate (1887b) introduced a new genus and species *Capistrocardia fragilis* for a South Australian specimen. This taxon has not been recognised by subsequent workers, the specimen probably representing *Panopea australis* (Cotton 1961; Noonan 1981; Ludbrook 1984; Ludbrook & Gowlett-Holmes 1989). Other Australian workers to include notes on this family are Hedley (1914b), Iredale (1930a), Cotton (1934) and Macpherson & Gabriel (1962).

Little is known of the biology of most species and the taxonomy is confused. In particular, the irregular shell of *Hiatella* species has led to the erection of numerous synonymous taxa (Hunter 1949; Beu 1971b; Yonge 1971). Present day workers (for example, Beu 1971b) consider that only two hiatellid species occur in Australian waters. They are *Hiatella australis* commonly known as the 'Southern Crypt Dweller', and *Panopea australis* which is known as the 'Southern Gaper'. *Hiatella australis* (Fig. 8.44A–C) is common in intertidal or shallow sublittoral waters in southern Australia and usually occurs 'nestling' or boring in soft rocks or sponges. *Panopea australis* (Fig. 8.44D–F), like other *Panopea* species (Hunter 1949; Yonge 1971), is a large, deep-burrowing bivalve living in subtidal sand and mud habitats (Ludbrook & Gowlett-Holmes 1989).

There have been no anatomical studies of Australian material. However, anatomical descriptions and details of functional morphology of some closely related extralimital species have been provided by Hunter (1949), Yonge (1971) and Narchi (1973).

In *Hiatella* the solid shell is whitish in colour with irregular striae, but is phenotypically variable and irregular in shape (Hunter 1949; Yonge 1971; Narchi 1973). The shells of *Panopea* tend to be greyish white, solid and rectangular in shape with smooth regular curves. The valves are equal and, compared to *Hiatella* species, have fairly regular commarginal ribbing (Noonan 1981). The byssus is absent in adult hiatellids except nestling individuals of *Hiatella* where it is reduced (Yonge 1962); it is absent in boring forms (Hunter 1949). The siphons are particularly large and elongate in *Panopea* species and shell gape is often as wide or wider than the depth of the shell (Yonge 1971, 1982b; Narchi 1973). The foot is digitate and extensible in the young – adapted for locomotion, but reduced in adults (Hunter 1949).

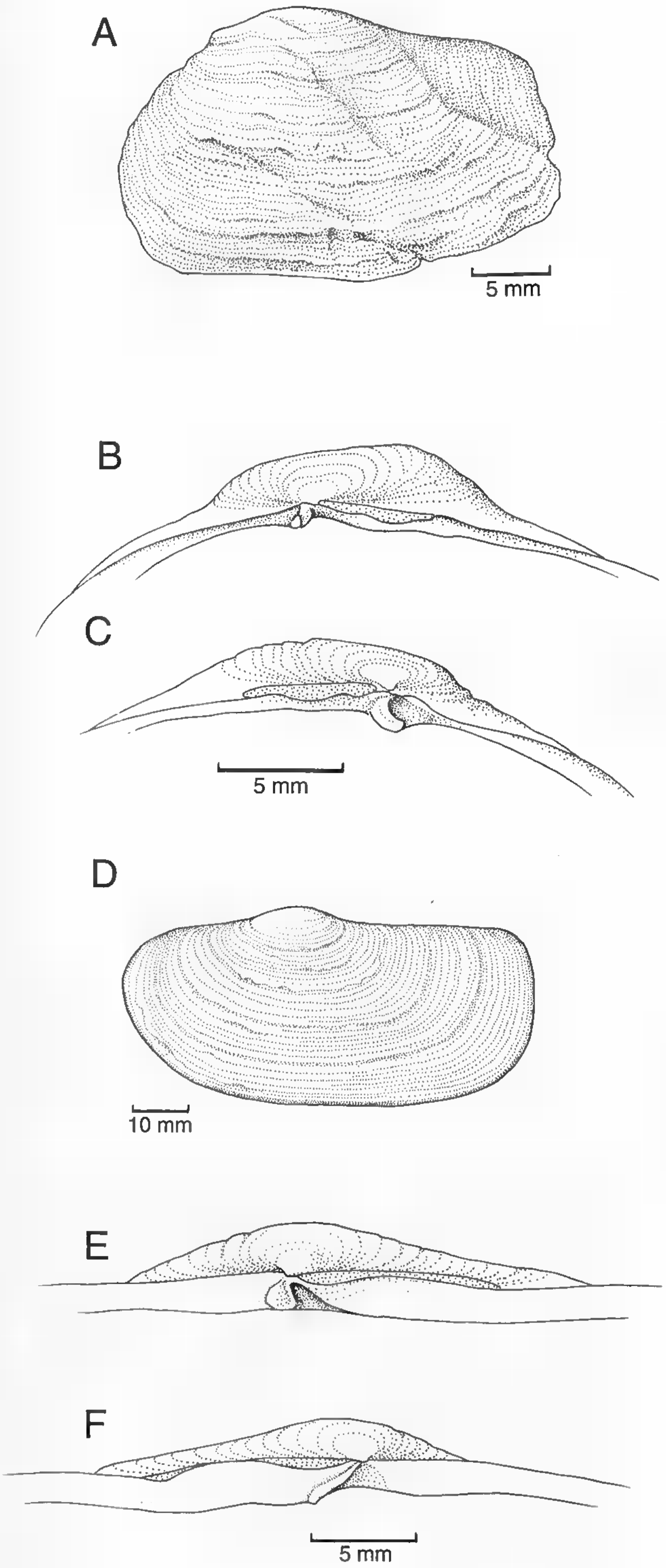


Figure 8.44 Family Hiatellidae. **A–C**, *Hiatella australis*: **A**, left shell valve, external view; **B**, right valve hinge; **C**, left valve hinge. **D–F**, *Panopea australis*: **D**, left shell valve, external view; **E**, right valve hinge; **F**, left valve hinge. [S. Weidland]

The long, narrow ctenidia are homorhabdic and synaptorhabdic (smooth or plicate) (Yonge 1971; Narchi 1973). The outer demibranch has a short supra-axial extension and is half the width of the inner demibranch. The gills may extend into the basal region of the siphons. The inner demibranch has a marginal groove but the outer demibranch lacks one (Hunter 1949; Yonge 1971; Narchi 1973). Frontal cilia are primarily responsible for the transport of particles (Narchi 1973). The palps are smooth and have several ridges and folds. A long oesophagus leads into the Type IV stomach antero-dorsally. A combined style sac and midgut enter the stomach postero-ventrally. The main typhlosole is sharply curved. The pericardium has an ovate ventricle through which the intestine passes. The paired auricles are large and lobate, and the pericardial gland is auricular (Yonge 1971; Narchi 1973).

The nervous system of hiatellids conforms generally with that of other heterodonts. Hunter (1949) reported a large central, visceral mass of ganglia with smaller cerebral and pedal ganglia, and a pair of siphonal ganglia.

Little is known of reproduction and development in the Hiatellidae. Representatives are gonochoristic and prolonged planktonic development appears to be common (Thorson 1936; Bernard, F.R. 1979).

Hunter (1949) reported the settlement and postsettlement behaviour in *Hiatella* species. The substratum type on which settlement occurs will determine the boring habit or otherwise of the adult. A smooth surface of soft, homogeneous rock or sponge will induce boring whereas hard, creviced rock will result in the adult nestling and anchoring by byssal threads. Hunter (1949) and Ansell & Nair (1969) considered boring in *Hiatella* to occur by mechanical abrasion, without chemical secretions. Trudgill & Crabtree (1987) reported bioerosion of fossil intertidal limestone by *Hiatella* species. Gallardo & Osorio (1978) reported bore holes of *Hiatella* in ascidians (*Polyandrocarpa*, *Phragmatopoma*), gastropods (*Concholepas*, *Fissurella*) and barnacle shells (*Megabalanus*). *Hiatella australis* occurs in similar epibiotic communities in southern Australian waters (Ludbrook & Gowlett-Holmes 1989), but no detailed studies have yet been undertaken.

The northern Pacific *Panopea generosa* ('geoduck') is considered a prized delicacy because of its large size and extensive fleshy siphons. Once common, it is now very rare in shallow waters because of over-collecting (Yonge 1971; Goodwin 1977; Gillingham 1984). In Australia, *P. australis* is not collected for food. Hiatellids are not economically important in Australia although *Hiatella* species may play a minor role in bioerosion and fouling (see Soldatova 1986; Trudgill & Crabtree 1987).

Superfamily PHOLADOIDEA

The Pholadoidea is a superfamily of bivalves comprising the Pholadidae and Teredinidae, all highly specialised for boring into firm substrata such as stiff clay, mudstone, peat, soft or friable rocks, poor-grade cement, shells, woody plant material, or even polyvinyl chloride (PVC) and styrofoam (Pls. 16.2, 16.3). Species of Pholadidae, commonly called piddocks, occur in one or more of these substrata, and are shallow-water, filter-feeders, with the exception of the deep-sea wood borers (Xylophagainae); their primary food source is wood. The Teredinidae, commonly called shipworms, pileworms or, by the Australian Aborigines, cobra (in the north) and warragárá (in the south). Pholadoideans have long worm-like bodies (Figs 8.45B, 8.51B) and occur in shallow water,

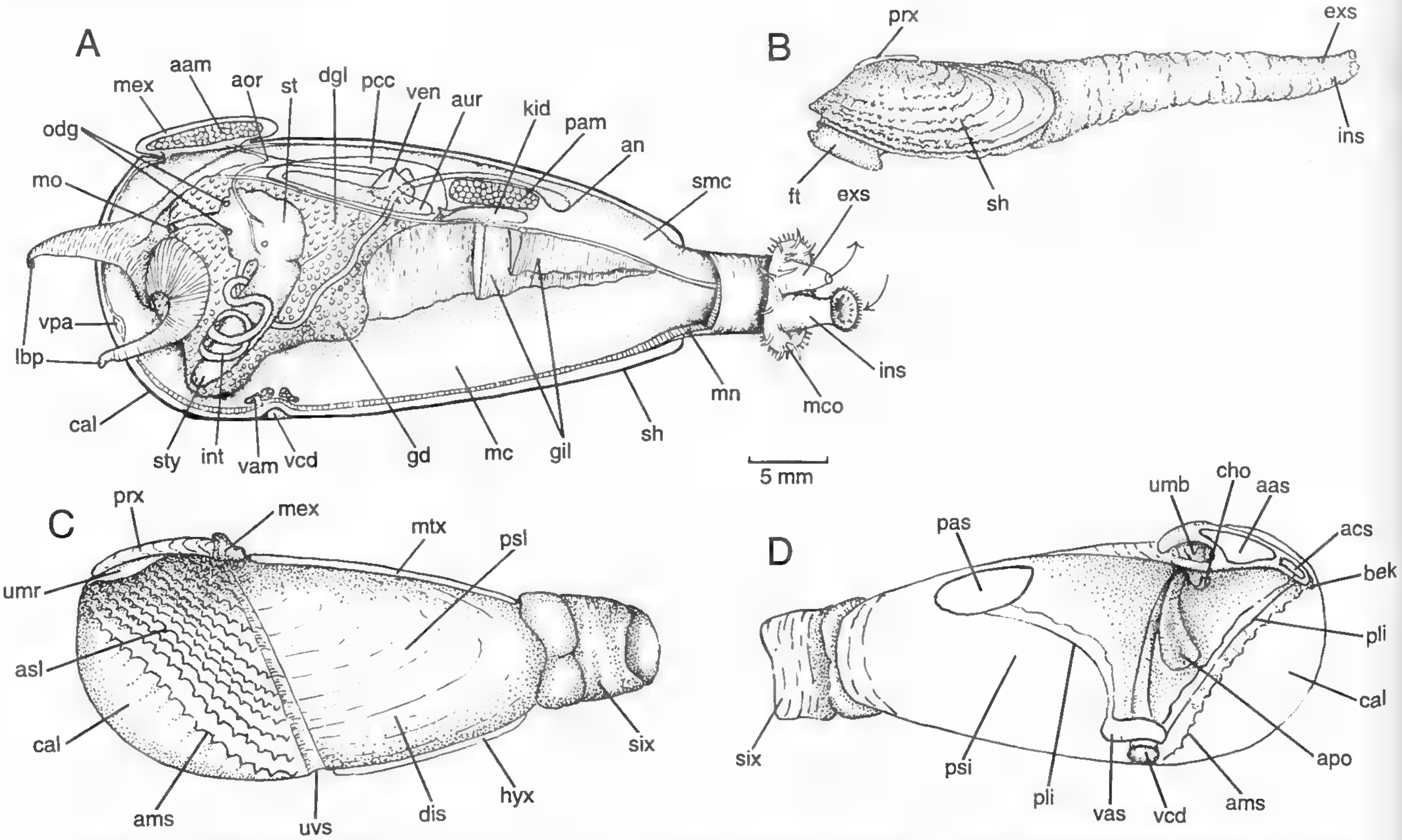


Figure 8.45 Family Pholadidae. A, internal anatomy of an adult *Martesia striata*, with callum fully developed. B–D, morphological features: B, animal; C, left shell valve, external view; D, left shell valve, internal view. **aam**, anterior adductor muscle; **aas**, anterior adductor muscle scar; **acs**, accessory adductor muscle scar; **ams**, anterior margin of shell; **an**, anus; **aor**, aorta; **apo**, apophysis; **asl**, anterior slope; **aur**, auricle; **bek**, beak; **cal**, callum; **cho**, chondrophore; **dgl**, digestive gland; **dis**, disc; **exs**, exhalant siphon; **ft**, foot; **gd**, gonad; **gil**, gills; **hyx**, hypoplax; **ins**, inhalant siphon; **int**, intestine; **kid**, kidney; **lbp**, labial palp; **mc**, mantle (or infrabranchial) cavity; **mco**, mantle collar; **mex**, mesoplax; **mn**, mantle; **mo**, mouth; **mtx**, metaplax; **odg**, openings of the digestive gland into stomach; **pam**, posterior adductor muscle; **pas**, posterior adductor muscle scar; **pcc**, pericardial cavity; **pli**, pallial line; **prx**, protoplax; **psi**, pallial sinus; **psl**, posterior slope; **sh**, shell; **six**, siphonoplax; **smc**, suprabranchial (or epibranchial) cavity; **st**, stomach; **sty**, crystalline style sac; **umb**, umbo; **umr**, umbonal reflection; **uvs**, umbonal-ventral sulcus; **vam**, ventral adductor muscle; **vas**, ventral adductor muscle scar; **vcd**, ventral condyle; **ven**, ventricle; **vpa**, ventral pedal palp. (A, after Turner 1971b)
[R.D. Turner]

boring into wood or other plant material which they utilise as food. Both families are distributed worldwide in marine and brackish waters with a few species extending into freshwater.

All pholadoideans, except adult Jouannetiinae, are equivalved, but inequilateral with the umbones located near the anterior end; the mantle is closed, except for the pedal gape anteriorly and siphonal openings posteriorly; a truncate, somewhat circular foot acts as a suction disc and aids in boring. Adult shells range in length from less than 5 mm for some Xylophagainae and Teredinidae to over 200 mm for some Pholadinae. The shells are white to tan and range from elongate elliptical to globular. The anterior margin of the valves may be rounded and the pedal gape narrow, sinuous with a moderate pedal gape, or highly rostrate with a deep embayment producing a large pedal gape. The extreme condition is reached in the wood boring species in which the ventral margin of the embayment is straight rather than sinuous and forms a very large, sharply angled pedal gape.

The dorsal margins of the valves anterior to the umbones are reflected and form the attachment areas for the anterior adductor muscle which is thus on the outside of the valves. Its contraction brings the valves together against the foot which, during boring, is securely attached to the anterior end of the burrow. The large posterior adductor muscle works antagonistically to the anterior adductor. Its contraction spreads the valves anteriorly, scrapes the denticulate ridges against the end of the burrow and thus enlarges it. The particles removed from the burrow are carried into the mantle cavity and pass out through the inhalant siphon as pseudofaeces in all pholadoideans except those wood borers that utilise the wood as food. The hinge (Figs 8.45D, 8.51C) is reduced to condyles and a small chondrophore for the attachment of the internal ligament which functions to hold the valves in position as they pivot on the condyles when boring. Apophyses, 'ribs', for the attachment of the pedal muscles extend from under the umbones in all pholadoideans except the Jouannetiinae and Xylophagainae. In these subfamilies, the pedal muscles insert in the typical bivalve position just anterior to the posterior adductor muscle. The anatomy of the Pholadidae and the Teredinidae is shown in Figures 8.45A, 8.51A. Only in the Teredinidae are the major vital organs located posterior to the posterior adductor muscle.

All Pholadidae except the deep sea wood borers, the Xylophagainae, are primarily filter-feeders, and all Teredinidae, except possibly *Kuphus*, utilise wood or other woody plant material as their primary food source. Popham & Dickson (1973) first demonstrated the presence of bacteria in the gills of *Bankia australis*. Waterbury, Calloway & Turner (1983) demonstrated

Figure 8.46 Family Pholadidae. Siphons of *Barnea dilatata* extended above the muddy substrate at Magnetic Island, North Queensland. The aperture of the inhalant siphon faces into the current; the exhalant siphon is behind.
[Australian Institute of Marine Sciences]

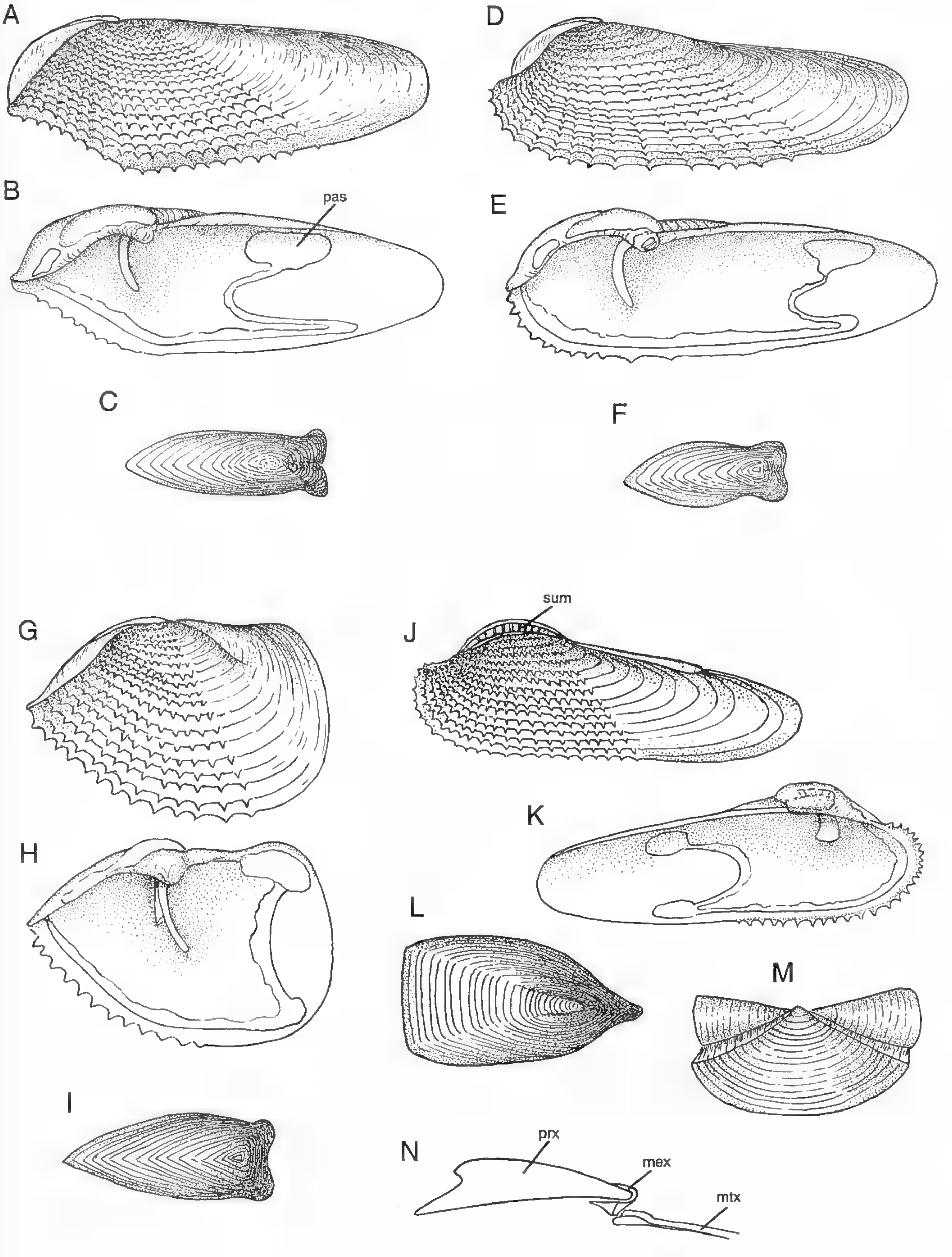


Figure 8.47 Family Pholadidae, subfamily Pholadinae. Shell valves and accessory plates of species in the Australian fauna. A–C, *Barnea obturamentum*: **A**, left shell valve, external view; **B**, right shell valve, internal view; **C**, protoplax. **D–F**, *Barnea australasiae*: **D**, left shell valve, external view; **E**, right valve, internal view; **F**, protoplax. **G–I**, *Barnea dilatata*: **G**, left shell valve, external view; **H**, right shell valve, internal view; **I**, protoplax. **J–N**, *Pholas orientalis*: **J**, left shell valve, external view; **K**, left shell valve, internal view; **L**, protoplax; **M**, mesoplax; **N**, arrangement of the accessory plates. **mex**, mesoplax; **mtx**, metaplax; **pas**, posterior adductor muscle scar; **prx**, protoplax; **sum**, septate umbone reflection. [R.D. Turner]

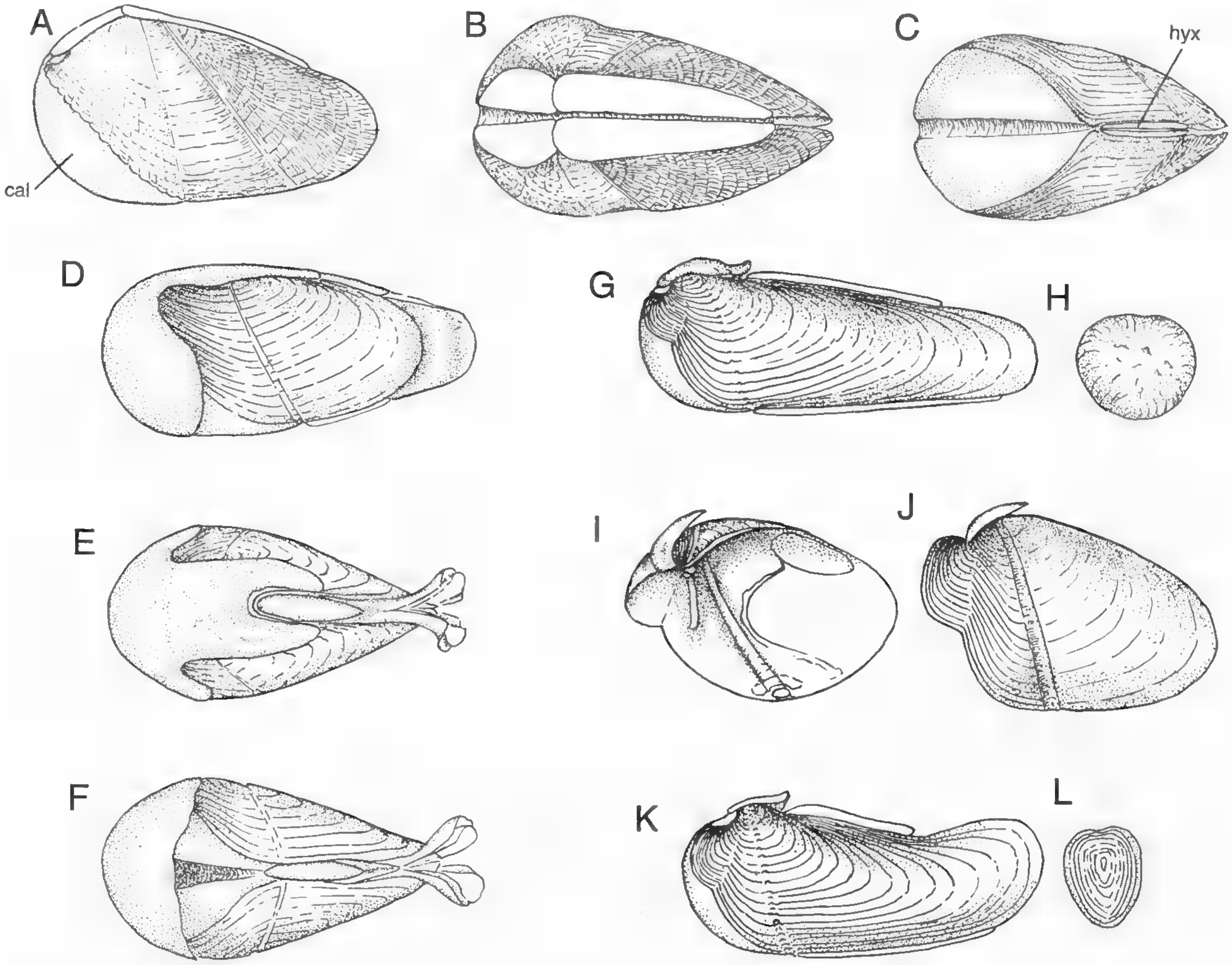


Figure 8.48 Family Pholadidae, subfamily Martesiinae. Shell valves, accessory plates and whole animals of species in the Australian fauna. **A–C**, *Parapholas quadrizonata*: **A**, left shell valve, lateral view; **B**, shell valves, dorsal view; **C**, closed shell valves, ventral view. **D–F**, *Aspidopholas obtecta*: **D**, left shell valve, lateral view; **E**, shell valves, dorsal view; **F**, shell valves, ventral view. **G–J**, *Martesia striata*: **G**, left shell valve, lateral view; **H**, mesoplax, dorsal view; **I**, right shell valve, internal view; **J**, left shell valve of a young specimen, external view. **K**, **L**, *Martesia fragilis*: **K**, left shell valve, lateral view, **L**, mesoplax, dorsal view. **cal**, callum; **hyx**, hypoplax. [R.D. Turner]

that bacteria isolated from the gills of six species representing four teredinid genera both digest cellulose and fix nitrogen. Teredinids have also been shown to utilise phytoplankton and dissolved organics. For a review of feeding in teredinids see Mann (1984, 1988).

All pholadids, with the possible exception of some *Xylophaga*, are oviparous as are all teredinids except *Lyrodus*, *Teredo* and *Zachsia*. Species in these genera are larviparous, brooding their young in the gills of the parent to the feeding stage (straight-hinge veliger) or the settling stage (pediveliger). Life histories of teredinids are reviewed by Turner (1966, 1971a, 1971b), Turner & Johnson (1971) and Calloway & Turner (1988) and the physiological and biochemical energetics of swimming larvae by Mann & Gallager (1985).

Information on the ecology of the 15 or more Australian pholad species is scattered and often anecdotal except for the coral borer, *Jouannetia cumingii* (see Morton, B. 1986a) and *Martesia striata* (see Moore 1947). *Martesia* species are typically wood borers, but do not utilise the wood as food and may be found in laterite, styrofoam and PVC. All other pholads, except the deep-sea wood borers, Xylophagainae, are shallow-water, marine, soft rock, shell and coral borers which live in Queensland and along the north coast, with only *Barnea australasiae*, *B. obturamentum* and *J. cumingii* extending into the temperate southern regions (Cotton 1961). This lack of biological data is probably a reflection of the difficulty in collecting these borers and their minor economic importance.

The major factors in the ecology and local distribution of teredinids are salinity, temperature, tidal height and presence of wood. *Bactronophorus*, *Dicyathifer* and *Nausitora* species are typical of low salinity mangrove areas, and also colonise wharves and boats in low salinity areas, whereas *Bankia*, *Teredo* and *Lyrodus* species are common in higher salinities, boring in boats, wharves and other waterfront structures made of wood.

Though generally considered pests, teredinids are of major importance in littoral ecology as recyclers of wood and woody plant material. They are also a delicacy with an oyster-like flavour, favoured by the Aborigines. The piddocks and shipworms become pests only when structures of interest to people are damaged or destroyed. *Martesia striata*, the only Australian pholad considered a pest, was first reported in Australia by Hedley in 1901 and by 1938 it was considered a menace in Middle Harbour, Sydney (Moore 1947). During the CSIRO marine borer survey of 1970–1973, it was collected from Waipa south to Sydney and on the north west coast in the vicinity of Port Hedland (Marshall & Turner 1974). The cost of protection and repair of wooden boats, wharves and other waterfront structures due to the activity of teredinid borers runs into millions of dollars annually. The enormous body of literature on the subject (up through 1954) was abstracted by Clapp & Kenk (1963) and includes some thirty-four Australian authors among them the biologists E.P. Wright, C. Hedley, C.T. Calman, T. Iredale and D.D. Moore. For further references see Marshall-Ihrahim's (1981) report on seasons of larval settlement conducted as part of the CSIRO marine borer survey.

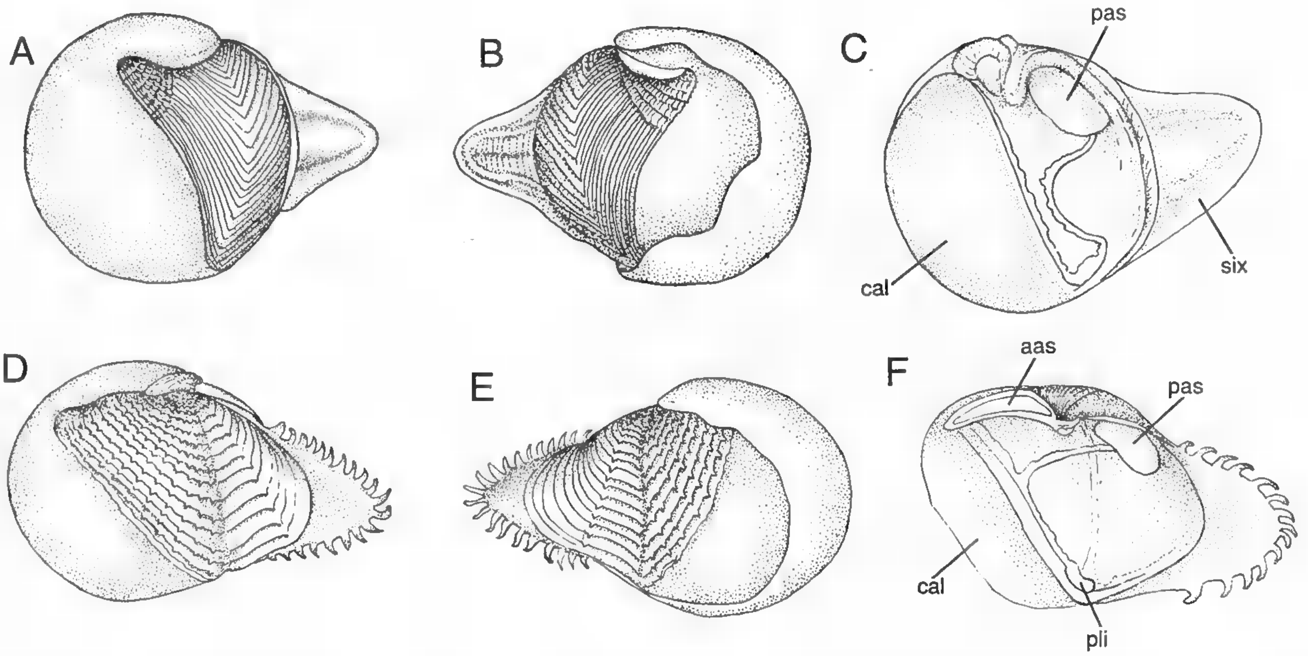


Figure 8.49 Family Pholadidae, subfamily Jouannetinae: shell valves and accessory plates of species in the Australian fauna. **A–C**, *Jouannetia cumingii*: **A**, left shell valve, lateral view; **B**, right shell valve, lateral view; **C**, right valve, internal view. **D–F**, *Jouannetia globosa*, shell valves: **D**, left, lateral view; **E**, right, lateral view; **F**, right, internal view. **aas**, anterior adductor muscle scar; **cal**, callum; **pas**, posterior adductor muscle scar; **pli**, pallial line; **six**, siphonoplax. [R.D. Turner]

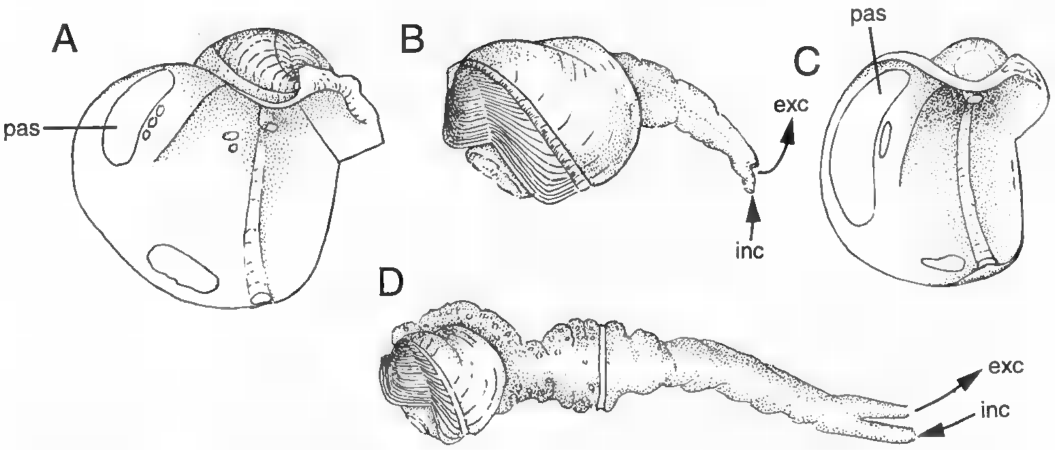


Figure 8.50 Family Pholadidae, subfamily Xylophagainae. Shell valves and whole animals of species in the Australian fauna. **A, B**, *Xylophaga* sp.: **A**, left shell valve, internal view; **B**, animal. **C, D**, *Xyloredo* sp.: **C**, left shell valve, internal view; **D**, animal. **exc**, exhalant current; **inc**, inhalant current; **pas**, posterior adductor muscle scar. [R.D. Turner]

Family Pholadidae

The family Pholadidae, with at least 15 species in Australia, is distinguished from the Teredinidae by lacking siphonal calcareous pallets, by having each gill consisting of two demibranchs (except in the Xylophagainae), and by the presence of accessory plates (hypoplax, mesoplax, metaplax, protoplax, siphonoplax) that cover the exposed anterior adductor muscles and protect the siphons (Fig. 8.45). The animals are capable of retracting into the shell valves. On the basis of the accessory plates, the presence or absence of the apophyses and the number of gill lamellae, the family Pholadidae is divided into four subfamilies (Turner 1969).

The subfamily Pholadinae comprises two fossil and five living genera, two of which, *Barnea* and *Pholas*, occur in Australia. They have elongate shells, apophyses, one to three dorsal accessory plates and grow throughout life (see Fig. 8.47). They live in firm to hard clay, peat or soft rock in the lower littoral or shallow sublittoral. Some live in the lower third of the shore. The siphons of *Barnea dilatata* are shown in Figure 8.47 and those of *Pholas obturamentum* in Plate 16.3.

The subfamily Martesiinae, the largest in the Pholadidae, comprises sixteen genera: eight fossil and eight extant, of which at least three, *Parapholas*, *Aspidopholas* and *Martesia*, occur in Australia. They have apophyses, a mesoplax, metaplax and hypoplax, but the most distinctive feature of the subfamily is the callum, a calcareous structure that closes the pedal gape when boring and growth ceases (see Fig. 8.48). At this stage the foot atrophies and the callum grows forward from the anterior margins of the valves until the two halves meet at the midline and are joined by a periostracal fold. This completely seals the anterior end of the shell except for a small pore in the periostracal connective, probably for water circulation. Some species protect the burrow entrance with a 'chimney' composed of faeces and/or pseudofaeces cemented with mucus from the siphons and shaped to fit snugly into the posterior end of the burrow. They bore into firm mud, mudstone, coral and soft rock, except for the wood-boring *Martesia* species which bore into mangroves, wharves and wooden boats and, because they do not utilise the wood for food, even into styrofoam, and PVC pipes. Martesiines range from low water to depths of about 100 m.

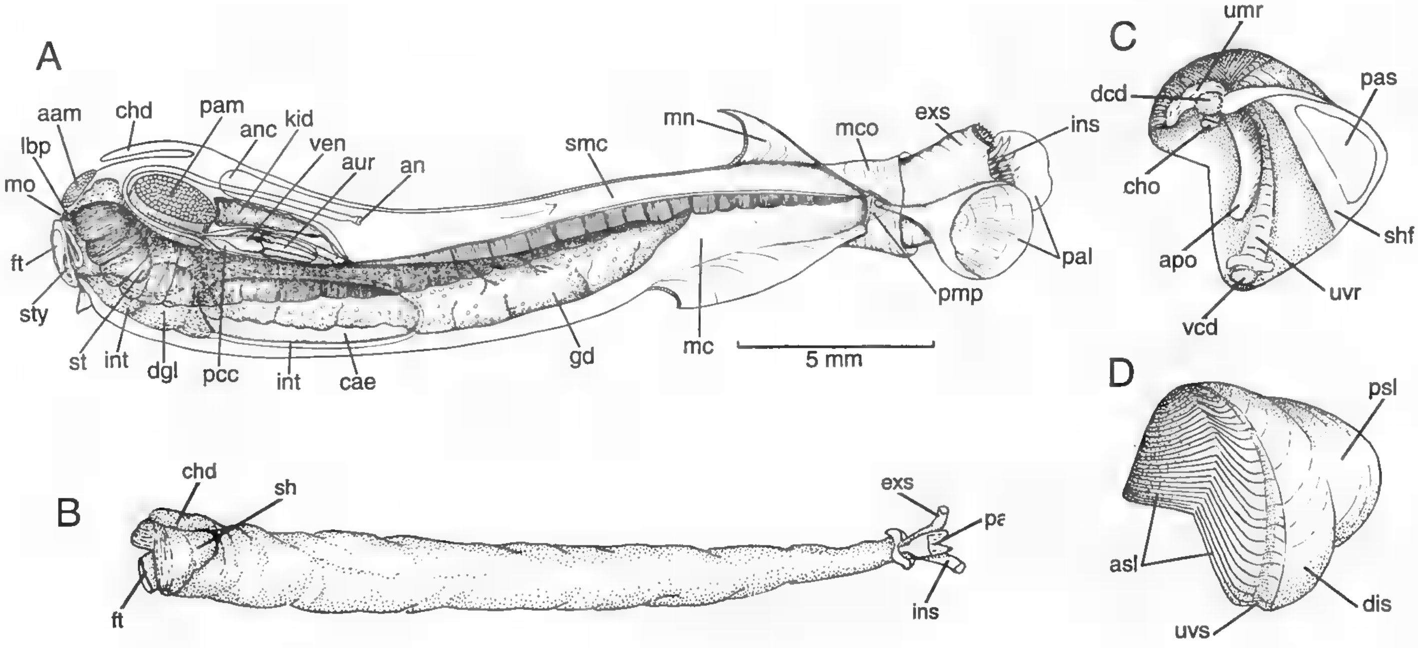


Figure 8.51 Family Teredinidae. **A**, internal anatomy of an adult *Teredora malleolus*, one of the least specialised teredinids. **B–D**, morphological features: **B**, animal; C, right shell valve, internal view; **D**, left shell valve, external view. **aam**, anterior adductor muscle; **an**, anus; **anc**, anal canal; **apo**, apophysis; **asl**, anterior slope; **aur**, auricle; **cae**, caecum; **chd**, cephalic hood; **cho**, chondrophore; **dcd**, dorsal condyle; **dgl**, digestive gland; **dis**, disc; **exs**, exhalant siphon; **ft**, foot; **gd**, gonad; **ins**, inhalant siphon; **int**, intestine; **kid**, kidney; **lbp**, labial palp; **mc**, mantle (or infrabranchial) cavity; **mco**, mantle collar; **mn**, mantle; **mo**, mouth; **pal**, pallet; **pam**, posterior adductor muscle; **pas**, posterior adductor muscle scar; **pcc**, pericardial cavity; **pmp**, protractor muscle of pallet; **psl**, posterior slope; **sh**, shell; **shf**, shelf; **smc**, suprabranchial (or epibranchial) cavity; **st**, stomach; **sty**, crystalline style sac; **umr**, umbonal reflection; **uvr**, umbonal-ventral ridge; **uvs**, umbonal-ventral sinus; **vcd**, ventral condyle; **ven**, ventricle. (A, after Turner 1966) [R.D. Turner]

The subfamily Jouannetiinae is composed of two genera, one of which, *Jouannetia* occurs in Australia. Jouannetiines lack apophyses and the pedal retractor muscles are inserted near the posterior adductor muscle. The active boring stage is equivalved, the pedal gape large; the adult nonboring stage of *Jouannetia* is inequivalved, the right siphonoplax is larger than the left and the enlarged callum of the left valve overlaps that of the right (see Fig. 8.49). The mesoplax, if present, is fused to the left half of the callum and displaced to the left by its growth. *Jouannetia* species burrow in coral, soft rock and sandstone.

The subfamily Xylophagainae includes one fossil and three living genera, two of which, *Xylophaga* and *Xyloredo* occur in Australian waters. They are deep-sea wood borers, with teredo-like shells that lack apophyses, have a small mesoplax, and do not produce a callum, and in which the gill consists of a single inner demibranch (see Fig. 8.50). They have a large wood-storing caecum, utilise the wood as food, and have been found in wood dredged from depths of 1051 and 4530 m off Sydney, New South Wales. Examination of wood dredged at other localities around Australia will no doubt produce additional material.

Family Teredinidae

The family Teredinidae, with at least 32 species in Australia, is distinguished by having a long worm-like body, a reduced shell with an angled anterior margin (Fig. 8.51D), a large pedal gape, a truncate foot, and calcareous siphonal pallets that close the burrow when the siphons are retracted (Fig. 8.52). The pallets may be in one piece (Fig. 8.53) or composed of numerous elements called cones (Fig. 8.54). Major vital organs are posterior to the shell and the long gills consist of inner demibranchs only (Fig. 8.51A). In *Teredora* and *Uperotus* species the gills extend from the mouth to the siphons (Fig. 8.51A); in all other genera they extend from the posterior end of the pericardium to the siphons. The burrow has a calcareous lining, which is thickened where the siphon and pallet muscles are attached. If the walls of the burrow become thin due to external erosion of the wood or the proximity of other borers, the tube is thickened (see Pl. 16.2). Consequently, a healthy borer may be found in a tube that is better than 60% exposed or the end of which protrudes from the eroded surface of the wood. Following settlement and metamorphosis, all teredinids except *Kuphus* and possibly some

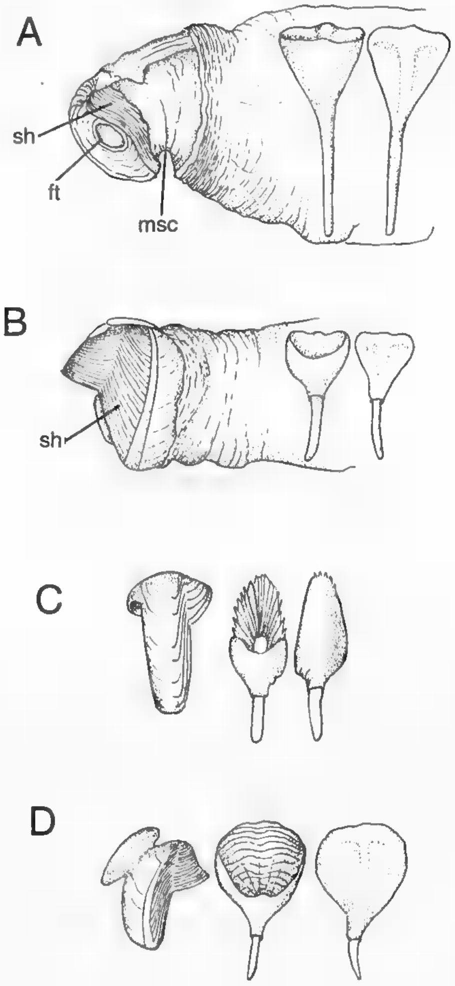


Figure 8.52 Family Teredinidae. **A**, subfamily Kuphinae, *Kuphus polythalamia*, anterior end of animal and outer and inner face of pallet. **B–D**, subfamily Teredininae: **B**, *Dicyathifer manni*, anterior end of animal and outer and inner face of pallet; **C**, *Uperotus clavus*, shell valve, exterior and outer and inner face of pallet; **D**, *Teredora princesae*, shell valve, exterior and outer and inner face of pallet. **ft**, foot; **msc**, muscular collar **sh**, shell. [R.D. Turner]

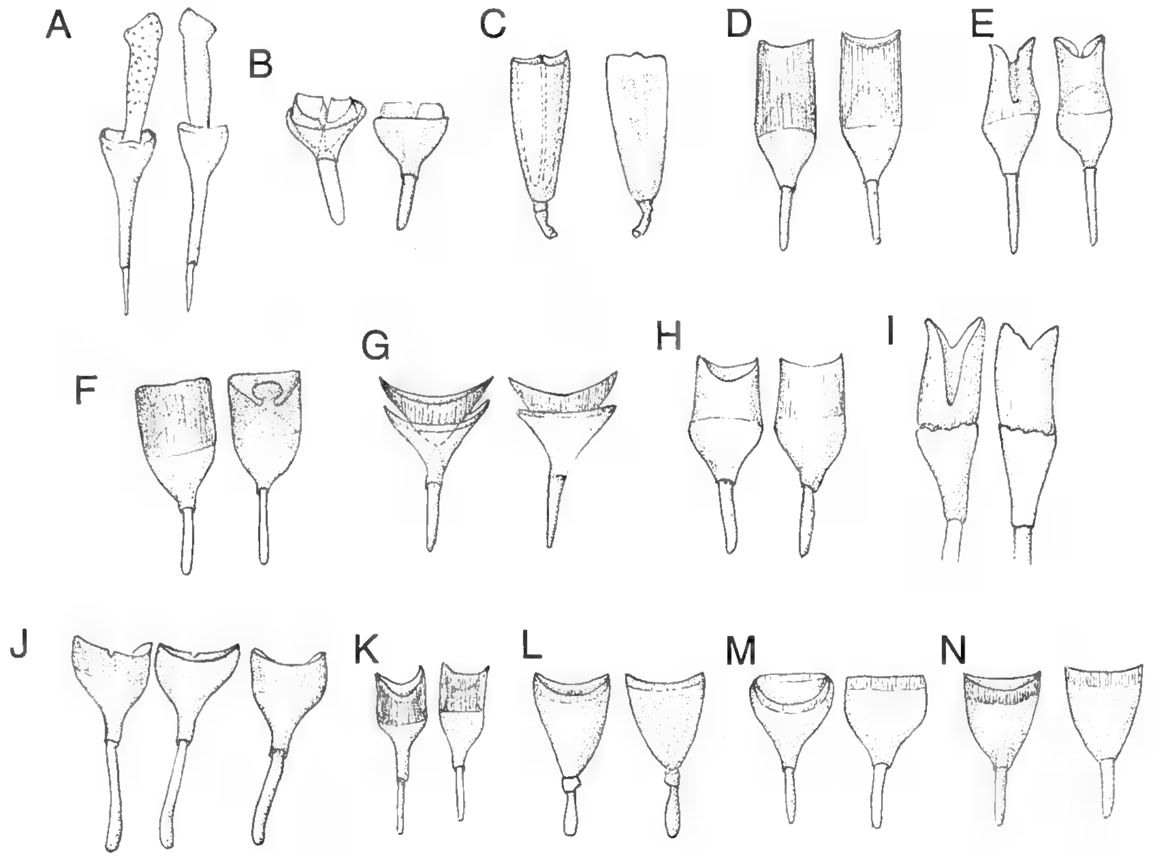


Figure 8.53 Family Teredinidae, subfamily Teredininae, pallets, outer and inner face. **A**, *Bactronophorus thoracites*; **B**, *Teredothyra matacotana*; **C**, *Teredothyra dominensis*; **D**, *Lyrodus pedicellatus*; **E**, *Lyrodus bipartitus*; **F**, *Lyrodus medilobatus*; **G**, *Lyrodus massa*; **H**, *Teredo navalis*; **I**, *Teredo furcifera*; **J**, *Teredo clappi*; **K**, *Teredo bartschi*; **L**, *Teredo mindanensis*; **M**, *Teredo poculifer*; **N**, *Teredo triangularis*. [R.D. Turner]

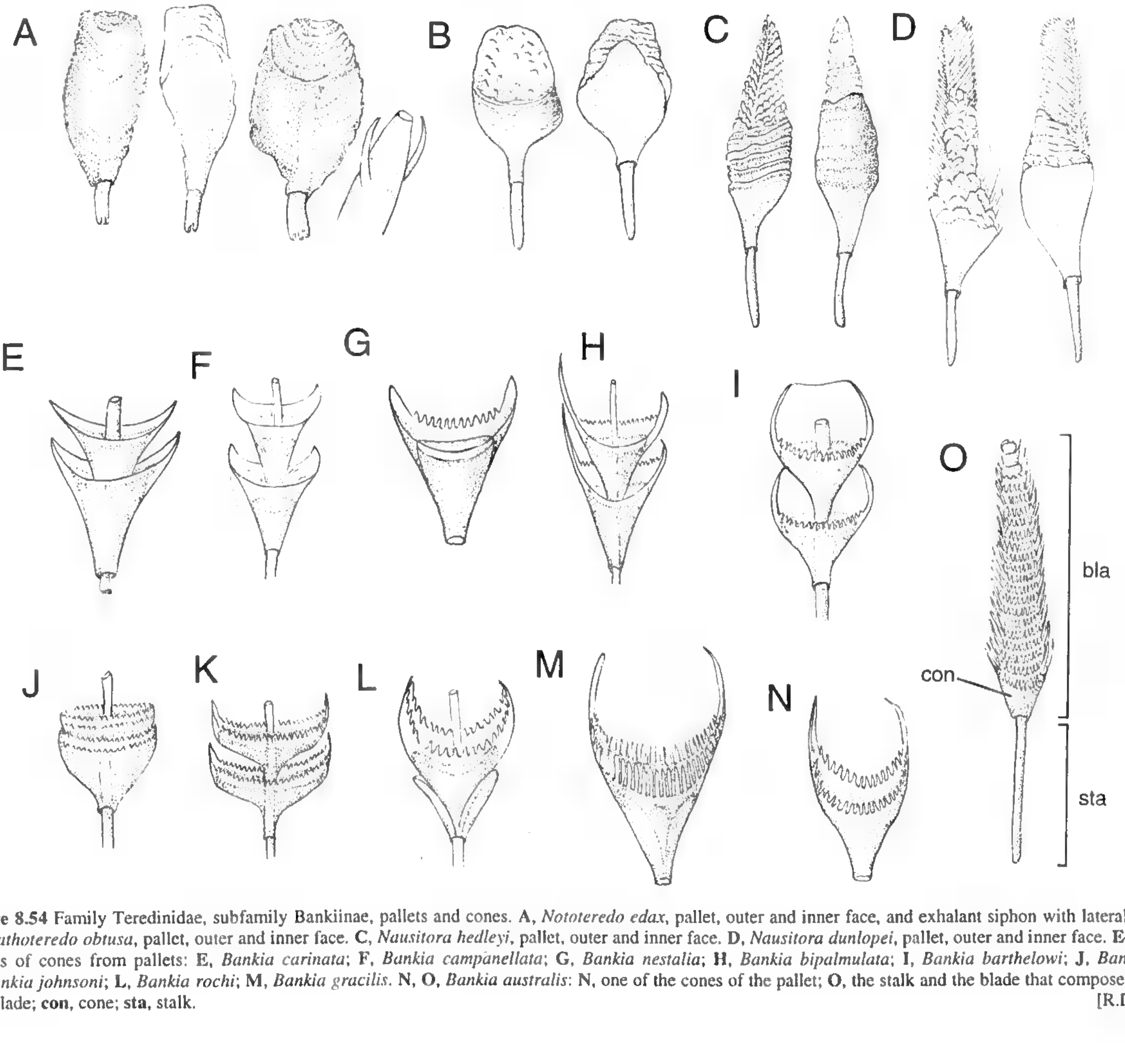


Figure 8.54 Family Teredinidae, subfamily Bankiinae, pallets and cones. **A**, *Nototeredo edax*, pallet, outer and inner face, and exhalant siphon with lateral tentacles. **B**, *Spathoteredo obtusa*, pallet, outer and inner face. **C**, *Nausitora hedleyi*, pallet, outer and inner face. **D**, *Nausitora dunlopei*, pallet, outer and inner face. **E–M**, cones or sets of cones from pallets: **E**, *Bankia carinata*; **F**, *Bankia campanellata*; **G**, *Bankia nestalia*; **H**, *Bankia bipalmulata*; **I**, *Bankia barthelowi*; **J**, *Bankia nordi*; **K**, *Bankia johnsoni*; **L**, *Bankia rochi*; **M**, *Bankia gracilis*. **N**, **O**, *Bankia australis*: **N**, one of the cones of the pallet; **O**, the stalk and the blade that compose the pallet. **bla**, blade; **con**, cone; **sta**, stalk. [R.D. Turner]

species of *Uperotus*, utilise wood or other plant material as food and bore throughout life or until no further space is available. If this happens they cap the tube anteriorly and, depending on the richness of the phytoplankton, live at a subsistence level or die. On the basis of the pallets and characters of the soft anatomy the family is divided into three subfamilies.

The subfamily Kuphinae comprises a single genus, *Kuphus*, and, on the basis of tubes only, has been reported from the middle Eocene. *Kuphus polythalamia* (Fig. 8.52A), the only living species, is not known in Australia, but is mentioned here because of its confusion with *Dicyathifer manni* (Fig. 8.52B) and because it might well be found on the north coast. Hedley (1895) observed *Kuphus* tubes in Papua New Guinea. Sivickis (1928) described a colony of sand-borers which he called *K. dubia* and said were closely related to *Kuphus arenarius* (= *K. polythalamia*). Anatomical studies by Turner (1966) on *Kuphus* show it to have a small shell, reduced adductor muscles, a muscular collar binding the valves posteriorly, long separate siphons, simple pallets, a reduced visceral mass largely posterior to the shell, and a long pericardium with the ventricular bulb traversed by the intestine. The large tube of an adult may reach 1.5 m in length, 55–60 mm in diameter, and the wall 8 mm in thickness. These enormous tubes are in many museum collections, but most lack data.

The subfamily Teredininae includes ten genera, seven known from Australia. All species bore into wood or woody plant material, have simple pallets, a large posterior adductor muscle, a moderate to large wood-storing caecum, and an intestine that does not traverse the pericardium. Identification of the 24 Australian species is based largely on the pallets and reproductive mode. Pallets of a selection of Australian species are illustrated in Figures 8.52B–D, 8.53. *Dicyathifer* (Fig. 8.52B) and *Kuphus* (Fig. 8.52A) species have similar pallets, but differ anatomically; the former are always found in wood. *Bactronophorus thoracites* (Fig. 8.53A) and *Dicyathifer manni* (Fig. 8.52B), the largest species in the subfamily, live in mangroves. Species of *Teredothyra* (Fig. 8.53B, C) are relatively rare, and are usually found in fully marine conditions from subtidal to depths of 100 m. *Uperotus* species (for example, Fig. 8.52C) in Australia are nut borers, generally found in old floating *Xylocarpus moluccensis* (a mangrove) as a cluster of closely packed tubes usually with the anterior ends closed, suggesting that they are filter-feeders. *Teredora* species (for example, Fig. 8.52D) typically bore into the underside of floating wood and so are not exposed by a receding tide. All are oviparous except species in *Teredo* (Fig. 8.53H–M) and *Lyrodus* (Fig. 8.53D–G) which are not only larviparous, but also the smallest of the teredinids.

The subfamily Bankiinae includes four genera, all known from Australia. They differ from the Teredininae in having pallets composed of numerous segments which may be closely packed and indistinct in *Nototeredo* (Fig. 8.54A) and *Spathoteredo* (Fig. 8.54B) species; distinct, but with fused segments in *Nausitora* species (Fig. 8.54C, D); or with individual segments (cones) set on a long stalk as in *Bankia* species (Fig. 8.53E–O). Species of *Spathoteredo* and *Nausitora* often have calcareous encrustations at the distal end of the pallets. They are all oviparous wood borers; many are found in brackish water.

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SUBCLASS ANOMALODESMATA

CHAPTER 9

DEFINITION AND GENERAL DESCRIPTION

The subclass Anomalodesmata, comprising the single order Pholadomyoida, includes some of the strangest and most specialised bivalves. All known anomalodesmatans are estuarine or marine. Most are small, nestling or burrowing forms with prismatonacreous shells, and have either modified eulamellibranchiate ctenidia (gills) with reduced and reflected outer demibranchs or septibranch ctenidia. Three families, the Cuspidariidae, Poromyidae, and to a lesser extent, the Verticordiidae, are considered to be septibranch. Their ctenidia, in association with their carnivorous lifestyle, are reduced to a muscular, pumping septum that lies horizontally along the ctenidial axis. The primary, opisthodetic ligament is internal or external and is often associated with a calcareous lithodesma. A thickened and fused periostracum forms a secondary ligament above the primary ligament and is thought to be involved with shell valve alignment (Yonge 1976; Yonge & Morton 1980). The hinge (Fig. 9.1) is typically edentulous although secondary teeth are present in some taxa. These teeth can be simple, single tooth and socket types (as in *Cleidothaerus*; Morton 1974) or composed of opposing paired and single teeth fitting into opposing sockets (as in Pandoridae; Yonge & Morton 1980). Boss & Merrill (1965) termed these secondary teeth anterior, posterior and median cardinal teeth respectively, although the analogy to other cardinal teeth is uncertain. The mantle lobes are fused, often leaving a pedal gape and a fourth pallial aperture in addition to the siphons. Arenophilic radial mantle glands, responsible for secreting glues that bond sand to the shell's exterior, occur in several families and are unique to the subclass. The Anomalodesmata includes filter-feeding, deposit-feeding and carnivorous bivalves. Large paired kidneys and a Type IV stomach are typical of the subclass. The carnivorous septibranchs have Type II stomachs. Except for cuspidariids which are predominantly dioecious, the anomalodesmatans are simultaneous hermaphrodites that produce large, yolky eggs.

Anomalodesmatans occur worldwide in habitats ranging from intertidal to abyssal. Newell, Cox, Keen, La Roque & Smith (1969) listed many Recent and fossil representatives dating right back to the early Palaeozoic. The Recent fauna is remarkably diverse. The numerous Australian fossil Anomalodesmata are discussed by Runnegar (1974). Cotton (1961) and Macpherson & Gabriel (1962) described many of the extant Anomalodesmata living in Australian waters. Excellent overviews of the evolution and adaptive radiation of the subclass are given by Morton (1981a, 1985a) and Runnegar (1974). Specific information on distributions and characteristics of Australian species are usually to be found in ecological reports (for example, see Stephenson, Williams & Cook 1974); there are few synoptic works on Australian Anomalodesmata. B.J. Smith (1971, 1976) reviewed the Australian members of the Clavagelloidea, and accounts of individual species of Australian Anomalodesmata (though not necessarily of specimens from Australia) are given by Morton (1973 on *Laternula truncata*; 1981b on *Offadesma angasi*; 1984a on *Clavagella australis*), and Macpherson (1951; on a new species of *Myadora*).

HISTORY OF DISCOVERY

Anomalodesmatans typically are rare and often occur in the deep sea. Early works on the subclass concentrated on describing taxa and detailing their gross anatomy. These works have provided a framework for recent studies and interpretations of anomalodesmatan phylogeny. Among these early works are important papers by Broderip (1834 on *Clavagella*); Adams & Reeve (1848–1850); Hancock (1853a, 1853b on *Myochama* and '*Chamostrea*'); Owen (1835 on *Clavagella*); Gray (1858a, 1858b); Reeve (1859 on *Thracia*); Angas (1869, 1872); de Lacaze-Duthiers (1870 on *Aspergillum*); Tate (1886 on Australian fossil Anomalodesmata); Pelseneer (1888a, 1888b, 1891); Dall (1890, 1915 including works on Anomalodesmata under the name 'Anatinacea'); Grobben (1892 on *Cuspidaria*); and Plate (1897 on 'septibranchs').

Early work including Australian anomalodesmatans was based on collections made by early expeditions to Australian waters (see Chapter 1). Knowledge of the Anomalodesmata expanded during the first half of the 20th Century. Ridewood (1903), Yonge (1928, 1937), Thiele (1935) and Atkins (1937) examined specific anatomical systems and gave details on the ctenidia, mantle and siphons.

MORPHOLOGY AND PHYSIOLOGY

External Features and Shells

Shell macrostructure is diverse in the Anomalodesmata. Shells can be equilateral or inequilateral, usually with the anterior rounded and the posterior truncate or rostrate. Shells can also be equivalve or inequivalve, some taxa having one valve flattened (Fig. 9.14D). Pandorid species have a flat right valve which faces upward in the substratum (Allen 1954, 1961a), whereas species of *Myadora* (Myochamidae) have a flat left valve which faces downward in the substratum (Morton 1977). Species of *Cleidothaerus* (Cleidothaeridae) have strongly inequivalve and inequilateral shells with the right valve deeply cupped and the left valve flat and reduced. These bivalves have strongly coiled umbones as a result of a tangential growth component (Morton 1974). The shell form of cleidothaerids reflects their cemented lifestyle. The most bizarre-appearing anomalodesmatans are in the family Clavagellidae, among them the so-called watering pot shells which have a small shell embedded within a long adventitious tube (Purchon 1956a, 1960; Smith, L.S. 1962a, 1962b; Smith, B.J. 1971, 1976; Soliman 1971; Morton 1984a). The anterior end of the tube is modified as a sieve-like plate through which water is pumped by action of 'septal' muscles associated with the pedal gape (Purchon 1956a, 1960). Most members of the group have thin shells, those of some burrowing laternulids being extremely thin. The Cleidothaeridae, however, are an exception, the attached cleidothaerids being very thick shelled. Variation in external shell sculpture is limited. Many anomalodesmatans have radial and commarginal ribs. Verticordiids and lyonsiids have thin, irregular radial ribs extending from the umbones to the shell margin. Thraciids have well-defined commarginal (concentric) ribs. Radially arranged spinules are common in some members of the subclass. The external shell of *Lyonsia* has small, truncated spinules (Prezant 1979a) whereas *Laternula* has small, conical spinules that are prefabricated by the mantle (Aller 1974). Similarly, spinules are characteristic of many verticordiids though it is not known if these are prefabricated. Deep radial and commarginal sculpture is found in several septibranch taxa.

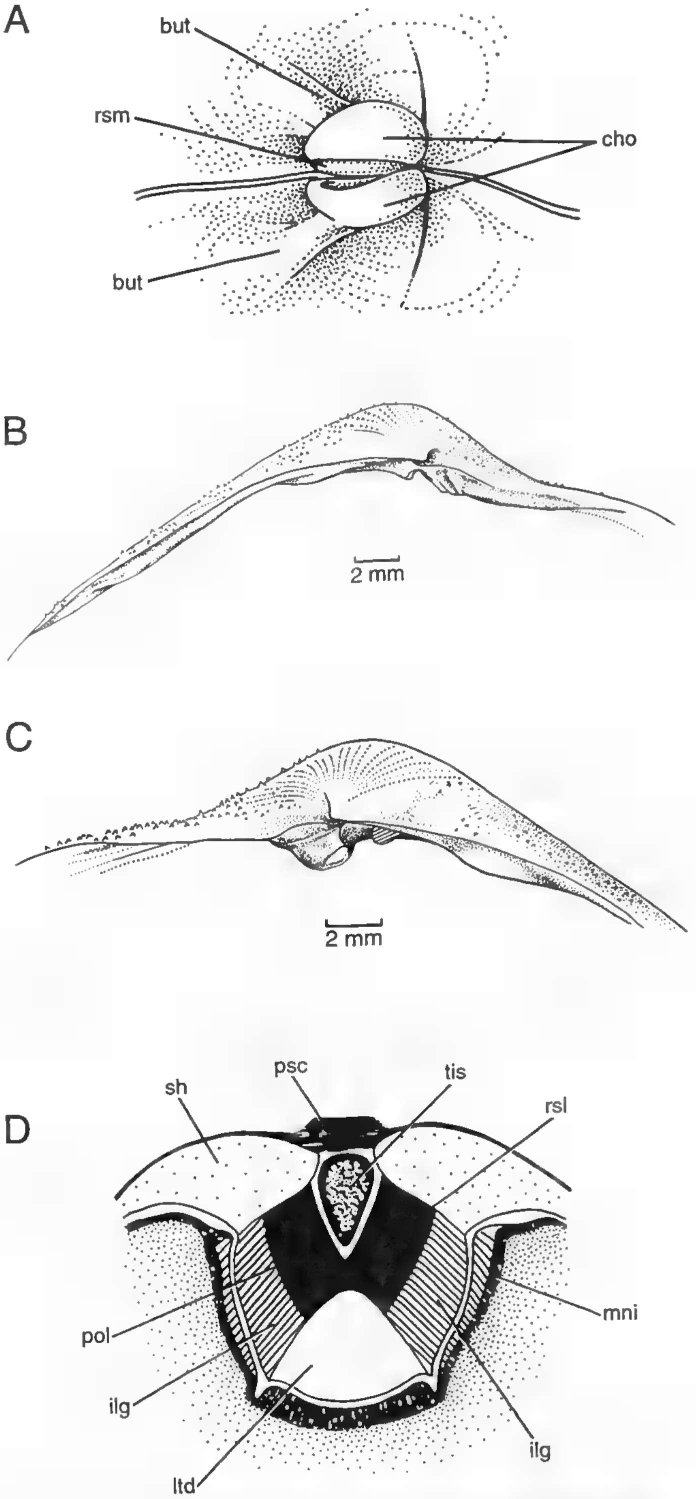

Figure 9.1 Anomalodesmatan hinges. **A**, *Offadesma angasi* (Periplomatidae), with spoon-shaped chondrophores mounted on strong posterior supporting buttresses and the internal ligament (resilium). **B, C**, *Poromya* cf. *buttoni* (Poromyidae): **B**, left valve; **C**, right valve. **D**, *Lyonsiella abyssicola* (Verticordiidae), transverse section through primary and secondary ligaments. **but**, supporting buttress; **cho**, chondrophore; **ilg**, inner ligament; **ltd**, lithodesma; **mni**, mantle isthmus; **pol**, posterior outer ligament; **psc**, fused periostracum; **rsl**, resilifer; **rsm**, resilium; **sh**, shell; **tis**, tongue of tissue. (A, modified after Cox 1969; D, after Yonge & Morton1980)
[A, D, R. Plant; B, C, A.J. Hill]

Most species have a prismatonacreous shell although the Cuspidariidae and some Thraciidae and Poromyidae have homogeneous shell microstructures (Taylor, Kennedy & Hall 1973). At least some species of *Entodesma* (Lyonsiidae) have a well-developed granular homogeneous shell layer in addition to a prismatonacreous layer (Prezant 1981a).

The hinge (Fig. 9.1) is typically edentulous, but some taxa (for example, *Thraciopsis*, and some taxa of the Pandoroidea, Poromyoidea and Cuspidarioidea) have secondary teeth (Boss & Merrill 1965; Morton 1974, 1984b; Yonge & Morton 1980). The primary ligament is external in the Pholadomyoidea, some Thraciidae, Poromyoidea and Clavagelloidea, but internal in the Pandoroidea, some Thraciidae, Laternulidae, Periplomatidae, Verticordioidea and Cuspidarioidea (Morton 1980, 1984a, 1985c; Yonge & Morton 1980). A local thickening of the periostracum above the primary ligament forms a characteristic secondary ligament (Fig. 9.1D), which assists in alignment of the valves (Yonge 1976; Yonge & Morton 1980). The lithodesma (Fig. 9.1D), when present, has a complex prismatic microstructure composed of densely packed small prisms produced in a dendritic fashion (Prezant & Carriker 1983) and is associated with abduction and valve alignment (Yonge 1976; Yonge & Morton 1980; Morton 1985a). The lithodesma reinforces the primary inner ligament by essentially dividing its mechanical effort in half. By avoiding the extensive pressures that would be associated with a single, very wide ligament, the lithodesma distributes a reduced force between portions of the inner ligament (Yonge & Morton 1980).

Mantle

Anomalodesmatans are typified by having fused mantle lobes with free lobes occurring only at the siphons, and at the pedal and fourth pallial apertures. Most (for example, members of the Pholadomyoidea, Verticordioidea and most of the Pandoroidea) have Yonge's (1976, 1982) Type B fusion, involving the inner and middle mantle folds (Yonge 1952; Allen 1954; Morton 1973, 1977, 1982, 1984a, 1985c). Type A fusion, involving only the inner fold, is present in the Poromyoidea and species of *Periploma* (Thracioidea) and *Cleidothaerus* (Pandoroidea) (Morton 1974, 1981a, 1981b, 1985a). Only clavagellids have a Type C mantle fusion, involving the inner and middle folds and inner surface of the outer fold (Morton 1984a, 1985c, 1984b). A fourth pallial aperture, located between the exhalant siphon and the pedal gape and of unknown function, is present in most Anomalodesmata except for the Laternulidae, Pandoridae, Poromyidae, Verticordiidae, and some Periplomatidae (Allen 1954, 1958; Morton 1973, 1981a, 1984a, 1985c). Morton (1980) suggests that the fourth pallial aperture acts mainly as a pressure-release valve in *Pholadomya* during pedal-feeding when pressure on shell or body organs can build up. The function in other anomalodesmatans has not been ascertained but in forms, such as *Lyonsia*, that are infaunal burrowers, it could serve as a pressure-release valve during burrowing. This is the proposed function in some non-Anomalodesmata that burrow rapidly (for example, *Ensis*, *Siliqua*) for which it could also serve to 'liquify' sediments during burrowing (Allen 1985). Yonge (1948) suggested this pallial opening in the Mactroidea could function in removal of body wastes.

Arenophilic radial mantle glands (Fig. 9.2) are unique to the Anomalodesmata although they are not present in all groups. The glands have been reported for some taxa in the families Verticordiidae (Allen & Turner 1974), Lyonsiidae (Prezant 1979b, 1981b, 1985), Periplomatidae (Morton 1981b), Parilimyidae (Morton 1982) and Clavagellidae (Morton 1984a, 1984c). These glands, in the Lyonsiidae, secrete a bilayered mucopolysaccharide and glycoprotein that adheres to the outside of the periostracum and functions to bond sand grains to the shell's exterior (Prezant 1981b). The sand coat can serve to protect the exposed posterior region (siphons) through camouflage or, in infaunal sand dwellers, to increase frictional resistance thereby affording them increased stability (Prezant 1981b). For infaunal species, such as *Lyonsia*, the sand coat could protect the bivalve from drilling by naticid gastropods (Prezant 1981b). In rocky crevice-dwelling species of *Entodesma*, as the bivalve grows and the shell thickens, the glands are gradually reduced in number. This does not occur in other lyonsiid genera but a possible corresponding decrease in gland number with shell growth remains unexamined in other anomalodesmatans.

In the Parilimyidae, arenophilic radial mantle glands are present along the mantle edge and, according to Morton (1982), are invaginations of the middle mantle fold. Prezant (1981b), however, found that these glands are modifications of the outer secretory mantle fold epithelium in the Lyonsiidae. In *Lyonsia*, the secretion appears as wrinkled, radially arranged strings running dorso-ventrally over the periostracum. In *Entodesma*, the secretion appears as a series of radially arranged tufts atop the periostracum. Prezant (1981b) suggested that the gland in *Entodesma* is distal to the periostracal groove and that secretion from the gland must periodically penetrate the periostracum to fulfil its adhesive function. To allow this process, Prezant speculated, the protein component of the gland secretion must contain a proteolytic enzyme which facilitates penetration of the periostracum. Morton (1987a) found this explanation overly complex and suggested a different arrangement of multiple periostracal grooves secreting around the arenophilic gland secretion thus accounting for the appearance of periostracal penetration. The differences in interpretation of these glands are addressed in Prezant (1985) and Morton (1987a).

Siphons are among the most variable of anomalodesmatan features. Long and short as well as fused and separate siphons occur. The predatory anomalodesmatans (Verticordioidea, Poromyoidea and Cuspidarioidea, *Parilimya*) have an inhalant siphon that is often expanded and may form a hood, possibly either to entrap small prey or to serve as a suctorial device to ensnare prey (Morton 1987b). In most anomalodesmatans, the siphons are crowned by simple tentacles. Members of the Parilimyidae (Morton 1987b) and Pholadomyidae (Morton 1980) lack tentacles or any other prominent ornamentation on their siphons. Morton (1987b) notes, however, that the siphons of *Parilimya fragilis* and *P. maoria* have very small papillae lining the internal surface of the enlarged and muscular inhalant siphon. See the section on Sense Organs and Nervous System for discussion of sensory structures associated with the siphons.

Musculature

Anomalodesmatans are dimyarian; Parilimyidae, Cleidothaeridae, Periplomatidae, Laternulidae and Thraciidae are heteromyarian, and the other families are isomyarian or slightly heteromyarian. Specialised taenioid muscles are present in the Parilimyidae and weakly developed in the Pholadomyidae and some Verticordiidae (Morton 1980, 1981a, 1982, 1985c); they are involved in retraction of the enlarged inhalant siphon in parilimyids. Other anomalodesmatans have typical bivalve siphonal retractor muscles. Pedal retractors are reduced in several of the more sedentary taxa, for example, *Cleidothaerus*, (see Odhner 1917; Morton 1974) living permanently attached by its right valve to rocks and algae, and the flattened infaunal *Myadora* (Morton 1977) living buried in sandy sediments. *Parilimya* lacks pedal retractors (Morton 1977). An unusual and unique muscle system associated with the pedal gape is found in *Pholadomya* species. In these a pair of pedal gape muscles crosses correspondingly from opposite sides of the gape to insert on the opposing shell valve (Morton 1980). The Poromyidae and Cuspidariidae have strong septal muscles associated with their septibranch ctenidia.

Locomotion

Most Anomalodesmata are sedentary or sessile. The foot is often reduced in association with a corresponding reduction in the pedal retractor muscles in these sedentary and sessile forms as noted above. It is well developed in the Cuspidariidae, Poromyidae, Verticordiidae, some Laternulidae, Periplomatidae, Lyonsiidae, Pandoridae and Parilimyidae, reflecting the burrowing abilities of these infaunal bivalves, but very few anomalodesmatans have a well-developed byssal groove, and only representatives of the Lyonsiidae and Verticordiidae are reported to have an adult byssus, usually consisting of a few byssal threads (Yonge 1952; Ansell 1967; Narchi 1968; Morgan & Allen 1976; Prezant 1981c). The well-developed foot of the verticordiid *Lyonsiella formosa*, is modified for burrowing and also has a byssal groove and byssal gland; however, no byssal threads have been discerned (Morton 1985c). Other verticordiids, however, have been found to produce a few, weak byssal threads (Allen & Turner 1974). Among the Lyonsiidae, *Entodesma* species produce numerous strong byssal threads that tightly secure the animal within rock crevices, but *Lyonsia* produces only a few, thin threads attached to individual sand grains (Prezant 1981c). It is likely that juvenile anomalodesmatans are usually more active than adults and can burrow more actively and 'search' for a 'home site'.

Feeding, Digestive and Ctenidial Systems

Anomalodesmatans are deposit-feeders, filter-feeders or predators. Feeding mode is well reflected in the form of the digestive system, ctenidia, palps and siphons. A recent account of the general anomalodesmatan digestive system, as exemplified in lyonsiid bivalves, was given by Thomas (1993). Most Anomalodesmata have a Type IV stomach (Purchon 1958) except the 'septibranchs' (Cuspidarioidea, Poromyidae and Verticordiidae) and *Parilimya* which have a Type II stomach (Purchon 1956b) adapted for reception of larger food items such as small crustaceans. *Parilimya* species have muscular stomach walls heavily lined with a chitinous layer for grinding, a small crystalline style, and relatively few primary digestive ducts with large lumina leading to the digestive glands (Purchon 1956b). The style sac and midgut are continuous in the Type IV stomach. Type II stomachs are adapted for handling and breaking down larger food items. As such they also produce strong digestive enzymes (Reid 1977). Among septibranchs, verticordiids show the least specialisation of the stomach for carnivory and some even have a Type IV stomach (Morton 1981a, 1982). The labial palps are variable, large or small and with or without deep sorting ridges according to the type of food collected by the bivalve. Most anomalodesmatan labial palps are of the typical bivalve plan and are involved with collecting and sorting food after it is delivered from the ctenidial food grooves. However, those of carnivorous bivalves including parilimyids, cuspidariids, verticordiids and Poromyidae, are modified. They are reduced, muscularised and ruffled, and have either very few or no sorting grooves (Allen & Turner 1974; Morton 1981a, 1985c). These features, too, are adaptations to a carnivorous lifestyle in which large prey such as copepods are caught.

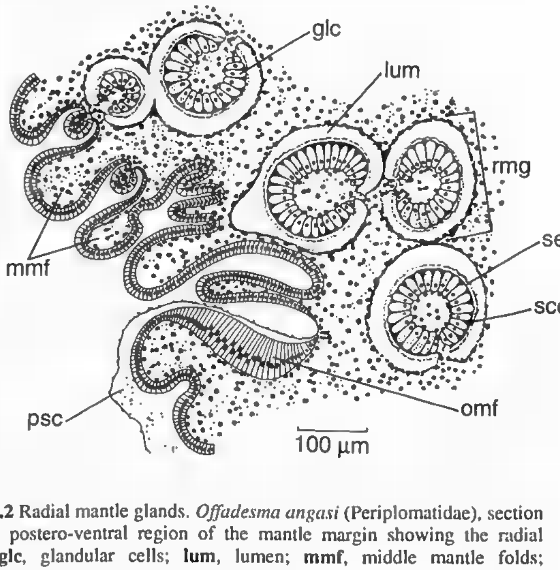

Figure 9.2 Radial mantle glands. *Offadesma angasi* (Periplomatidae), section from the postero-ventral region of the mantle margin showing the radial glands. **glc**, glandular cells; **lum**, lumen; **mmf**, middle mantle folds; **omf**, outer mantle fold; **psc**, periostracum; **rmg**, radial mantle gland; **sce**, supporting cell; **sec**, secretion. [R. Plant]

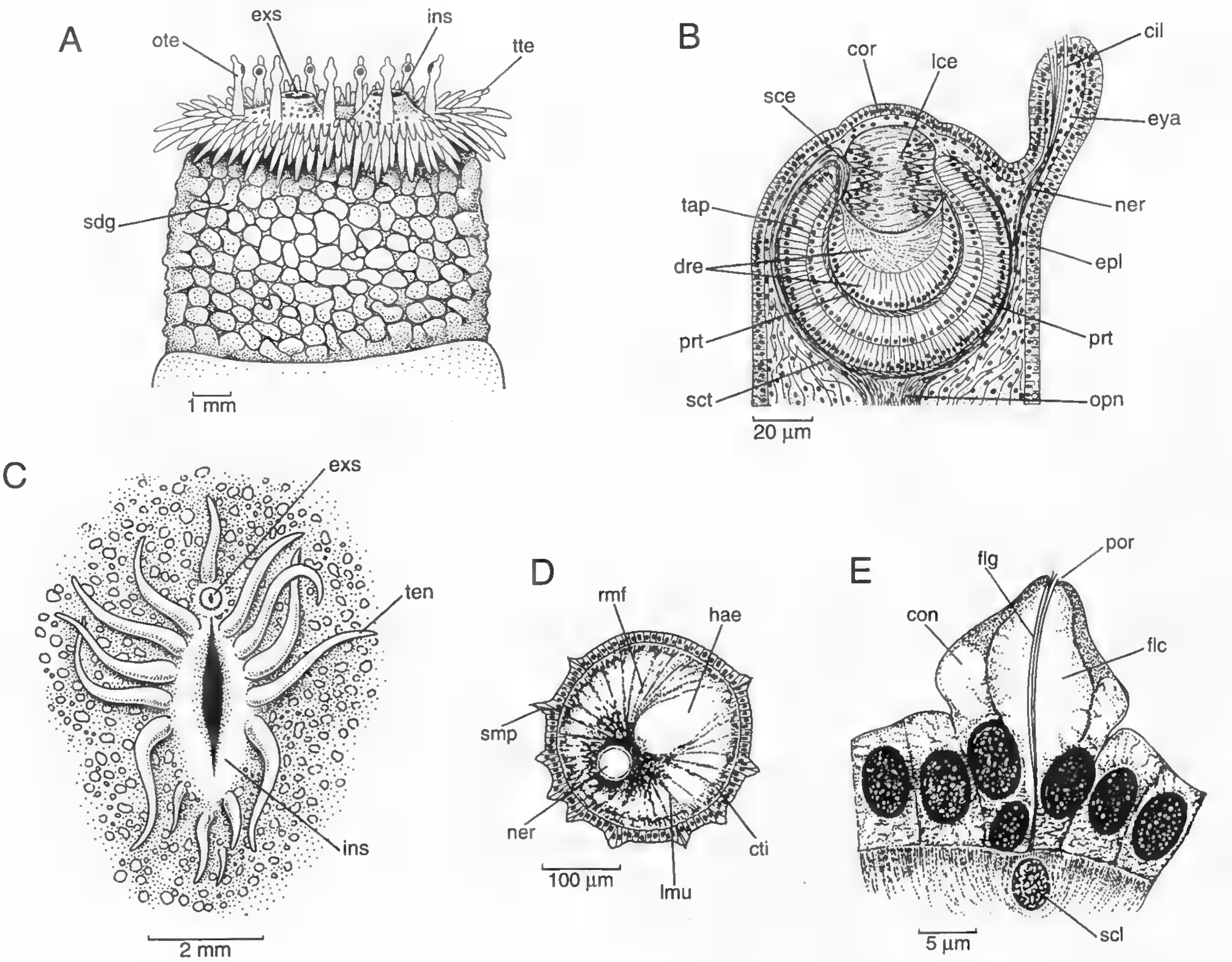

Figure 9.3 Anomalodesmatan sensory structures. A, **B**, *Laternula truncata* (Laternulidae): **A**, lateral view of the siphons showing the optic tentacles; **B**, longitudinal section through an eye on the tip of an optic tentacle. **C–E**, *Poromya granulata* (Poromyidae): **C**, siphons and tentacles as seen posteriorly with shell buried in the sand; D, transverse section through a single siphonal tentacle; E, detail of single sensory papilla of a siphonal tentacle. **cil**, cilia; **con**, cone-shaped cell; **cor**, cornea; **cti**, connective tissue; **dre**, distal retina; **epl**, epithelium; **exs**, exhalant siphon; **eya**, eye appendage; **flc**, flask-shaped chamber; **flg**, flagella; **hae**, haemocoel; **ins**, inhalant siphon; **lce**, lens cell; **lmu**, longitudinal muscle; **ner**, nerve; **opn**, optic nerve; **ote**, optic tentacle; **por**, pore; **prt**, proximal retina; **rmf**, radial muscle fibres; **sce**, supporting cell; **scl**, sensory cell; **sct**, sclerotic; **sdg**, sand grains; **smp**, small epithelial projection; **tap**, tapetum; **ten**, tentacle; **tte**, tactile tentacle. (A, B, after Adal & Morton 1973; C–E, after Morton 1981) [R. Plant]

The ctenidia of most anomalodesmatans are Type E (Atkins 1937). They are modified eulamellibranchiate ctenidia comprising an entire inner demibranch and a reduced outer demibranch consisting only of the descending lamella, which is reflected dorsally. The ctenidia are typically plicate and heterorhabdic. The Cuspidariidae and Poromyidae have septibranch ctenidia, effectively a muscularised septum that lies horizontally in the mantle cavity. The septum is used to create a negative hydrostatic pressure during feeding (Reid & Reid 1974; Morton 1987b). It has highly reduced, remnant ctenidial filaments which are retained only as septal ostia. The origin of the septum is a topic of long standing and vigorous debate (Dall 1890; Ridewood 1903; Yonge 1928; Bernard 1974; Allen & Morgan 1981). Whether its origin is to be found in the ctenidium itself or in an invasion of pallial, taenioid or pedal gape musculature is discussed by Bernard (1974, 1979), Morton (1981a) and Allen & Morgan (1981).

Dall (1890) suggested that the septum developed as an extension of the intersiphonal septum and that siphonal retractor muscles and the ostia developed secondarily. Ridewood (1903) supported the concept that the septum is a muscularised ctenidium with reduced branchial pores. Yonge (1928) agreed with this interpretation, but Bernard (1974) argued that the septum arose in an ancient stock that lacked ctenidia and developed a secondary outgrowth of mantle tissue. An evolutionary series leading to the septibranch condition was outlined by Allen & Morgan (1981) who suggested that the septum was derived from the gill. They documented occurrence of ctenidial filaments within the septum ostia system and hypothesised an evolutionary series from typical eulamellibranchiate ctenidia that includes regression of filaments, loss of skeletal support rods, and increased muscularisation. Strong emphasis has been placed on the origin of the septum and its potential use in taxonomy of the 'septibranchs'. Morton (1985a) supported a polyphyletic origin from a variety of pholadomyoidean ancestors.

In general, anomalodesmatans are filter-feeders, drawing in plankton in the inhalant current, trapping them on their highly folded ctenidia and using ciliary currents to bring the food ventrad to the food groove and then forward to the palps for primary sorting. Ctenidia and palps are joined in a Type III junction (Stasek 1963) with only a few ctenidial filaments of the inner demibranch extending between the palps. Lyonsiids have the ventral portion of the anterior ctenidial filaments of the inner demibranch fused to the anterior oral groove, a Type II junction (Narchi 1968).

The siphons of the Parilimyidae, Poromyidae, Verticordiidae and Cuspidariidae are modified for predatory feeding. The inhalant siphons of poromyids and some verticordiids are modified as hoods or cowls possibly to entrap prey; those of cuspidariids and parilimyids are muscular and extensible and possibly function by extending and 'inhaling' prey (for a review see Morton 1987b). Prey thus brought into the mantle cavity are transferred to the mouth by the extensible labial palps. Strong proteolytic enzymes have been discovered in the stomach of some cuspidariid species (Reid 1977).

Circulatory System

The thin-walled pericardial chamber contains a typical bivalve heart composed of a muscular ventricle and paired auricles. Several species that have been examined have anterior and posterior aortas, for example *Offadesma angasi* (Morton 1981b). The rectum penetrates the ventricle in laternulids, myochamids, parilimyids and poromyids (Morton 1973, 1977, 1981a, 1982). It passes above the heart in the Pandoridae and Cleidothaeriidae and below it in *Pholadomya* (Allen 1954; Morton 1973, 1980; Thomas 1994). A pallial lacunal system, associated with predatory feeding habits and corresponding hydraulic activities, is present in the Poromyidae, Cuspidariidae and Verticordiidae (Allen & Turner 1974; Reid & Reid 1974; Morton 1982). This lacunal system, containing blood cells, is extensive in some verticordiids (Allen & Turner 1974), infiltrating a large portion of the mantle surrounding the suprabranchial chamber. Morton (1985c) speculated that shell adduction forces blood from the pallial lacunal system into the siphonal hood of septibranchs allowing it to evert and thus entrap prey. Allen & Morgan (1981) described a complex sinus system that opens into the auricles of the Cuspidariidae and ramifies through the gonads, kidneys, siphons, septum and mantle. These too are associated with changes in hydraulic pressure that occur during septal movement and shell closure in these predatory bivalves.

Excretion

Most anomalodesmatan species examined have large paired kidneys, often showing round and lamellate excretory concretions in the distal limb. The kidneys usually drain the 'coelom' by a pair of nephrostomes located postero-ventrally in the pericardial chamber. The narrow proximal kidney limbs are usually tubular and surrounded by the more spacious distal limbs which open by paired nephridiopores into the posterior suprabranchial chamber. In laternulids, the nephridiopores empty into a cloacal aperture along with the gonopores (Morton 1973).

Sense Organs and Nervous System

The nervous system of the Anomalodesmata is of the typical bivalve plan, comprising cerebral, pedal and visceral ganglia and connectives. Statocysts are present and range from very simple (Pandoridae) to complex (Pholadomyidae) (Morton 1985b). In most Anomalodesmata (Morton 1985b), as is typical in bivalves, the statocysts are adjacent to or even appear embedded within the pedal ganglia. The anomalodesmatan statocysts variably comprise relatively few or numerous cells and contain either solitary statoliths or numerous, smaller statoconia.

Type A statocysts occur only in *Pholadomya candida* and are perhaps the most complex statocyst system within the Anomalodesmata. They occur in the foot, separate from the pedal ganglia, and are composed of a solid statolith surrounded by a complex ovoid chamber encased by nerves. Cuspidariids have simple Type C statocysts composed of few cells containing a single large statolith (Morton 1985b). These balance organs do not abut the pedal ganglia but are separated from them. In all species investigated, the statocysts are innervated by the cerebral ganglia.

Other sensory structures in the Anomalodesmata (Fig. 9.3) are associated with protection or feeding. The tentacles that fringe the siphons of many Anomalodesmata typically are mechano-, chemo- or photosensitive. A siphonal ganglion is present in some lyonsiids and is associated with numerous ciliary-based photoreceptors (Prezant 1977). Even more complex photoreceptors, tipping siphonal tentacles, are present in laternulids (Fig. 9.3A) (Adal & Morton 1973). The eyes of *Laternula* are remarkably complex. Associated with the siphonal tentacles are nine photoreceptors, each composed of an apical lens, a surrounding pigment cup and a bilayered, ciliary based retina (Adal & Morton 1973). These eyes function as shadow receptors. Similarly, the simpler eyes of *Lyonsia*, comprising an apical lens capped by a nucleus and covered by a thin epithelial cornea, surrounded by a pigment cup containing melanin, and tapering to a ciliary-based retina, are also shadow receptors that when stimulated induce retraction of siphons (Prezant 1977, 1984).

The 'septibranch' bivalves often have ciliated siphonal sense organs (Fig. 9.3E) that act as mechano- or chemoreceptors (Adal & Morton 1973; Reid & Crosby 1980; Morton 1987b). In the carnivorous anomalodesmatans, siphonal mechanical receptors probably detect movement of prey.

An opisthopodium, a small bifurcating finger-like projection, is located postero-ventrally on the visceral mass in the Pholadomyidae and some Verticordiidae and perhaps *Euciroa* in the Verticordiidae. This is likely to have a sensory function based on the innervation it receives from the pedal ganglia (Morton 1980). Morton (1980, 1985a) suggested that this structure monitors inhalant water flow of *Pholadomya candida*, and he further speculated that this allows greater control during pedal-feeding in this infaunal bivalve.

Reproduction, Embryology and Development

All Anomalodesmata are simultaneous hermaphrodites, except for the Cuspidariidae which are dioecious. Gonads are paired and in mature individuals can fill a large volume of the visceral mass, surrounding and infiltrating the digestive gland, and amassing around the nephridia and pericardial chamber. In some taxa (for example *Cleidothaerus*; Morton 1974), the ovaries are found dorsally and testes ventrally. The testes form large follicles with mature spermatozoa tails directed inwards, and spermatids arranged outermost. The mature *Laternula limicola* spermatozoan is the only one known that has its acrosome located posterior to midpiece mitochondria (Hosokawa & Noda 1994). Either separate gonopores or a fused urogenital cloaca is present. The Anomalodesmata have large, yolky eggs, often surrounded by a number of external ('capsule') layers. In *Entodesma cuneata*, the outer layer is composed of mucins that swell upon contact with sea water and may entrap sperm or make the eggs buoyant (Campos & Ramorino 1981). Prezant (1981c) repeatedly found ova in the suprabranchial chamber of three other species of *Entodesma* and suggested the possibility of brooding. Indeed the separation of the ctenidia from the viscera to create a large and spacious chamber may be an adaptation for brooding (see Burne 1920 for *Laternula*; Morton 1981b for *Offadesma*, and 1982 for *Parilimya*).

Information on the embryology and development of the Anomalodesmata is inferred from a limited number of studies on some Pandoroidea from the Atlantic and southern Pacific and a rare laboratory spawning event in the septibranch *Cardiomya pectinata* recorded by Gustafson, O'Foighil, & Reid (1986). Allen (1961a), Chanley & Castagna (1966), and Campos & Ramorino (1981) have examined, respectively, the development of *Pandora inaequivalvis*, *Lyonsia hyalina* and *Entodesma cuneata*. From these studies and from the fact that the suprabranchial chamber is often capacious and eggs are yolky, it is suggested that direct development occurs within a brood chamber or, if a planktonic larva is produced, the planktonic period is very short. In *L. hyalina*, a 'straight hinge stage' is reached in 24 hours with metamorphosis beginning after three days (Chanley & Castagna 1966). In *P. inaequivalvis* (Fig. 9.4), gastrulae are present about nine hours after fertilisation, with gastrulation occurring by epiboly (Allen 1961a). *Pandora inaequivalvis* spends about 24 hours in the plankton and complete metamorphosis occurs in less than four days (Allen 1961a). Gustafson *et al.* (1986) monitored spawning and early development, in the laboratory, of the cuspidariid *Cardiomya pectinata*. They found that *C. pectinata* underwent non-planktotrophic, encapsulated development to a prejuvenile stage. Non-buoyant developing embryos have prolonged encapsulation and would presumably be benthic and thus undergo limited dispersion.

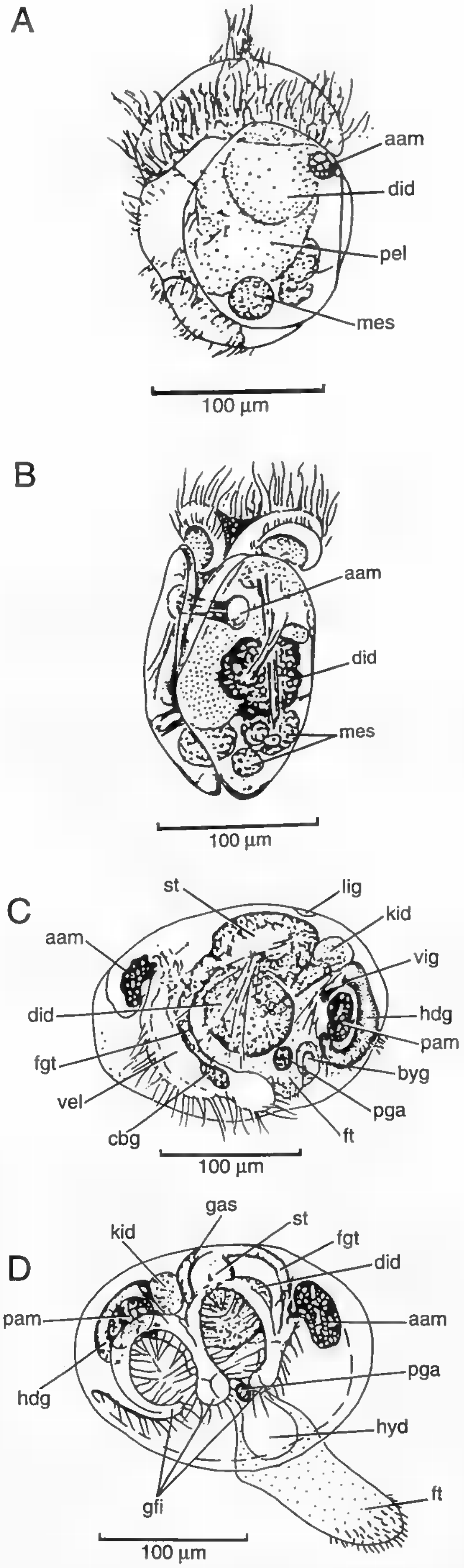

Figure 9.4 Development of *Pandora inaequivalvis* (Pandoridae). **A**, a veliger at 25 hours, lateral view, showing the bivalve prodissoconch. **B**, a veliger at 38 hours, dorso-lateral view, the velum can be completely retracted within the shell ventral to the mouth. **C**, a veliconcha at 48 hours. **D**, spat at 140 hours, foot extended and the first three gill filaments shown. **aam**, anterior adductor muscle; **byg**, byssus gland; **cbg**, cerebral ganglion; **did**, digestive diverticula; **fgt**, foregut; **ft**, foot; **gas**, gastric shield; **gfi**, gill filaments; **hdg**, hindgut; **hyd**, hydrocoele; **lig**, ligament; **kid**, kidney rudiment; **mes**, mesoderm; **pam**, posterior adductor muscle; **pel**, limit of the pellicle; **pga**, pedal ganglia; **st**, stomach; **vel**, velum; **vig**, visceral ganglion. (After Allen 1961) [R. Plant]

NATURAL HISTORY

Life History

Direct or rapid development of sedentary or sessile organisms limits their dispersal capabilities. Allen (1961a) suggested that rapid metamorphosis in pandorids reduces the risk of removal from appropriate habitats already successfully occupied by parental stock. Morton (1985a) concurred, seeing selective advantages to many Anomalodesmata in remaining in their particular microhabitats. With limited populations that are narrowly distributed, simultaneous hermaphroditism is also a key to local success. These constraints on reproductive success at broad levels are reflected in the relatively limited distribution of a variety of anomalodesmatan taxa across the Indo-Pacific. No information is available on longevity of any Anomalodesmata.

Ecology

The Anomalodesmata are today represented by a number of specialised taxa with restricted distributions, yet are as diverse in habitat as they are in form. They are limited to estuarine and marine environments, however, and occupy niches ranging from intertidal to abyssal. Shallow-water members are usually uncommon, with localised exceptions, whereas deep-water 'septibranchs' are an important component of the benthos (Knudsen 1979). Many pandorids occur in shallow, sometimes intertidal, waters along muddy shores (Yonge 1937), and *Cleidothaerus* species are found cemented to hard substrata (Morton 1974). Some lyonsiids are so specialised in microhabitat as to occur only as select endosymbionts. For example, *Mytilimeria nuttalli* from the eastern Pacific only embeds within compound tunicates (Yonge 1952). The type of habitat occupied varies within single families and even single genera; for example members of the genus *Laternula* may live from the mid- to low-tidal levels of sandy shores (*L. anatina*; Vohra 1971), commonly burrow in sands of eel grass beds (*L. tasmanica*; Morton 1973), along the exposed shores of mangroves in Singapore and Hong Kong (*L. rostrata*; Morton 1973), and in coarse sands (*L. truncata*; Purchon 1958).

The Anomalodesmata of Australian waters range from infaunal in soft sediments to epifaunal on hard substrata. For example, *Parilimya tasmanica* burrows in soft sediments in deep waters off the coast of South Australia and *Myochama tabida* lives in shallow waters cemented to *Eucrassatella cumingii* in South Australia, Victoria, Tasmania and New South Wales. Most 'septibranchs' occur in deep water whereas many of the Pandoroidea form part of the shallow-water fauna. Diversity is exemplified, not only by the variety of habitats occupied, but by the remarkable adaptations for feeding, particularly for predation. Most predatory Anomalodesmata occur at great depths and have highly specialised means of capturing and digesting small animals. Anomalodesmata that occur in shallow, more turbid waters are well adapted to handling the sediment that enters the mantle cavity and would otherwise foul the ctenidia.

Little is known of commensals or parasites of any Anomalodesmata. Prezant (1977) reported a large infection of Sporozoa in the kidneys of *Lyonsia hyalina* from the western Atlantic, perhaps producing a dwarfed population. Stunkard (1974, 1976) also reported sporocysts and cercaria infections in the gonads and digestive glands of *L. hyalina* from the western Atlantic.

Behaviour

Much of the published information concerning behaviour of anomalodesmatan bivalves is based on interpretation and inference from preserved museum specimens. For instance, the conceptualised methods of feeding in various septibranchs (Fig. 9.5; for review see Morton 1987b) are based almost solely on histological sections and dissections of preserved animals.

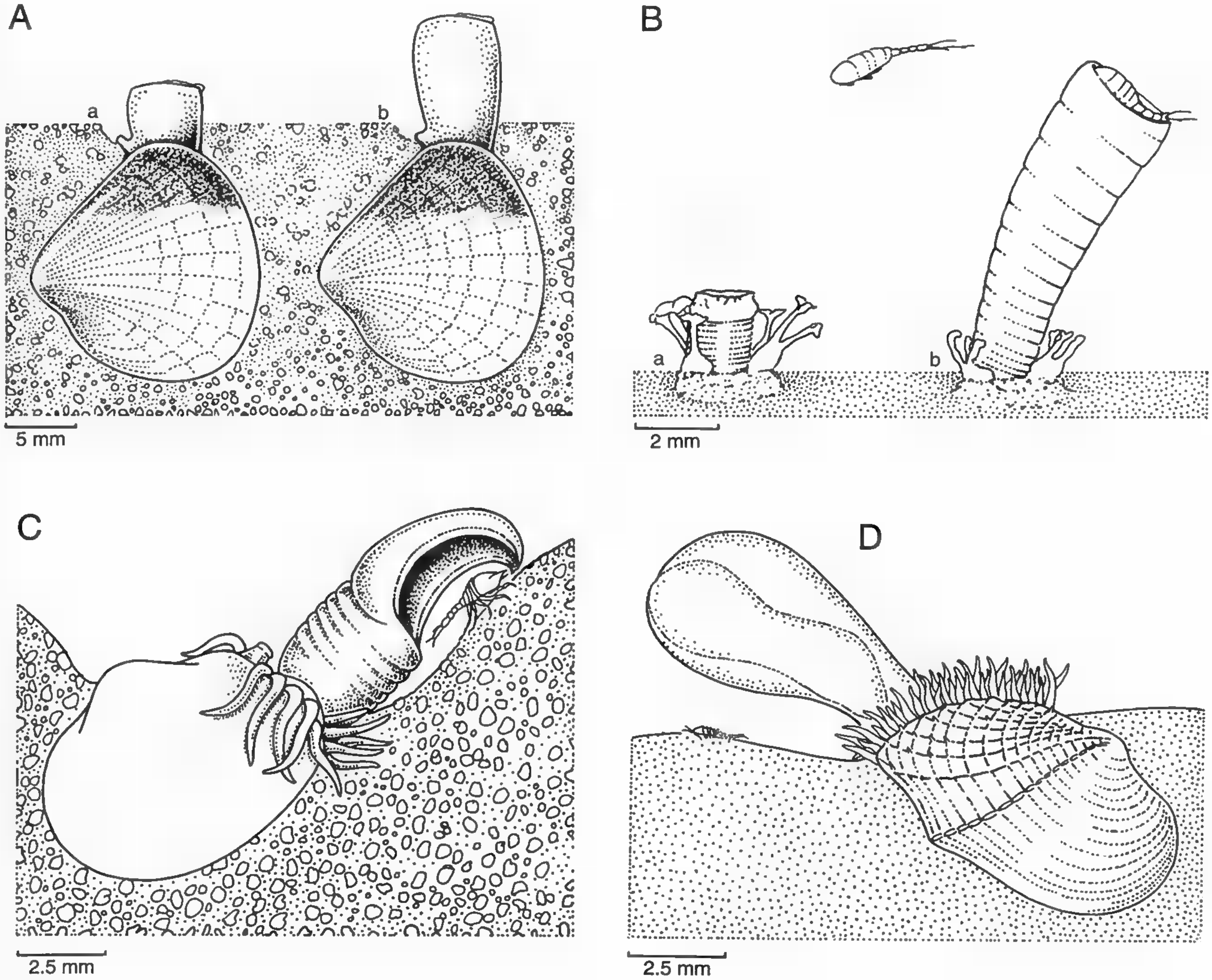

Figure 9.5 Observed and postulated prey capture in four anomalodesmatans. **A**, *Parilimya fragilis* (Parilimyidae) in its postulated natural position in the sand: **a**, the animal is has its valves widely opened and siphons half extended and is ventilating its respiratory surfaces; **b**, the inhalant siphon is extended for entrapping food. **B**, *Cuspidaria cuspidata* (Cuspidariidae): **a**, the animal is lying in the sand with the inhalant siphon retracted; **b**, the inhalant siphon is extended to capture mobile prey. **C**, postulated feeding behaviour of *Poromya illevis* (Poromyidae); the animal is shown in a natural position in the sand with the inhalant siphon fully extended ready to capture a bottom-dwelling crustacean. **D**, postulated feeding posture of *Lyonsiella formosa* (Verticordiidae); the animal is in a natural position in the sediment with the cowl of the inhalant siphon fully extended, about to capture a bottom-dwelling copepod. (A, after Morton 1982; B, after Reid & Reid 1974; C, after Morton 1981c; D, after Morton 1985c) [R. Plant]

Morton (1985c) examined a single, preserved specimen of *Lyonsiella formosa*, a deep-water verticordiid from off the coast of Hawaii. He speculated that stimulation of sensory papillae on the siphonal tentacles induced the eversion of a large 'hoodlike cowl of the inhalant siphon' allowing prey to be trapped and brought into the mantle cavity (Fig. 9.5D). In a rare observation of living specimens, Morton (1981c) examined two specimens of *Poromya illevis* (= *Poromya granulata*) dredged off the coast of Norway from a depth of 80 metres. Based on observation of living and then preserved specimens of these poromyoideans, Morton described an active predatory feeding mechanism (Fig. 9.5C), involving a hood similar to that of *Lyonsiella formosa*. Similar feeding mechanisms led Morton (1985c) to suggest a close familial linkage between the Verticordiidae and Poromyidae.

Burrowing activity has been examined in a few anomalodesmatans, including species of *Lyonsia* (Ansell 1967) and *Periploma* (Fig. 9.6; Rosewater 1984). Although most infaunal forms are considered to be 'passive burrowers', only gradually submerging in the sediment with growth, some periplomatids and lyonsiids are active burrowers that basically follow Stanley's (1970) stages of burrowing. Thus, *Lyonsia* species initially probe the substratum with the foot, close the siphons and quickly adduct the valves to force a jet of water into the sediment allowing the foot to probe deeper and then gain anchorage. Pedal retractor muscles contract pulling the shell deeper into the sediment. Rosewater (1984) found periplomatids to be 'sluggish burrowers'. He suggested that the thin-shelled bivalve *Periploma margaritaceum* uses its muscular exhalant siphon to help cleanse the mantle cavity of sand debris accumulated during burrowing and in doing so, helps to clear the way forward when entering the sediment. The bellows-like exhalant siphon closes off and forms a 'bulb'; sudden contraction of the siphon creates the previously noted currents. This action avoids undue physical stress on their thin valves. Other periplomatids, such as *Offadesma angasi* (Morton 1981b), have a reduced foot and associated pedal retractors and if removed from their buried position are unable to re-bury. Narchi (1968) timed a 20 mm specimen of *Lyonsia californica*; it buried itself completely in 25 minutes.

At least some periplomatids are preyed upon by naticids (Rosewater 1980) and some laternulids by echinoderms (Zamorano, Durate & Moreno 1986). Like many other anomalodesmatans, clavagellids may have arenophilic radial mantle glands along their mantle margins, which secrete a 'glue' to which sand grains adhere. The resultant sand coat can serve to protect the exposed posterior region (siphons) through camouflage or, in the case of infaunal sand dwellers, to increase frictional resistance thereby affording them increased stability (Prezant 1981b). In *Lyonsia* species, at least, the sand coat gives protection from drilling by naticid gastropods (Prezant 1979b, 1981b).

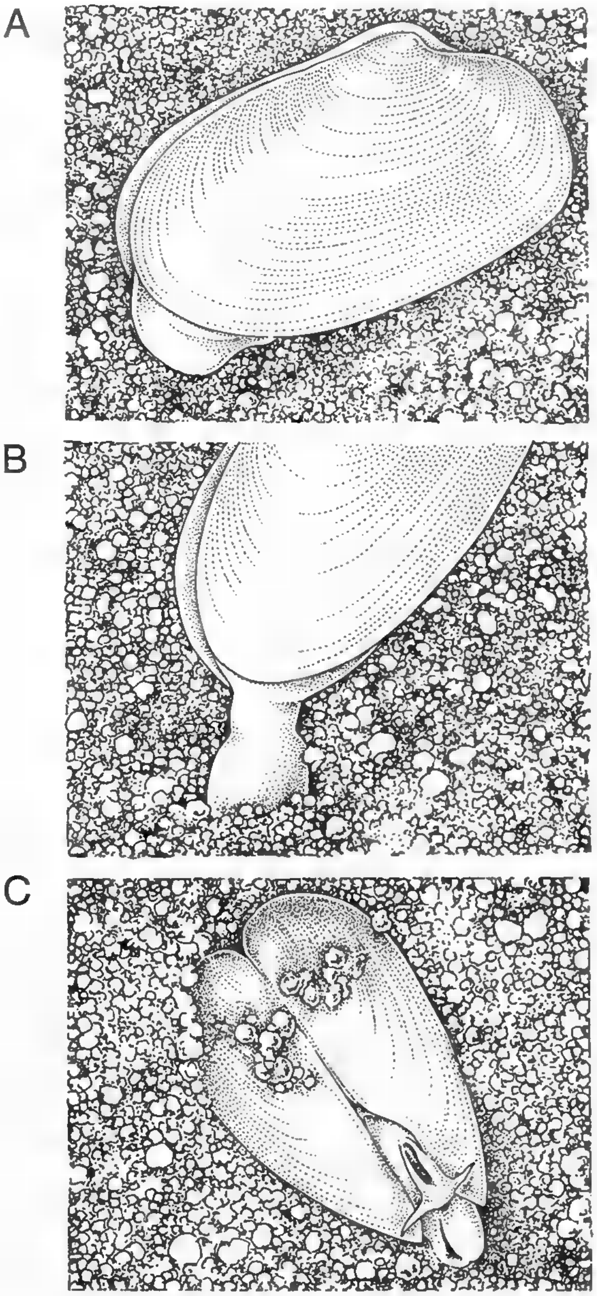

Figure 9.6 Stages of burrowing in *Periploma margaritaceum* (Periplomatidae). **A**, individual lying on right valve with foot protruding slightly antero-ventrally from mantle pedal aperture. **B**, foot digging into substratum; note enlarged tip of foot. **C**, individual partially buried, siphons beginning to protrude; note elongate opening of exhalant siphon with two tentacles. (After Rosewater 1984) [R. Plant]

The well-developed photoreceptors present on the exhalant siphons of some lyonsiids respond to shadows and may thus react to passing predators, prompting the bivalve to retract its sensitive siphons (Prezant 1977). The photoreceptors of *Laternula*, also located along the siphons and also showing a shadow reflex (Adal & Morton 1973), are among the most complex in the Mollusca.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Anomalodesmata are distributed worldwide, with several groups widespread in the Indo-Pacific. The highly diverse carnivorous Verticordioidea, Poromyoidea and Cuspidarioidea live predominantly in deep waters throughout the Indo-Pacific. The Laternulidae also occur widely in the Indo-Pacific, and Morton (1977) suggested that another family which is well represented in the region, the Myochamidae, had its primary radiation across the Indo-Pacific, stemming from the subgenus *Myadora (Myadora)*.

Anomalodesmata are represented by a sparse, but diverse assemblage in Australian waters. Most families, with the exception of the Pholadomyidae and Lyonsiidae, are represented to varying degrees, and most taxa appear to be southern in distribution. Laternulids are the most widely distributed, occurring in sandy substrata from tropical mangrove habitats to the Antarctic; only one species, *Laternula creccina*, is found on all Australian coasts (Macpherson & Gabriel 1962; Wells 1984; Wells & Bryce 1985).

The family Cleidothaeridae is endemic to Australia and New Zealand and may be monotypic, with *Cleidothaerus albidus* as its sole representative. Several families are represented by one or two species within Australian waters. *Parilimya tasmanica*, the only commonly cited species in the family Parilimyidae found in Australian waters, has only been recorded from deep waters off South Australia and Port Arthur, Tasmania. *Parilimya haddoni* is recorded from Torres Strait but little information is available on this species. Only two species of *Pandora*, *Pandora (Frenamya) patula* and *Pandora elongatus*, have been reported, both from South Australia. *Offadesma angasi* is the only verified member of the Periplomatidae reported from Australia; its type locality is Spencer Gulf although it seems to be widely distributed in South Australia and Victoria and also occurs in New Zealand. Hedley (1901) described *Periploma (Pendaloma) micans* from New South Wales, but this also awaits taxonomic validation.

Cleidothaerus albidus the sole cleidothaerid, lives attached to rocks, shells and algal holdfasts, along exposed rocky shores and subtidally. *Cleidothaerus* has been discussed in some detail by Beu & Maxwell (1990) who concluded that there are probably two Recent species, the second being *C. pliciferus*.

In contrast, the Myochamidae are represented in Australia by some 17 species occurring in mid-energy sand flats just below low tide, or epibiotically on other bivalves. Species of *Myochama* are restricted to Tasmania, south-eastern Australia and New Zealand. *Myadora*, a more speciose taxon, has a wider Indo-Pacific distribution.

There are probably some eight laternulid species in the Australian fauna. *Laternula elliptica* occurs in Antarctica (Burne 1920) and *L. truncata* lives in tropical mangrove habitats (Morton 1973). *Laternula anserifera* is found along the southern Australian coast (Iredale 1930); *L. creccina*, as mentioned above, is found on all coasts; and *L. recta* is common on mud flats of southern Australia (Ludbrook 1984). Poore (1982) listed *Laternula tasmanica* from Gippsland Lakes, Victoria but this was probably a misidentification of *L. truncata* or *L. creccina*.

Several species (about 16) of Thraciidae occur in the Australian benthos at depths of 7–540 m. Thraciids have only been collected in continental Australia off the South Australian coast.

Fossil Record and Phylogeny

Runnegar (1974) gave a detailed account of the evolutionary history of the Anomalodesmata, and Morton (1981a) discussed the origins of various superfamilies. The earliest recognisable member of the Anomalodesmata is found in the Middle Ordovician (Pojeta 1971). In the middle to late Palaeozoic and Mesozoic they became common, but dwindled in numbers in the Tertiary (Pojeta 1971). Early anomalodesmatans were shallow burrowers, but fossil evidence reveals two evolutionary trends from ancient stock. Over their 440 million year history, the Anomalodesmata have developed many infaunal, deeper-burrowing forms and many byssate forms. Some of the epibyssate forms may be part of the stem group for the extant cemented anomalodesmatans, which are confined to Australasia (Runnegar 1974). Stanley (1972) suggested that these bivalves, which attach by byssi to hard surfaces, evolved from infaunal or partially buried relatives. Alternatively, bivalves that are infaunal and produce byssi, may have retained a byssus through neoteny (Yonge 1962).

Many deep-sea bivalves are predatory and most belong to the septibranch Anomalodesmata (Knudsen 1979), a group that apparently radiated into the deep-water habitats in the late Mesozoic (Runnegar 1974; Morton 1987b). The fossil record of Anomalodesmata from Australia is excellent (Tate 1887; Ludbrook 1978; Darragh & Kendrick 1980; Waterhouse 1987). Tate (1887) described a Tertiary bivalve fauna of the Muddy Creek beds, Victoria, that includes several species of *Myadora* and a species of *Thracia*, *T. persacrosa*. A single Late Eocene specimen of *Verticordia* sp. was described by Darragh & Kendrick (1980) from Pallinup Siltstone. This added to the known verticordiid Tertiary fauna detailed by Tate (1887) and Pritchard (1901). A diverse bivalve fauna of the Early Pleistocene of the western Eucla Basin of southern Australia, described by Ludbrook (1978), includes representatives of the Myochamidae (*Myadora pervalida*) and Clavagellidae (*Brechites australis*, *B. veitchi*). The extinct pholadomyoidean families Megadesmidae, Edmondiidae and Chaenomyidae, are well represented in the Late Palaeozoic of eastern Australia and are discussed and described by Waterhouse (1987). This diverse anomalodesmatan fauna of the south-eastern Bowen Basin, Queensland, is taxonomically uncertain. Waterhouse, however, has clarified many synonymies and added some new taxa to this important molluscan fauna, including a new subfamily for *Myonia*, the Myoniinae.

The oldest anomalodesmatans were equivalve. The earliest known inequivalve species, *Pyramus barringtonensis*, is from the Middle Carboniferous of eastern Australia (Runnegar 1974). The number of anomalodesmatan taxa with asymmetrical valves appears to have increased over time. The shell form of species of *Cuneamya* among the early Palaeozoic Grammysiidae gives significant clues to the life styles of the Grammysiidae, Megadesmidae and Edmonidiidae, as well as all extinct anomalodesmatan families (Runnegar 1974). Adaptations for deep burrowing are clearly evident from the elongate shells, with pedal and siphonal gapes, and deep pallial sinus, of the Permian megadesmid bivalves *Vacunella curvata*, *Myonia elongata*, and *Pyramus laevis* from New South Wales, and *Myonia morrisi* and *M. carinella* from Queensland (Runnegar 1965, 1974; Newell *et al.* 1969). *Australomya waterhousi* from the Permian of New South Wales, with a shallow pallial sinus, is thought to have been endobyssate (Runnegar 1974; Morton 1985a).

CLASSIFICATION

Over the last 30 years, interest in the Anomalodesmata has grown, in part because of their unusual representatives, and in equal part because of the paucity of information on these intriguing bivalves. The increase in studies on the subclass is also reflected in the proliferation of proposed classifications for the group. At least eight attempts to reclassify the Anomalodesmata have been made since 1969. Among these are proposals by Newell *et al.* (1969), Knudsen (1970), Runnegar (1974), Bernard (1974, 1979), Allen & Morgan (1981) and Morton (1982); these classifications have been reviewed by Morton (1985a). The taxonomic confusion arises from problems of dealing with organisms as disparate as the watering pot shells, *Brechites* species, the superficially oyster-like *Myochama* species, and the carnivorous septibranchs. This chapter follows the classification outlined by Morton (1982) and recognises only one order, the Pholadomyoida, erected by Newell (1965). This classification (Table 9.1) is based, in large part, on the palaeontological work of Runnegar (1974) and thus imparts a strong evolutionary basis.

Much of the confusion in anomalodesmatan taxonomy centres on the placement of the septibranch bivalves. There has been substantial debate concerning the actual phylogenetic position of verticordiids, poromyids and cuspidariids. Purchon (1987) retained the Anomalodesmata at the ordinal level with the suborder Septibranchia containing the superfamily 'Poromyacea' all within the subclass Lamellibranchia. Here all 'septibranch' families are linked within the 'Poromyacea' based on the lack of hinge teeth, the similar gill type, and similarities in sexuality. Aside from these features, which are not universal among the so-called septibranchs, Purchon listed others including such variable features as taenioid muscles, arenophilic radial mantle glands, stomach type, and byssus system. Allen & Morgan (1981) divided the suborder Septibranchia into two superfamilies, the Poromyoidea, containing the Verticordiidae and Poromyidae, and the monotypic Cuspidarioidea. Morton (1985a, 1987b), however, found sufficient differences between the two poromyoidean families and the Cuspidariidae to justify placing each in its own superfamily. Because of significant differences in shell microstructure, ligament, hinge, lacunal and sinus systems, gill types, palp structure, stomach type and sexuality, and in the presence or absence of arenophilic mantle glands and taenioid muscles, the three families are here retained in separate superfamilies.

The subclass comprises the sole order Pholadomyoida. The familial classification is outlined in Table 9.1. Except for the Lyonsiidae and Pholadomyidae, all families of Anomalodesmata occur in Australian waters.

Guianadesma sinuosum, described as a freshwater member of this subclass from streams of Guyana (Morrison 1943), is not an anomalodesmatan, but its true taxonomic affinity is unknown.

Order PHOLADOMYOIDA

Superfamily PHOLADOMYOIDEA

The Pholadomyoidea arose in the early Palaeozoic and is the oldest living superfamily in the subclass. The superfamily is composed of nine families, only two of which are extant. Morton (1982) removed parilimyids from the family Pholadomyidae and erected the new family Parilimyidae, consisting of the deep-water genera *Parilimya*, *Panacca* and *Nipponopanacca*. Although the parilimyid shell and hinge resemble those of *Pholadomya*, (external ligament, shell with radial ribs), the internal structures of the body are more reminiscent of other anomalodesmatans, in particular the septibranch bivalves (muscular inhalant siphon, palps, stomach Type II) (Morton 1982, 1985a). The superfamily is at least partially defined by the possession of specialised taenioid muscles, reduced in pholadomyids, but well developed and assisting in the retraction of the large inhalant siphon in parilimyids.

Pholadomyoidea are small to large bivalves with thin prismatonacreous shells. The shells are aragonitic, inequilateral, equivalve to slightly inequivalve and have radial ribs and commarginal lines or ribs. The anterior margin is rounded and the

Table 9.1 Family classification of extant Anomalodesmata. Families indicated by an asterisk have not been recorded from Australia.

Subclass ANOMALODESMATA

Order PHOLADOMYOIDA

- Superfamily PHOLADOMYOIDEA
  - Family Pholadomyidae*
  - Family Parilimyidae
- Superfamily THRACIOIDEA
  - Family Thraciidae
  - Family Periplomatidae
  - Family Laternulidae
- Superfamily CLAVAGELLOIDEA
  - Family Clavagellidae
- Superfamily PANDOROIDEA
  - Family Lyonsiidae*
  - Family Pandoridae
  - Family Myochamidae
  - Family Cleidothaeridae
- Superfamily VERTICORDIOIDEA
  - Family Verticordiidae
- Superfamily POROMYOIDEA
  - Family Poromyidae
- Superfamily CUSPIDARIOIDEA
  - Family Cuspidariidae

posterior margin truncate. The shells gape both anteriorly and posteriorly. The primary ligament, which is opisthodetic and seated in a well-defined chondrophore, is external and complemented by a thin secondary ligament of periostracum. The pholadomyoidean external ligament is considered to be primitive (Morton 1981a). Although members of the order are typically edentulous, some species have small secondary teeth. A lithodesma is lacking. Well-defined pallial and adductor muscle scars are present as is a deep pallial sinus which houses the elongate siphons.

Among pholadomyoideans is the very rare extant *Pholadomya candida* from the western mid-Atlantic, only two living specimens of which have ever been examined (Morton 1980). There is perhaps a single species of Australian parilimyid, *Parilimya tasmanica*. The functional morphology of *Parilimya* has been described by Morton (1982) and that of *Pholadomya* by Runnegar (1972) and Morton (1980). A New Zealand species, *Pholadomya maoria*, was described by Dell (1963), from about 600 m depth between Aldermen and Red Mercury Island, who noted that it is very similar to *Pholadomya pacifica* from the north-western Pacific and Japan. Morton (1980, 1981a), suggested that aside from *Pholadomya candida*, all extant pholadomyoideans are referable to the genera *Panacca* and *Nipponopanacca* in the Parilimyidae.

Members of the superfamily Pholadomyioidea are characterised by having the mantle margins fused, with only four apertures remaining: two siphonal, an elongate pedal, and a small pallial. Arenophilic radial mantle glands are present in parilimyids, but not pholadomyids (Morton 1980). Siphons are long and fused along their length in *Pholadomya*. *Parilimya* has an extensive inhalant, but a very short, free exhalant siphon. Well-developed taenioid muscles are present in *Parilimya*, and similar, but greatly reduced taenioid muscles are present in *Pholadomya* (Morton 1980). These bivalves are heteromyarian, with elongate anterior and rounded posterior adductors. Pedal retractors are present in *Pholadomya*, but not *Parilimya*. All pholadomyoideans are sedentary and probably unable to burrow if disinterred.

The ctenidia are typical anomalodesmatan plicate gills with reduced and reflected outer lamellae. The labial palps are short in *Parilimya*, long in *Pholadomya*, and contain few to many sorting ridges respectively (Morton 1980, 1982). *Pholadomya* has a Type IV and *Parilimya* a Type II stomach (Purchon 1956b, 1958). The latter is heavily muscularised and *Parilimya* is probably carnivorous with some adaptations parallelling those of the 'septibranchs'. *Pholadomya* has a large sac-like stomach with extensive sorting regions, but few primary ducts. *Pholadomya candida* may be a deposit-feeder perhaps using its foot to 'pump' organic sediment into the mantle cavity through the pedal gape (Morton 1981a).

The pericardial system is ventral to the umbones and contains the heart with ventricle and paired auricles. The rectum passes below the heart in *Pholadomya*, but pierces the ventricle in *Parilimya* (Morton 1985a). The kidneys are large and paired.

The nervous system is simple with cerebropleural, pedal and visceral ganglia and connectives (Morton 1980, 1982). Statocysts are present but are of different types in each family. *Parilimya* has Type B_1 statocysts, abutting the pedal ganglia with ovoid statoliths and numerous statoconia; *Pholadomya* has Type A (Morton 1985b).

Pholadomyoideans are simultaneous hermaphrodites. A large branchial chamber may serve as a brood pouch, but little is known of reproduction or development in this group. The reproductive systems of both families have been examined by Morton (1980, 1982). Ovaries and testes open into a cloaca.

The superfamily, though presently low in diversity and numbers, is a remnant of a group of bivalves that was abundant in the late Palaeozoic (Stanley 1972). The fossil bivalves *Megadesmus*, *Myonia* and *Vacunella* from the Australian Permian are related to *Pholadomya* (Dickins 1963; Waterhouse 1966, 1969; Runnegar 1972).

Family Parilimyidae

The family Parilimyidae was established by Morton (1982) who discussed the basic characteristics and history of the family.

Parilimyids are characterised by the presence of a mid-anterior taenioid muscle scar on the interior of the shell, elongate inhalant and short exhalant siphons and a digestive system adapted to handle large food items.

The shells are small (*Parilimya tasmanica* being about 25 mm long), thin, typically white, equivalve and strongly inequilateral with a longer posterior side leading to a rounded margin. The shorter anterior portion of the shell terminates in a truncate margin. Narrow anterior and posterior shell gapes are the only regions where the valves do not meet fully. The umbones are entire and slightly incurved. Some species have a granulose exterior, others are prominently radially ribbed. An external ligament, composed of periostracum, is present. Parilimyids are typically edentulous although a single secondary tooth is present in some species. Internally, there is a complete pallial line, a rounded posterior adductor scar and an ovoid anterior adductor scar as well as a subcircular taenioid muscle scar.

The family is rare in Australian waters. The southern *Parilimya tasmanica* and the northern (Torres Strait) *Parilimya haddoni* (Fig. 9.7A–C) are the only extant parilimyids recorded from Australia. The fragile shell is rounded-triangular in shape with the umbones situated very close to the anterior end. Radial ribs decorate the shell's surface. Muscular siphons are associated with the well-developed and deep pallial sinus.

The mantle lobes of *Parilimya* are only fused along the inner folds (Morton 1982), unlike those of many other Anomalodesmata that have the inner and middle mantle lobes fused. Openings into the mantle cavity are the inhalant and exhalant siphons, pedal aperture and fourth pallial aperture. Arenophilic radial mantle glands are present along the mantle edge. A long, but truncate foot may protrude through the antero-ventral pedal gape, but may not be active in burrowing as the animal usually is sedentary after settlement (Morton 1982). An elongate inhalant siphon dwarfs the much smaller exhalant siphon. Two very long retractor muscles form a pair of taenioid muscles that function to withdraw the enlarged inhalant siphon (Fig. 9.7D). The bivalves are heteromyarian, but both adductor muscles are small.

The enlarged inhalant siphon (which is similar to that in some of the septibranch bivalves) is thought to be raptorial (Fig. 9.5A; Morton 1982, 1985a). The short labial palps are muscular with a few, deep ridges. The overall structure of the palps is not unlike that of the septibranch Anomalodesmata (Morton 1985a). The mouth leads to a muscular oesophagus and opens anteriorly into the stomach. Parilimyids have a Type II stomach (Purchon 1956b) as is also found in the Poromyoidea. This type of stomach could be adaptive for handling large food particles as in a predatory life style (Morton 1982). The rectum extends above the elongate kidney, which is anterior to the pericardium, and penetrates the ventricle to exit on the distal side of the posterior adductor muscle. The pericardial system is typical of the subclass. The renal apertures are separate from the gonoducts as in the Pholadomyidae (Morton 1980).

The ctenidia are typically anomalodesmatan, comprising a complete inner demibranch and a reflected and reduced outer demibranch with only descending lamella. Ctenidial filaments are glandular, discharging secretions of unknown function into the suprabranchial chamber. The plicate gill could be modified along its central region as a marsupium and the ctenidial secretions could be related to brooding (Morton 1982).

The parilimyid nervous system is simple, composed of cerebropleural and pedal ganglia with cerebropleural-pedal connectives. *Parilimya fragilis* has Type B_1 statocysts abutting the pedal ganglia, each with a single ovoid statolith. *Parilimya maoria* has a Type B_2 statocyst, also abutting the pedal ganglia and with an ovoid statolith, but also with a number of smaller statoconia (Morton 1985b).

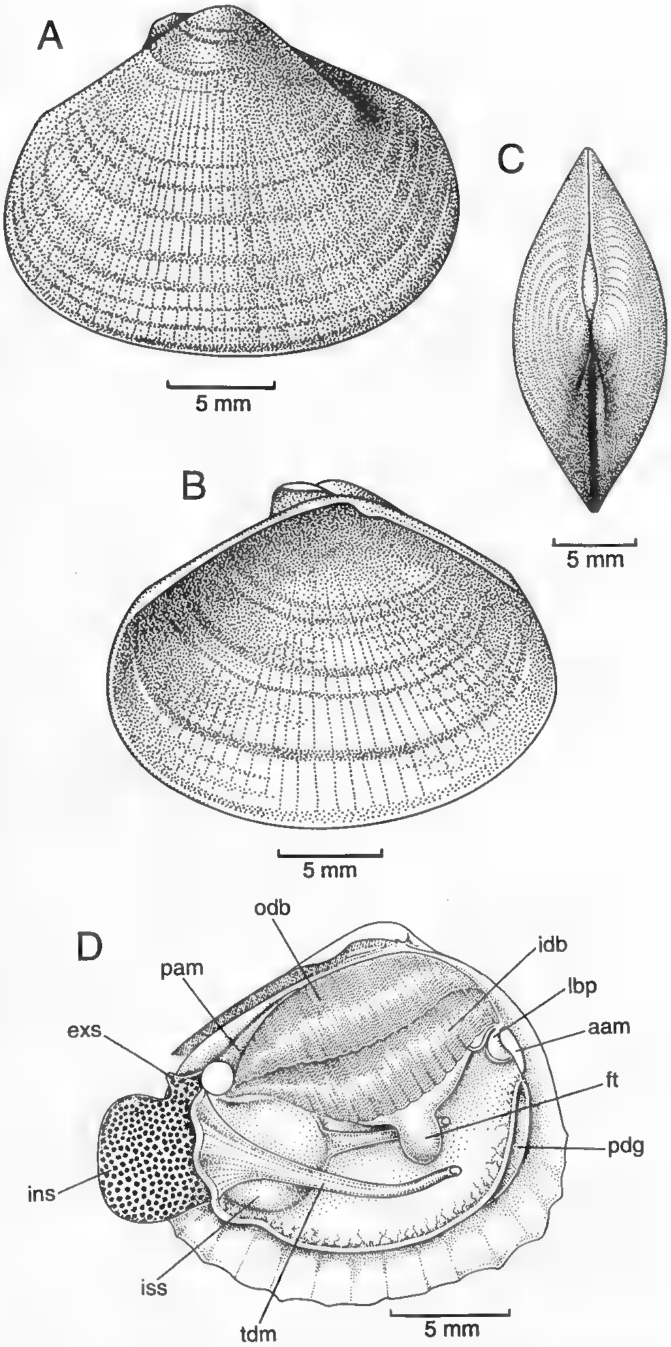

Figure 9.7 Family Parilimyidae. **A–C**, *Parilimya haddoni*, shell valves: A, right valve in external view; **B**, left valve in internal view; **C**, paired valves, dorsal view. **D**, *Parilimya fragilis*, organs of the mantle cavity, including the everted inhalant siphon; left shell valve and mantle lobe removed. **aam**, anterior adductor muscle; **exs**, exhalant siphon; **ft**, foot; **idb**, inner demibranch; **ins**, inhalant siphon; **iss**, inter-siphonal septum; **lbp**, labial palp; **odb**, outer demibranch; **pam**, posterior adductor muscle; **pdg**, pedal gape; **tdm**, taenioid muscle. (A–C, after Melvill & Standon 1899; D, after Morton 1982) [A–C, C. Eadie; D, R. Plant]

Parilimyids are simultaneous hermaphrodites and have paired ovaries and testes, which empty via united gonoducts on each side of the posterior suprabranchial chamber. The mature eggs of *Parilimya fragilis* are large and yolky with an external capsule. Morton (1982) found that the suprabranchial chamber of *P. fragilis* was filled with mature sperm and eggs. Nothing is known of embryology within this family.

Parilimyids live predominantly in moderately deep water; only one species (from Japan) is known to occur in shallow waters. *Parilimya maoria* is recorded from 610 m off the coast of New Zealand (Powell 1979). The Parilimyidae comprise three genera: *Parilimya*, *Panacca* and *Nipponopanacca*. Most species are found in deeper waters, however several have been recorded from shallower Pacific (especially around Japan), Atlantic and possibly Antarctic waters (Soot-Ryen 1951; Cotton 1961; Morton 1980).

The type locality of *Parilimya tasmanica* is off Port Arthur, Tasmania, in 90 m water, and it has been recorded from deep water in South Australia (Cotton 1961). *Parilimya tasmanica* was originally described as *Pholadomya tasmanica*, which Cotton (1930) made the type species of his new genus *Notomya* in the Pholadomyidae. Cox (1969) synonymised *Notomya* with *Panacca*, but Morton (1982) referred it to *Parilimya*. *Parilimya haddoni* was described from Torres Strait by Melvill & Standon (1899). *Panacca adelaidis* and *P. mawsoni* from Victoria Land, Antarctica (Soot-Ryen 1951), may be parilimyids.

The Parilimyidae may be closely related to the 'septibranch' bivalves; the latter may have evolved from Parilimyidae in the Mesozoic (see Morton 1982, 1985a). Morton (1982) suggested that the Parilimyidae could be an evolutionary conduit between the primitive Pholaomyoidea and the Recent septibranchs.

Superfamily THRACIOIDEA

The Thracioidea comprises three families, the Thraciidae, Periplomatidae and Laternulidae. The Thracioidea, Mesozoic in origin, are mainly thin-shelled bivalves with an external or internal, opisthodetic primary ligament situated in large, cup- shaped chondrophores (Yonge & Morton 1980). A lithodesma is variably present, developed to some degree in most Thraciidae studied, as well as in *Cochlodesma* in the Periplomatidae, and in some laternulids (for example, *Laternula truncata*, *L. boschansina*). This calcareous ossicle, however, is absent from the periplomatid genus *Periploma*, and from the laternulids *L. elliptica* and *L. anserifera* (Allen 1958, 1960; Morton 1976, 1981a, 1981b). Aside from the deeper water 'septibranchs', Thracioidea is perhaps the most speciose anomalodesmatan superfamily within Australian waters.

Thracioideans have white shells, often with fine commarginal ribs, but only rarely radial ribs. The shells of laternulids and periplomatids more closely resemble each other than they do the shells of thraciids, being thinner, gaping at both ends and having an internal primary ligament. Periplomatids and laternulids have a perpendicular umbonal crack in the shell dorsum supported internally by a corresponding buttress. This structure is absent in Thraciidae. Pallial and adductor scars are evident. The shells of most thraciids have a homogeneous microstructure compared to the prismatonacreous shell of the other thracioideans. The mantle edges are fused with the typical paired siphonal, pedal and, except in laternulids, fourth pallial apertures remaining. Siphons are well developed, fused in laternulids, but separate in periplomatids and thraciids. Complex photoreceptors associated with the siphonal tentacles occur in laternulids. Some but not all periplomatids have arenophilic radial mantle glands along the mantle edge. These are involved with adhesion of sand grains to the shell's exterior (Morton 1981a, 1981b).

The adductor muscles are small and slightly heteromyarian. The foot is small and reflects the animals' sluggish life style. Only some species, for example *Periploma margaritaceum* (Rosewater 1984), are capable of active burrowing after attaining adulthood, with perhaps most being passive burrowers that are not able to reburrow if removed from the substratum. Pedal retractor muscles are poorly developed.

All Thracioidea have typical anomalodesmatan ctenidia that are plicate and heterorhabdic with reduced and reflected outer demibranchs. Purchon's (1958) Type IV stomach is present in all members of the superfamily as are a conjoined midgut and a style sac. The hindgut passes through the ventricle. The pericardium contains the usual ventricle and paired auricles and is drained by large kidneys that empty into the suprabranchial chamber through paired nephridiopores.

All known Thracioidea are simultaneous hermaphrodites with paired male and female gonoducts fused into a 'cloaca' that empties near the nephridiopores. The eggs are large and yolky, and although nothing is known of development in this group, a very short planktonic larval stage or direct development is likely (Ockelmann 1959).

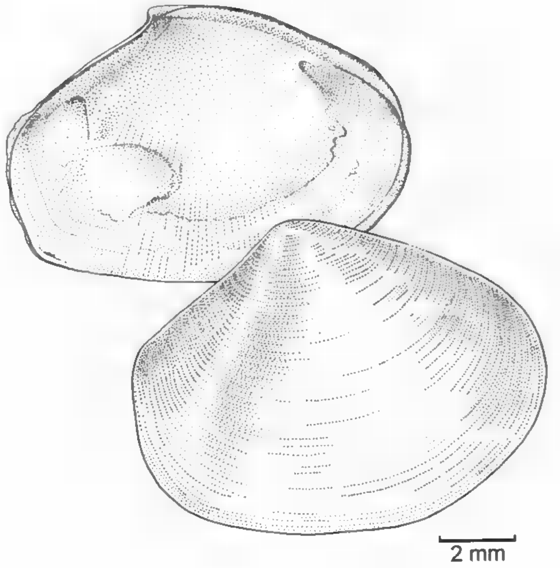

Figure 9.8 Family Thraciidae. *Thracia ovalis*, left shell valve in internal view, right shell valve in external view. [A.J. Hill]

All members of this superfamily are infaunal, living buried in sands and muds intertidally and down to over 500 m. The Thraciidae and Laternulidae mostly live positioned vertically, several centimetres below the sediment surface, although at least one species of *Thracia* is reported to live on its side (Thomas 1967). From such positions in the sediment, they extend their siphons to the surface, sometimes in association with siphonally produced mucoid-lined tubes. Periplomatids also live infaunally, typically lying on their flatter, left valve. From this position they too extend long siphons to the surface in association with mucoid tubes, but in at least *Cochlodesma praetenue* the exhalant siphon lies parallel to the surface and remains out of direct contact with the overlying water column (Allen 1958).

The superfamily contains 20 extant genera (Vokes 1980) seven of which occur in Australian waters. The Thraciidae are cosmopolitan in distribution and several species occur in Australian waters. They can be distinguished by the absence of the subumbonal crack and, in addition to an internal ligament in many, the presence of a small external ligament. The Periplomatidae also have a cosmopolitan distribution, but have fewer species than the Thraciidae, and are represented in Australian waters only by *Offadesma angasi*. The Periplomatidae have inequivalve shells with the right valve slightly larger and more inflated than the left, a subumbonal crack, an internal ligament and a smooth exterior. The Laternulidae are predominantly Indo-Pacific with several members in Australian waters, but one species has a circum-Antarctic distribution. Laternulids have slightly inequivalve shells with the left valve barely larger and more inflated than the right, grainy shell sculpture as well as a subumbonal crack, and an internal ligament.

The earliest thracioideans date from the Jurassic (Boss 1978). Pandoroideans, which in the past have been assembled with Thracoidea into a single superfamily (Newell *et al.* 1969; Runnegar 1974), arose in the Cainozoic. The difference in ages as well as significant hinge and ligament differences prompted Yonge & Morton (1980) to distinguish the Thraciidae, Periplomatidae and Laternulidae as a separate superfamily.

Family Thraciidae

Members of the Thraciidae are small (most Australian species being less than 20 mm long), thin-shelled bivalves with fine commarginal and, rarely, radial ribs, although the latter are sometimes eroded and not discernible (Fig. 9.8). Thraciids do not have a subumbonal crack as do periplomatids and laternulids, and the ligament is normally small and external. Among the Australian thraciids, two genera, *Phragmorisma* and *Thraciopsis*, are unique in having an internal primary ligament and no apparent external primary ligament.

The Thraciidae have not been studied extensively. A review of the eastern Pacific thraciids was completed by Coan (1990), and Allen (1961b) described the shell characters of British species. Limited additional information on the biology, form and function, and ecology of thraciids is provided by Kiener (1834), Morse (1913), Iredale (1924), Lamy (1931), Thomas (1967), and Keen (1969). Thomas (1967) found that *Thracia conradi*, off Prince Edward Island in the Gulf of St Lawrence, Canada, inhabited muddy sands in relatively shallow waters (4 m). There it burrowed to depths of 140–260 mm living with its right valve uppermost, very much like *Periploma* species. Thomas reported that in *T. conradi* both siphons reached the surface of the sediment where they were separated by about 80 mm. No published reviews are available for Australian members; most of the information available is in the form of brief notes and checklists (Cotton 1961; Iredale & McMichael 1962; Macpherson & Gabriel 1962). Several species have been recorded from Australian waters, but their taxonomy remains uncertain.

Recent thraciids have an aragonitic, granular homogeneous shell microstructure (Taylor *et al.* 1973) whereas Runnegar (1974) found that thraciids from the Mesozoic have 'nacreous' shells. Most thraciid shells are white, equivalve, very thin, and have a finely granular surface. The shells (Fig. 9.8), some twice as long as tall, have the anterior margin rounded and posterior margin truncate. The umbones are located close to the centre of the dorsal margin in some species, but well behind it in others. The parivincular ligament, located posterior to the umbones, is typically external and associated with a variably structured, anteriorly placed lithodesma. The hinge is typically edentulous, but teeth are present in species of *Thraciopsis*. The pallial line is well defined and a deep pallial sinus extends to beneath the hinge line. The posterior adductor muscle scar is large and kidney-shaped, the anterior scar is smaller and lemon-shaped. The valve margins are fused except for the slight, posterior siphonal gape, elongate pedal gape, and extensive fourth pallial aperture.

Little is known of the internal anatomy of thraciids. The bivalves are slightly heteromyarian, with the anterior adductor muscle only slightly smaller in size. The deep pallial sinus is indicative of elongate siphons; Costa (1829) and Morse (1913) illustrated thraciids with highly extensible, separate siphons. The long siphons have strong siphonal retractor muscles (Morton 1981a). The inhalant siphon can be much longer than the exhalant. The foot has variously been described as large (Morton 1985a) or small (Kiener 1834). Thraciids have been reported to be, as is typical for the Anomalodesmata, simultaneous hermaphrodites (Ockelmann 1959) with either a very short planktonic stage or none at all.

Thraciids usually occur subtidally; most species have been reported from 7–110 m. They are infaunal burrowers that lie positioned vertically in sand with their inflatable siphons extended to the surface through separate canals (Yonge 1937). The posterior 10–20 mm of these canals is lined by mucus produced by the siphons. This arrangement, which also occurs in the Periplomatidae (*Offadesma angasi*), allows the animal to remain deep in its burrow and withdraw its siphons to just below the surface so as not to expose the delicate siphonal tips to the surface and potential predation (Yonge 1937).

A discussion of the nomenclatural and taxonomic position of the family and type genus is presented by Coan (1990). The family comprises eight genera: *Thracia*, *Asthenothaerus*, *Bushia*, *Cyathodonta*, *Lampeia*, *Parvithracia*, *Phragmorisma* and *Thraciopsis*. The affinities of another genus, *Thracidora* (described by Iredale 1924), are unclear and it has been placed in the Verticordiiae following the works of Thiele (1935) and Soot-Ryen (1966). The genus-group names, *Eximiothracia* and *Cetothrax*, proposed for some Australian species by Iredale (1924, 1949 respectively) were synonymised by Keen (1969) with *Thracia*, but Coan (1990) treated *Eximiothracia* as a subgenus of *Thracia*.

The family occurs around Australia, although most species are rare. *Thracia meridionalis* has a wide Antarctic and Subantarctic distribution (Dell 1964) and is recorded from off the coast of Victoria Land (Soot-Ryen 1951). The Australian thraciid fauna is at least moderately diverse if published faunas and checklists are valid. Four genus-group taxa, *Eximiothracia*, *Cetothrax*, *Phragmorisma* and *Thraciopsis*, have been proposed in the family for Australian species. *Phragmorisma* and *Thraciopsis* are distinctive taxa that differ from other Australian thraciids in having an internal rather than an external primary ligament; several species of *Thracia* have been recorded from Australia.

Cotton (1961) recorded seven species within three genera – *Thracidora* now in the Verticordiidae, *Eximiothracia* (five species) and *Thraciopsis* – from South Australian waters. A single additional species, *Eximiothracia modesta*, was listed by Macpherson & Gabriel (1962) from Victoria. Iredale & McMichael (1962) listed four species of *Eximiothracia*, one species of *Cetothrax* and five species of *Thraciopsis*. Stephenson *et al.* (1974) found an unidentified species of *Phragmorisma* from southern Moreton Bay. *Thracia alciope* is listed by Hedley (1916) as the sole representative of the Thraciidae in Western Australia; no thraciids were noted by Wells & Threlfall (1980) for Cockburn Sound just north of Perth.

The family dates from the Jurassic (Boss 1978). Morton (1980, 1985a) discussed the origins of the family. Those members with an external opisthodetic ligament are considered to be the more primitive (Runnegar 1974). Morton (1980) also suggested that the relatively simple body structure (siphons, mantle, foot) of some thraciids previews that of the more complex periplomatids and laternulids.

Only two thraciid species have been described from the Australian Tertiary (Darragh 1970). One of these is an Oligocene species of *Phragmorisma*, a distinctive genus apparently endemic to Australia.

Family Periplomatidae

The Periplomatidae are a small family of thin-shelled, burrowing bivalves that usually lie horizontally within the substratum with siphons extended to the surface (Fig. 9.9C). These bivalves are characterised by having a small to large (up to 90 mm) inequivalve shell with the right valve more inflated than the left, and each valve containing a subumbonal 'crack' (Fig. 9.9A, B). Only a single species, *Offadesma angasi* (the type species of the genus), is reported from Australian waters; although widespread, it is rarely collected. This intertidal to just subtidal bivalve has a large shell, at times reaching more than 90 mm in length and 65 mm in height. It has a wide western Pacific distribution, and in Australia is found along the coasts of South Australia, Victoria, and New South Wales, where it burrows in muddy sands on protected, low energy beaches (Cotton 1961; Rosewater 1968). Hedley (1901) described *Periploma micans* from off Sydney but no additional records of this species have been found in the literature. Iredale (1930) disagreed with Hedley's generic assignment for this species and erected the genus *Pendaloma*, designating *Pendaloma micans* as the type. Bernard (1989), noted that *Offadesma* is considered to be a subgenus of *Periploma*, based on the absence of a calcified lithodesma (typically replaced by a proteinaceous ligamental pad). The lack of a calcified lithodesma diagnoses *Offadesma* as a valid genus, with the species *O. angasi*.

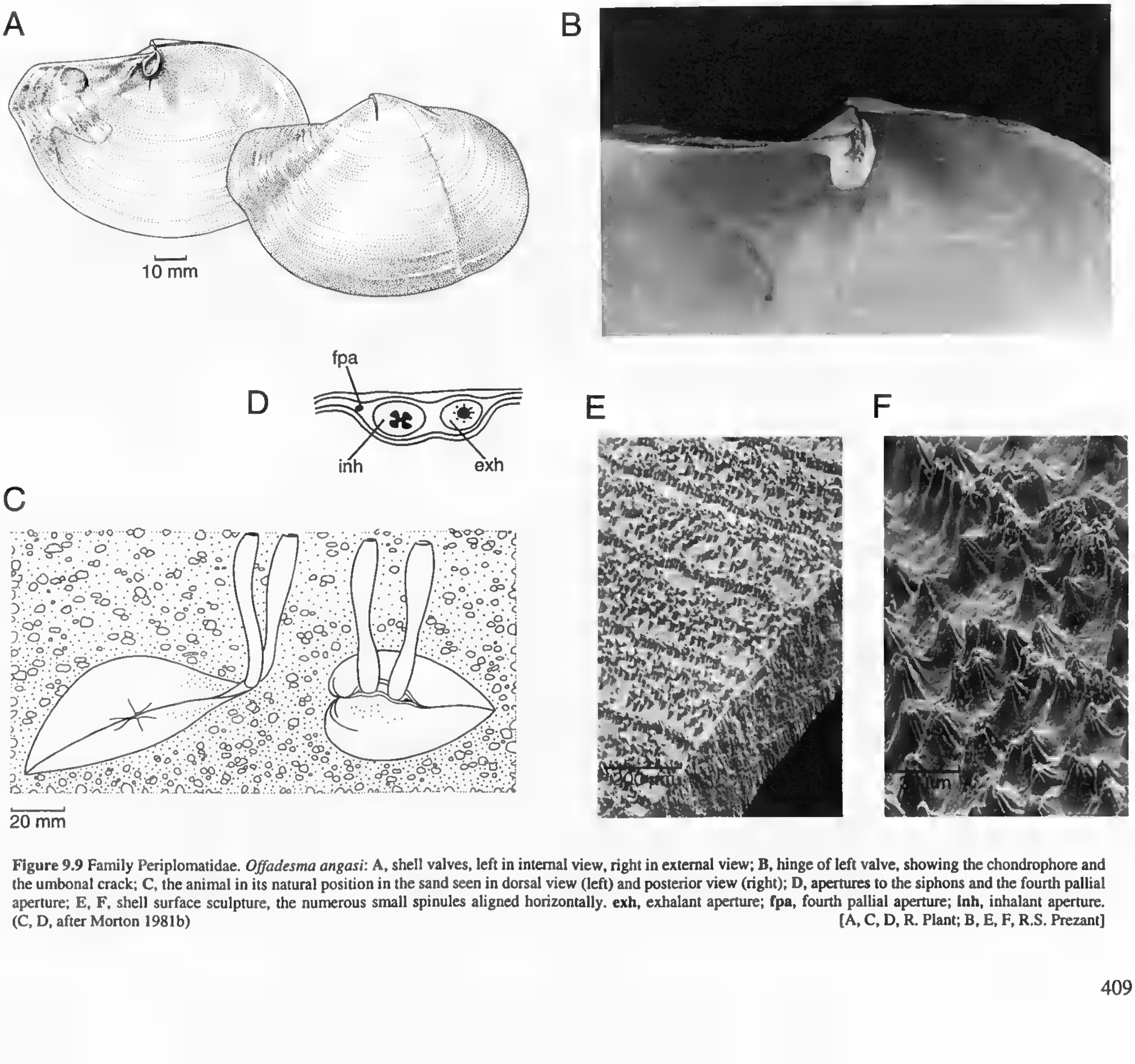

Figure 9.9 Family Periplomatidae. *Offadesma angasi*: **A**, shell valves, left in internal view, right in external view; **B**, hinge of left valve, showing the chondrophore and the umbonal crack; **C**, the animal in its natural position in the sand seen in dorsal view (left) and posterior view (right); **D**, apertures to the siphons and the fourth pallial aperture; **E**, **F**, shell surface sculpture, the numerous small spinules aligned horizontally. **exh**, exhalant aperture; **fpa**, fourth pallial aperture; **inh**, inhalant aperture. (C, D, after Morton 1981b) [A, C, D, R. Plant; B, E, F, R.S. Prezant]

There are no major reviews of this family, but some members have been studied: *Cochlodesma* (Allen 1958, 1960), *Periploma* (Rosewater 1968, 1980, 1984) and *Offadesma* (Morton 1981b). Bernard (1989) briefly reviewed the Periplomatidae of the Pacific and Indo-Pacific, recognising five genera from this region: *Periploma, Albimanus, Halistrepta, Offadesma* and *Takashia.* An unpublished manuscript on western Atlantic Periplomatidae by Rosewater (1991), obtained after his death, also listed five genera, based on shell characters. Bernard (1989) described *Gricoploma* and *Septentrioploma* as subgenera of *Periploma* and also considered *Albimanus, Halistrepta,* and *Galaxura,* to be subgenera. Clearly, a careful taxonomic review of the family is required.

The shell (Fig. 9.9A) is thin, inequivalve and has a more deeply concave right valve with its umbo sitting higher than and over-riding that of the left valve. The anterior shell margin of periplomatids is rounded. Posteriorly, the margin is rostrate and truncate with the posteriormost region directed slightly dorsad. A distinct subumbonal crack (Fig. 9.9B) is present in both valves directly below the umbones and running vertically downward for about the same distance as the internal, spoon-shaped chondrophores. This crack, supported internally by shell ridges or buttresses running dorso-ventrally, is covered by a thin brown periostracum. The aragonitic shells are prismatonacreous in structure (Taylor *et al.* 1973) with an inner layer of sheet nacre, a middle layer of lenticular nacre, and an outer prismatic layer. On the shell interior, the lenticular nacre is iridescent, whereas the sheet nacre inside the pallial line is a dull white. The thin translucent shell shows numerous appressed commarginal lines. The outer shell surface of *O. angasi* is shown in Figure 9.9E, F. The anterior adductor scar is thin and elongate and situated close to the anterior shell margin. A small anterior pedal retractor muscle scar is present on the mid to dorsal posterior region of this adductor scar. The posterior adductor muscle scar is larger and round to triangular in outline. The pallial line is evident and a deep pallial sinus is present. Large spoon-shaped chondrophores are directed ventrally, but also angled to the right in vertical orientation. The thick primary, opisthodetic ligament is internal and sits in the chondrophores (Fig. 9.1A). It is composed of a small anterior and larger posterior layer. A secondary ligament composed of periostracum fuses a long portion of the dorsal shell margin. Hinge teeth are not present.

As in most Anomalodesmata, the mantle margins are fused leaving only the siphonal and pedal gapes, and the fourth pallial aperture (Fig. 9.9D). The small fourth aperture in *Offadesma angasi* is located directly beneath the inhalant siphon (Morton 1981b). The middle and outer folds of the mantle edge are long in *O. angasi* and thus, unless retracted into the shell by pallial retractor muscles, the mantle edge protrudes between the shell valves in life (Morton 1981b). Some periplomatid species, including *O. angasi* (Morton 1981b), have arenophilic radial mantle glands (Fig. 9.2), but these have not been found in *Periploma fragile* from the east coast of the United States or in *Cochlodesma praetenue* from Isle of Cumbrae, Scotland (Prezant 1981b). Putative hypobranchial glands that function in the removal of pallial debris, have been found in the branchial chamber of *O. angasi* Morton (1981b). Long, muscular, separate siphons (Fig. 9.9C) with fine tentaculate tips, can be withdrawn completely into the pallial sinus of the shell. The siphons undergo peristaltic movements that could be associated with mucoid tube formation (Yonge 1937; Morton 1981b).

The foot and pedal gape are small. In the laboratory, *Offadesma angasi* appeared incapable of reburrowing when extracted from sediment Morton (1981b). Rosewater (1984), however, described the burrowing behaviour of *Periploma margaritaceum* from south-eastern United States of America (Fig. 9.6). During burrowing, this species used its siphons as 'bellows' to clear the mantle cavity of extraneous sediment.

Periplomatids are typical filter-feeding bivalves with adaptations for life in turbid waters. The mouth, located just above the posterior region of the anterior adductor muscle, is roofed over by a pair of bulbous 'sacs' that prevent material from entering the gut without prior sorting by the long, strongly ridged labial palps (Morton 1981b). *Offadesma angasi* has a Type IV stomach with a conjoined midgut and style sac, as is typical of some other Anomalodesmata (Purchon 1956b). The rectum penetrates the ventricle and kidney. The circulatory and excretory systems are also typical, with a single ventricle and paired auricles. Single anterior and posterior aortas are present. Paired kidneys with large distal limbs, exit via small nephridiopores into the suprabranchial chamber. These pores are separate from the gonopores (Morton 1981b).

The ctenidia are also typical of the Anomalodesmata, being plicate, heterorhabdic and eulamellibranchiate. Each ctenidium is composed of two demibranchs, the outer demibranch being reduced and reflected upwards.

The position of the periplomatid gonads varies. For example, in *Offadesma angasi* the ovaries are located antero-dorsally and testis postero-ventrally in the visceral mass (Morton 1981b) and in the British species, *Cochlodesma praetenue*, the ovaries are located postero-dorsally and the testis antero-ventrally (Allen 1958). Separate gonoducts exit from male and female gonads and merge to empty via gonopores close to the nephridiopores, into a 'cloaca' (Morton 1981b). Mature eggs, up to 100 µm in diameter, develop in large vacuous follicles. The eggs, as is characteristic of the subclass, are rich in yolk (Morton 1981b).

Periplomatids typically live buried several centimetres below the sediment surface (Fig. 9.9C) where they lie on their flatter left valve (although in the laboratory Allen (1958) found a weak preference for the right valve to be directed downward in *Cochlodesma praetenue*). Morton (1985a) considered *Offadesma angasi* and other periplomatids to be passive burrowers as adults. Thus, they are inactive and, with few exceptions, unable to reburrow if extracted from their buried position. Most have elongate siphons that extend to the sediment surface and are capable of building mucoid tubes. In *Cochlodesma*, the exhalant siphon apparently lies parallel to the sediment surface, whereas the inhalant siphon turns sharply upward to the surface (Allen 1958). *Offadesma angasi* lives in sheltered zones adjacent to high energy beaches. Long labial palps with dense and deep sorting grooves, a hooded mouth, rejectory currents over the visceral mass, hypobranchial glands, and tentaculate siphonal tips, are all adaptive for life in an environment prone to heavy siltation (Morton 1981b). Rosewater (1980) has documented naticid on several periplomatid species. It is likely that other predatory shore dwellers prey on these thin-shelled, shallowly burrowed bivalves.

Offadesma angasi lives intertidally and down to about 14 m in the muddy sands of sheltered embayments at numerous localities in southern Australia (Cotton 1961; Macpherson & Gabriel 1962). It also lives in New Zealand (Powell 1979) where it has a reasonable fossil record, possibly extending back to the early Miocene (Beu *et al.* 1990).

The earliest known periplomatids are from the Upper Cretaceous (Speden 1970). Darragh & Kendrick (1991) have described '*Periploma*' species from the Upper Cretaceous of Western Australia. The oldest fossil *Offadesma* is recorded from the Middle Eocene of New Zealand (Powell 1979; Beu *et al.* 1990).

Family Laternulidae

Laternulids, commonly known as lantern shells, have medium-sized shells (20–100 mm) that are usually thin and delicate (Fig. 9.10A, B). Typically, they live buried in sandy or muddy sediments in shallow waters, sometimes in eel grass beds. The shell, usually white, has a granular surface and numerous radially arranged spinules (Fig. 9.10C, D; Aller 1974). Laternulids, with *Laternula* the sole valid extant genus, are well documented from Australia with several species described in the literature. The exact taxonomy and number of species, however, are unresolved although Morton (1976) suggested there are eight valid species worldwide. The family is diagnosed by a thin, equivalve or slightly inequivalve shell with a wide anterior and posterior gape. An umbonal crack is located adjacent to the sunken primary ligament. Laternulids have a well-developed umbonal buttress (Fig. 9.10B, E) and are further characterised by long, fused siphons tipped by tentacles with complex photoreceptors (Figs 9.3A, B, 9.10F; Adal & Morton 1973). There have been no recent systematic reviews of this family.

The ovoid to cylindrical shell of *Laternula* (Fig. 9.10A, B) is equivalve or slightly inequivalve with the left valve usually deeper and slightly larger than the right; the valves are usually very thin. Typically, the shell is prismatonacreous. The external surface is covered with minute spikes (Fig. 9.10C, D) that are preformed in the mantle and function to increase the clam's stability in the substratum by increasing frictional resistance to dislocation (Aller 1974). The anterior region of the shell is inflated and rounded along the margin whereas the posterior shell margin is narrower and truncate. Fine sand grains often adhere to the shell exterior on top of the thin, two-layered periostracum. An external periostracal ligament covers part of the dorsum. The shell gapes widely both anteriorly and posteriorly. The prominent umbones have a slit or crack which is covered by periostracum in life. The shell is reinforced internally by significant buttresses that appear as flattened columns running at a slight angle posteriorly from the inner margin of the large chondrophores (Fig. 9.10B, E). There is a small internal ligament located between the cupped chondrophores. A lithodesma (Fig. 9.10E), sometimes strongly arched, is present in only some species. Among Australian laternulids a lithodesma is absent in *Laternula anserifera*, *L. elliptica* and *L. anatina*. The pallial line is evident and has a deep sinus. Adductor scars are clearly delineated and situated quite high on the shell.

The mantle is fused along the inner and middle folds leaving only the siphons and a small pedal aperture as openings into the mantle cavity. Morton (1973) reported no fourth pallial aperture

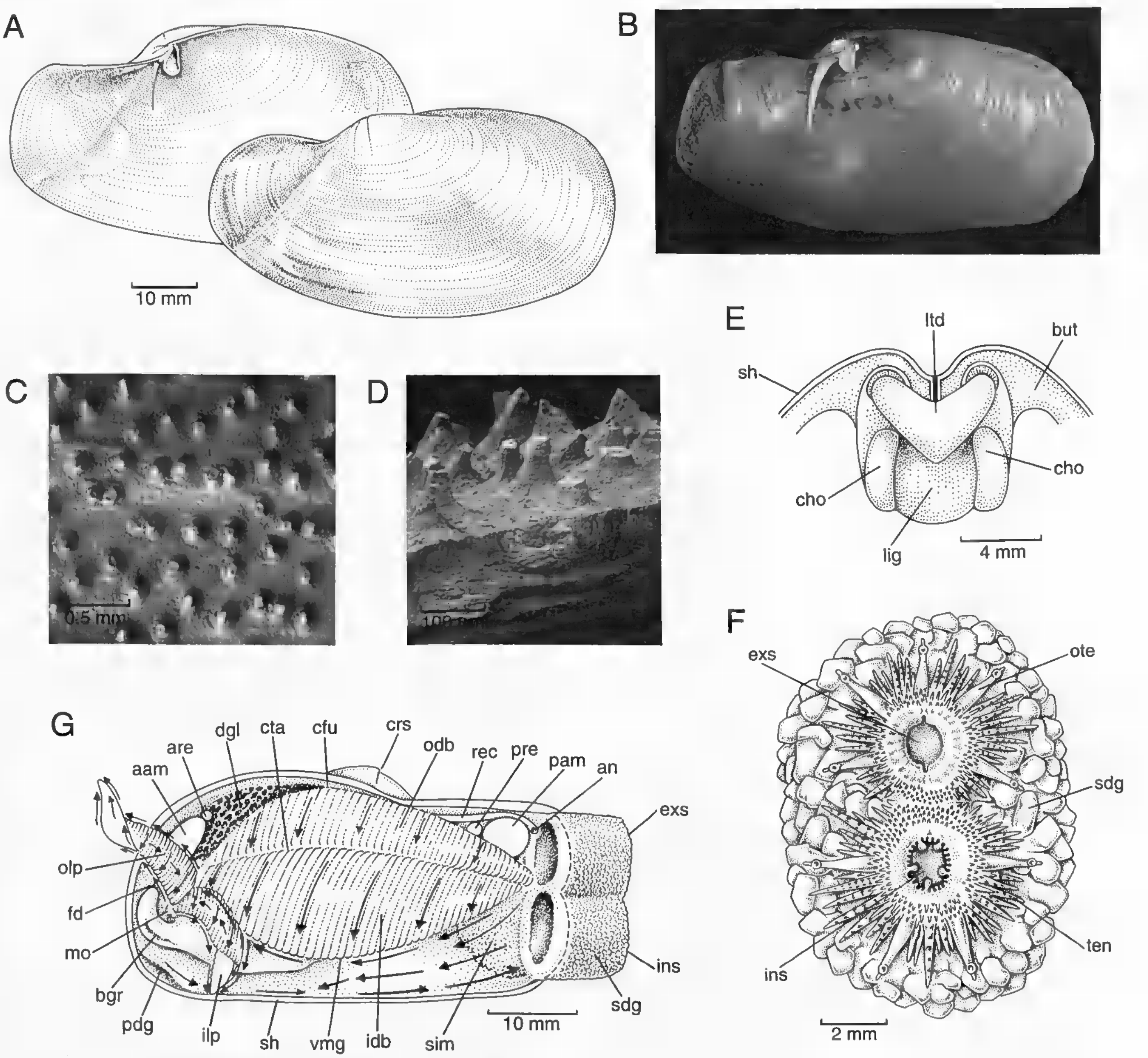

Figure 9.10 Family Laternulidae. **A–D**, *Laternula creccina*: **A**, shell valves, left valve in internal view, right valve in external view; **B**, left valve, showing the chondrophore and the buttress below the umbonal crack, the posterior periostracum overlaps the shell margin; **C**, shell surface sculpture, truncated spinules of the shell exterior; **D**, the truncated spinules, lateral view. **E–G**, *Laternula truncata*: **E**, hinge, anterior view, showing the lithodesma. **F**, siphons; **G**, organs of the mantle cavity, left mantle lobe and shell valve removed, showing the anatomy and the ciliary currents. **aam**, anterior adductor muscle; **an**, anus; **are**, anterior retractor muscle; **bgr**, byssal groove; **but**, buttress; **cfu**, point of cuticular fusion between the ascending lamella of the outer demibranch and the visceral mass; **cho**, chondrophore; **crs**, crack in shell; **cta**, ctenidial axis; **dgl**, digestive gland; **exs**, exhalant siphon; **fd**, food; **idb**, inner demibranch; **ilp**, inner labial palp; **ins**, inhalant siphon; **lig**, ligament; **ltd**, lithodesma; **mo**, mouth; **odb**, outer demibranch; **olp**, outer labial palp; **ote**, optic tentacle; **pam**, posterior adductor muscle; **pdg**, pedal gape; **pre**, posterior retractor muscle; **rec**, rectum; **sdg**, sand grains; **sh**, shell; **sim**, siphonal musculature; **ten**, tentacles; **vmg**, ventral marginal groove. (E, after Morton 1976; F, G, after Morton 1973)

[A, E–G, R. Plant; B–D, R.S. Prezant]

in *Laternula truncata* from Hong Kong. The extensive siphons, fused along their entire length, can reach half the shell length and are covered in part by a thick periostracal layer. This layer, in turn, is often covered with sand grains although no arenophilic radial mantle glands have been reported for any laternulid. The inhalant siphon is tipped by four eyes mounted on optic tentacles; the exhalant siphon has five such eyes (Adal & Morton 1973). These elaborate and complex photoreceptors (Fig. 9.3B) have retinal receptors composed of flattened whirls of cilia (Adal & Morton 1973). Additionally, the siphons are crowned by numerous shorter tentacles (Fig. 9.10F) that are flecked and banded with brown, white and yellow pigment spots, providing excellent camouflage when extended against a sand background.

Adult laternulids have a small foot that, although retaining a reduced byssal groove, lacks a functional byssal gland (Morton 1973). Small pedal retractor muscles serve to move the foot. Most adult laternulids are unable to reburrow if removed from their infaunal habitat, however, the foot is used for burrowing in juveniles. Adult *Laternula elliptica* from the Antarctic can slowly reburrow following eviction (Zamorano *et al.* 1986). The anterior and posterior adductor muscles are both small, the posterior being rounder and larger and both are located high in the valves. Strong orbital muscles line the mantle edge. The small and dorsally situated adductor muscles of laternulids probably could not act sufficiently in opposition to the abduction forces of a fully formed ligament. In *Laternula*, however, the ligament is reduced and the very thin valves do not undergo strong adduction in opposition to a strong elastic ligament. Instead, the shell is well adapted to the burrowed infaunal habit that, as adults, leaves them permanently buried. Contraction of the small adductor and strong orbital muscles brings the valves together along the fulcrum of the small primary ligament. The laterally arranged anterior and posterior orbital muscles, modifications of the pallial musculature, in conjunction with the adductors, act to bring anterior and posterior valve closure and alignment as described by Morton (1976). The umbonal slit in the laternulid shell effectively divides the shell into four functional shell portions.

Features of internal anatomy are illustrated in Figure 9.10G. The ctenidia are typically anomalodesmatan, plicate and heterorhabdic with a reduced and reflected outer demibranch. Long labial palps sort and carry food to the mouth. The stomach is of Purchon's Type IV (1958) and has a conjoined midgut and style sac. The rectum passes through the kidney and the ventricle of the heart. The pericardium is situated far forward and contains a single ventricle and two auricles. A single renopericardial aperture drains from the posterior portion of the pericardium into the kidney. The single renopericardial duct is short and quickly splits into two ducts that lead to the proximal limbs of the kidneys. The convoluted kidneys exit via nephridiopores mounted on urogenital papillae that open on each side of the body at the level of the umbones (Morton 1973).

Laternula anserifera, from intertidal eel grass beds, has a Type B_2 statocyst (Morton 1985b). The statocysts, each under 100 µm in diameter, abut the top of the pedal ganglia. The ovoid statolith of each is accompanied by small statoconia. Statoconia are not present in all laternulids. Morton (1985b) found *L. truncata* to have Type B_1 statocysts, possessing solitary statoliths and lacking statoconia.

Laternulids are simultaneous hermaphrodites with ventral testes and dorsal ovaries. In most Anomalodesmata, the gonads open via separate gonoducts into the suprabranchial chamber. In laternulids, however, a vas deferens runs from each testis posteriorly and opens into the urinogenital duct. Similarly, short oviducts from each ovary open into the vasa deferentia. From this point of junction outward the duct is considered an hermaphroditic duct (Morton 1973). Nothing is known of laternulid embryogeny.

The siphonal photoreceptors are responsive to shadows. The animal reacts to shadows by 'flicking' the optic tentacle. This is thought to serve a defensive role or a siphonal cleansing function when a passing predator (bird, crab, etc.) disrupts sediment stability and deposits silt on the photoreceptor (Adal & Morton 1973). The animals do not burrow or even retract their well-hidden siphons when a shadow passes over the eyes; the definitive function of the eyes may still be unresolved.

Morton (1976) suggested that shell thickness in laternulids is correlated with latitude. Tropical laternulids have thin shells and more temperate species have thicker shells. This general trend seems to be true, but several thin-shelled species have an overall geographic range overlapping with, for instance, that of the thick-shelled *Laternula truncata*, and the maxim holds only for the centre of distribution. Nevertheless, there does seem to be a significant correlation between decrease in shell thickness and depth of burial as well as a trend towards a cylindrical shell of circular cross-section (Morton 1976).

The strong orbital and small adductor muscles are responsible for adduction of the shell and thus facilitate flow of seawater into and out of the mantle cavity (Morton 1976, 1985a). The ligament is essentially immobile in most laternulids, and adduction and valve movement are assisted by flexion of the valves along the umbonal 'crack' with the buttress supporting this potentially weak region. In an edentulous group like the Laternulidae, the lithodesma may assist in alignment of valves.

Laternulids are weakly burrowing infaunal bivalves, living vertically or near vertically in soft sediments, usually sand or mud. *Laternula* is a suspension-feeding bivalve that, when found in large populations, is an important contributor to the organic particle flux in an ecosystem. Ahn (1993) found that *L. elliptica* along King George Island, Antarctica, plays an important role in benthic-pelagic coupling through production of large amounts of faeces and pseudofaeces, contributed to the water column and sea bottom. Large populations of *Laternula* along Australian coasts probably play similar roles in organic carbon contributions.

Laternulids are mostly Indo-Pacific in distribution, but some species (for example, *L. elliptica*) occur in Antarctic waters. Morton (1976) noted eight living species in this family with several occurring in Australian waters. They occur in sandy substrata and because of their infaunal habits and camouflaged siphons, they can be difficult to find. Species in the Australian fauna have been listed by Cotton (1961), Macpherson & Gabriel (1962), and Iredale & McMichael (1962). *Laternula creccina* is present down to 18 m in New South Wales, Southern Australia, north-western Australia, Queensland, Tasmania and Victoria. *Laternula anserifera* occurs intertidally in south-western Western Australia and South Australia (Cotton 1961; Macpherson & Gabriel 1962). *Laternula elliptica* is a circum-Antarctic species, widely distributed in soft sediments in 15–20 m of water, where it lives buried as deep as 500 mm or more (Zamorano *et al.* 1986), and has been collected off Oates Coast, Victoria Land, Antarctica (Soot-Ryen 1951). At least for the latter species, which are periodically uprooted by ice scouring, seastars are important predators (Zamorano *et al.* 1986).

Runnegar (1974) suggested that the earliest laternulid was *Cercomya* of the Late Triassic. This genus contains shells with an umbonal crack similar to that of extant species of *Laternula*, but the exact hinge structure is unknown and the ligament could have been external. Runnegar (1974) noted that the earliest known laternulids are the Cretaceous species of *Periplomya* and *Anatimya*.

Superfamily CLAVAGELLOIDEA

The superfamily Clavagelloidea comprises the single family Clavagellidae, commonly called the watering pot shells. It is one of the most enigmatic and bizarre bivalve groups; its ancestry is obscure (Morton 1985a). It shows extreme adaptation to an infaunal existence with the adult contained within a sealed adventitious calcareous tube. It has been postulated (Smith, B.J. 1978; Morton 1984c) that the juveniles are free bivalves that either burrow into sediment or bore into soft calcareous rock. The animal then lines this burrow with the adventitious calcareous tube material to which either one or both of the valves are fused. The anterior end of this tube terminates in a series of either simple or branched tubules which are open in most groups, allowing water movement to and from the inside of the tube. The valves are nacreous and lack the hinge plate. The animals are typical anomalodesmatans, but the musculature and organs of the visceral mass are reduced, and there is hypertrophy of the siphons and ctenidia.

Savazzi (1982) postulated an adaptive radiation in the clavagelloideans from an obligate boring ancestor, with the *Clavagella* group being the most primitive. Morton (1985a) on the other hand suggested that since the ligament of *Clavagella* is internal and that of *Brechites* external, *Brechites* might be of earlier origin. He suggested that because of a similarity between *Brechites* and *Pholadomya candida* in mode of feeding from deep deposits via the pedal gape,an origin for the infaunal Clavagelloidea might be sought among the Pholadomyoidea.

Family Clavagellidae

The Clavagellidae (formerly known as the Aspergillidae) are the most aberrant of the bivalve families with respect to shell form and life style. Clavagellids are marine and mainly known from fairly shallow water where they either live attached to a solid surface or bore into soft rock or are infaunal, buried vertically in soft sediments with their posterior end protruding into the water.

The Recent species of the world were revised by B.J. Smith (1976) following his revision of the Australian clavagellid species in which he described one new Recent and one new fossil species (Smith, B.J. 1971). Prior to this, L.A. Smith (1962a) and Keen & Smith (1969) listed the species in the Clavagelloidea. Purchon (1956a) reported on his observations of a live animal, and Morton (1984a, 1984c) described the functional morphology of several species together with further information on their biology. Soliman (1971) and Appukuttan (1974) added further distributional and taxonomic information.

The family consists of three genera, *Clavagella*, *Humphreyia* and *Brechites* (after Smith, B.J. 1976; *Brechites* taking priority over *Penicillus* suggested by Smith, L.A. 1962a). In species of *Clavagella*, the left valve is fused or cemented to the tube, but the right valve is entirely free inside the chamber of the tube (Fig. 9.11A, B). Species of *Clavagella* either bore into calcareous rock, probably by chemical means (Morton 1984a), or are attached by the anterior end to a hard substratum. The burrow is lined with adventitious calcareous material although in some an area under the free right valve may be left unlined. The valves are inequilateral with hinge teeth absent. In *Clavagella australis*, the ligament is simple, flanked by a thickened area of fused periostracum which assists in the alignment of the valves (Morton 1984a). *Clavagella* species are heteromyarian with large adductor muscles. In *Humphreyia*, the valves are large, making up most of the anterior end of the tube and both are fused into the tube structure (Fig. 9.11C). The smaller Australian species may be attached by the anterior end to a hard substratum or live burrowed into soft sediment. The large Japanese species lives buried vertically in sediment with the posterior siphonal end protruding into the water. The anterior adductor muscle is lost and the posterior adductor is greatly reduced and probably non-functional (Smith, B.J. 1971). In *Brechites* both valves are fused to the tube, but they are very small and insignificant compared to the size of the tube (Fig. 9.11D). They are equivalve and inequilateral and are set into a 'saddle' which in turn is set into the adventitious tube. The ligament is covered externally by a thick pad of fused periostracum. The anterior end of the tube is perforated by many small holes which in some species form a regular 'rose' structure which gives the group its common name of watering pot shells.

The tube comprises a single homogeneous shelly layer and there is strong evidence that this is secreted just once as a single structure (Smith, B.J. 1978; Savazzi 1982; Morton 1984c). It fuses with one or both valves, which are present in the juvenile, and there is some evidence (Morton 1985a) that the 'watering pot' perforated anterior end may either be secreted at a slightly different time or more likely that the secretion for this arises from a different series of glands. In

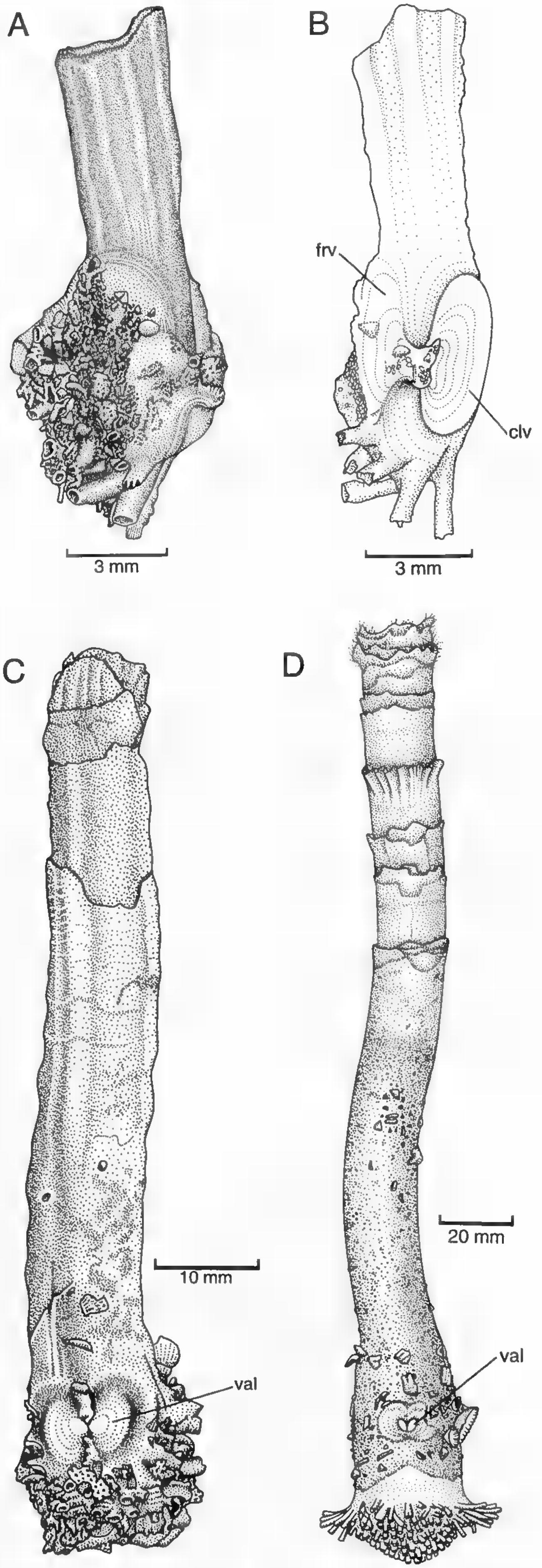

Figure 9.11 Family Clavagellidae. Shells: **A**, **B**, *Clavagella (Clavagella) multangularis*, **B**, showing position of the free, internal right valve and the cemented left valve; **C**, *Humphreyia (Humphreyia) strangei*, showing the two large valves; **D**, *Brechites (Brechites) vaginiferus australis*, showing the small valves and the typical watering-pot anterior end. **clv**, cemented left valve; **frv**, position of free right valve as indicated on the tube; **val**, shell valve. [C. Eadie]

Brechites, the tiny true valves and the external ligament are locked into the tube in a small 'saddle' structure. This means that before the tube is secreted, a juvenile slug-like stage must exist, the animal consisting of a large muscular mantle bearing the small true shell. This shell must be inflated by muscular and hydrostatic pressure into the final shell size and shape and then the tube shell secreted (Smith, B.J. 1978), however, this has never been observed. All the species have some small perforations in the tube at the anterior end and a single opening at the posterior end for the siphonal discharge. The form of the anterior perforations varies between genera and species and their function is largely unknown. Morton (1984c) suggested that the juvenile stage is buried infaunally, retaining motility only in the vertical plane. Shelly material secreted by the general mantle surface under the original valves produces the typical 'saddle'. The calcareous material forming the adventitious tube and the perforated basal plate is then secreted from the siphonal aperture glands and the anterior mantle cavity respectively, via the pedal gape.

The general anatomy (see Fig. 9.12) of most of the Australian species was described by B.J. Smith (1971), and Morton (1984a) described the biology and functional morphology of *Clavagella (Dacosta) australis*. *Clavagella* has two adductor muscles as it has one valve free (Fig. 9.12A, B), but in the other genera the adductor muscles are lost. The body is entirely contained within a thick muscular integument which is extended posteriorly into a contractile siphon tube. The foot is reduced to a small protuberance on the visceral mass. Feeding is by filtration of currents drawn in through the inhalant siphon and across the eulamellibranchiate ctenidia where the filaments are continuous with the descending lamella of the descending demibranchs. Purchon (1956a, 1960) demonstrated ciliary pathways and feeding and water currents in a *Brechites* species. Morton (1985a) speculated that in species of *Brechites* there may be some food gathering and water interchange from the sediment around the anterior end via the tube perforations. The labial palps are moderate in size and trigonal, and the stomach has a style sac united with the mid-gut. Pericardial glands are present in the auricle, and the visceral ganglion occurs below the rectum.

Clavagellids are hermaphroditic, but nothing is known about the life history, though B.J. Smith (1978) has speculated on the possible existence of a slug-like juvenile stage prior to tube secretion. Little is known of the ecology of members of the family as few have been observed alive in their natural environment.

The Recent world fauna consists of 17 species and subspecies occurring in the Mediterranean and many parts of the Indo-West Pacific (Smith, B.J. 1976). The genus *Clavagella* is divided into four subgenera with nine species and subspecies worldwide. The Australian fauna comprises *Clavagella (Clavagella) torresi* which

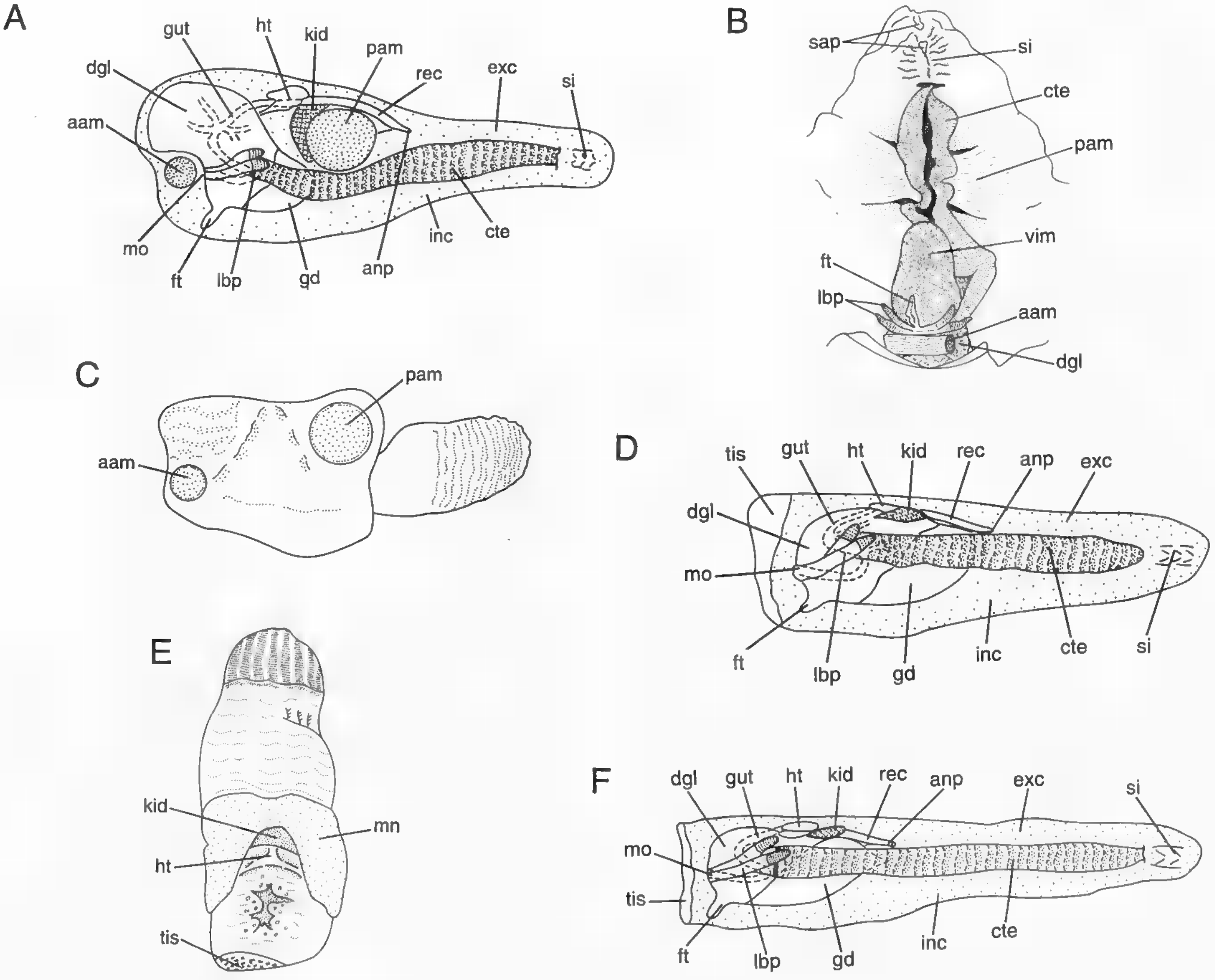

Figure 9.12 Family Clavagellidae. Internal and external anatomy. **A–C**, *Clavagella (Dacosta) australis*: **A**, general internal anatomy, lateral view; **B**, the pallial chamber, ventral view; **C**, exterior of the animal, lateral view, showing the position of the two adductor muscles. **D, E**, *Humphreyia (Humphreyia) strangei*: **D**, general internal anatomy, lateral view; **E**, the exterior of the animal, diagrammatic dorsal view. **F**, *Brechites (Brechites) vaginiferus australis*, general internal anatomy. **aam**, anterior adductor muscle; **anp**, anal papilla; **cte**, ctenidium; **dgl**, digestive gland; **exc**, exhalant chamber; **ft**, foot; **gd**, gonad; **gut**, gut; **ht**, heart; **inc**, inhalant chamber; **kid**, kidney; **lbp**, labial palps; **mn**, true mantle area; **mo**, mouth; **pam**, posterior adductor muscle; **rec**, rectum; **sap**, siphonal aperture; **si**, siphons; **tis**, pad of soft tissue; **vim**, visceral mass. (After Smith, B.J. 1971) [C. Eadie]

occurs from North Queensland to Singapore, *Clavagella (Clavagella) multangularis* which is found only in southern Australian waters, and *Clavagella (Dacosta) australis australis* which is restricted to south-eastern Australia where it can be found intertidally attached to rocks. A related sub-species, *Clavagella (Dacosta) australis mullerae*, is found in South Africa; species of *Clavagella (Bryopa)* are found from the Mediterranean to Mauritius, Sri Lanka and the Philippines, and the only species in *Clavagella (Stirpulina)* is found in Japan.

The genus *Humphreyia* comprises two subgenera, each represented by one Recent species. *Humphreyia (Humphreyia) strangei* is confined to south-eastern Australia and *Humphreyia (Nipponoclava) gigantea* is only found in southern Japan.

The genus *Brechites* contains three subgenera, each of which has Australian representatives. The Australian fauna comprises *Brechites (Brechites) vaginiferus australis* which occurs along the Western Australian coast north of Perth – it has been found alive at extreme low water at Broome; *Brechites (Penicillus) philippinensis* which occurs around the western and northern parts of Australia from Rottnest Island to central Queensland and north-west to the Philippines; *Brechites (Foegia) novaezelandiae* which occurs only in the waters of tropical Australia from Perth to Torres Strait; and the larger *Brechites (Foegia) veitchi* known only from off Eyre Peninsula, South Australia. Species outside the Australian fauna are *Brechites (Brechites) vaginiferus vaginiferus* which occurs in the northern part of the Indian Ocean and the Red Sea and *Brechites (Penicillus) penis* which is found throughout the northern Indian Ocean, from Mozambique, and eastwards to Borneo.

Clavagella (C.) multangularis is known from the Upper Eocene, Upper Oligocene and Miocene at several localities in Victoria and South Australia, along with a second species of *Clavagella sensu stricto* from the Upper Oligocene of Victoria. *Humphreyia (H.) strangei* is known from the Pliocene beds in South Australia; *Brechites (B.) v. australis* has been collected as a Lower Pleistocene fossil in Western Australia and *B. (F.) veitchi* is also known from the same beds (Smith, B.J. 1971).

Superfamily PANDOROIDEA

The Pandoroidea consists of four families, some of which are well represented in the Indo-Pacific, and one family which is restricted to Australia and New Zealand. The superfamily is characterised by a prismatonacreous shell, sunken primary ligament with a lithodesma, and, typically, unequal valves. Members of this superfamily are diverse, and include cemented epifaunal forms as well as byssally attached infaunal species. It is a relatively young group, apparently arising in the Cainozoic (Boss 1978). The oldest extant family is the Lyonsiidae (Yonge & Morton 1980) which is absent from Australia; some poorly known Antarctic species may occur in Australian territorial waters. Definitions of genera and an outline of evolution within the family Lyonsiidae are given by Prezant (1981a, 1981b, 1981c). The general characters of this diverse superfamily are discussed by Morton (1985a). The Pandoridae and Cleidothaeridae are poorly represented in Australia, but the Myochamidae are a rich and speciose component of the fauna.

The shells are inequilateral, and inequivalve except for lyonsiids which are equivalve. The Pandoridae and Myochamidae respectively have the right and left valves flattened. The epifaunal Cleidothaeridae, cemented by their strongly keeled right valve to hard substrata, have very heavy shells that tend to coil as a result of a tangential growth component (Yonge 1967). Other families in the superfamily are thin shelled. Pandoroideans have a prismatonacreous shell (Taylor *et al.* 1973; Prezant 1981a) and are characterised by having an internal primary ligament. At least some members of each family have a lithodesma (Yonge & Morton 1980; Prezant & Carriker 1983). A thin secondary ligament of periostracum covers the hinge region. Secondary teeth are present in some members of all families except the Lyonsiidae.

As is characteristic of the subclass, the mantle lobes are fused with only siphonal and pedal apertures remaining. Only the Pandoridae lack a fourth pallial aperture. Arenophilic radial mantle glands are present in the Lyonsiidae (Prezant 1979b, 1981b, 1985). Siphons are short and usually fringed with short tentacles. Complex photoreceptors are present, embedded in the exhalant siphon of some lyonsiids (Prezant 1984). The Pandoroidae are typically isomyarian or only slightly heteromyarian, but cleidothaerids, all attached, are strongly heteromyarian. A large, usually laterally compressed foot is present in all but the Cleidothaeridae and *Myochama* (Myochamidae). The latter have a small, inactive foot, reflective of their attached life styles. Production of byssal threads in adult pandoroideans is noted only in the Lyonsiidae. Ctenidia are large, plicate and heterorhabdic. Palps are small to large. All have a Type IV stomach (Purchon 1958). The rectum passes above the ventricle in all but the Myochamidae in which it penetrates this chamber of the heart. The statocysts are all variations of the Type B system, as defined by Morton (1985b). External fertilisation is characteristic of these simultaneous hermaphrodites.

All pandorids and lyonsiids and many myochamids live buried in fine sands. Cleidothaerids live attached to hard substrata.

The Pandoroidea arose in the Cainozoic (Morton 1985a). Lyonsiid bivalves, the oldest pandoroideans, first appeared in the Eocene (Runnegar 1974) as did the Pandoridae (Boss & Merrill 1965). The Cleidothaeridae have a fossil record dating back to the Early Miocene in Australia (Darragh 1985). Runnegar (1974) and Morton (1985a) described an evolutionary trend in this group towards an epifaunal, sessile lifestyle. The Pandoroidea probably stem from stock similar to that which gave rise to the Thracioidea (Boss 1978) some time in the Jurassic (Morton 1985a).

Family Pandoridae

The Pandoridae are poorly represented in the south-western Pacific, the only species recorded from Australia being the rare subtidal *Pandora (Frenamya) patula* (Fig. 9.13A). Carpenter (1864) described *Pandora (Frenamya) elongatus* (Fig. 9.13B) from southern Queensland, but the status of this taxon is not confirmed. *Pandora*, the only genus recognised within the family, reaches its highest diversity in northern regions of eastern Asia and on the east and west coasts of North America (Boss & Merrill 1965). The family is defined by small to medium-sized white shells (maximum 60 mm long) which are inequivalve, the right valve being flat and the left convex (Fig. 9.13). The primary ligament is depressed, often with a long lithodesma between shallow resilifers. Variably developed secondary hinge teeth may be present, often in the form of a centrally positioned 'cardinal' tooth in the right valve and weaker anterior and posterior 'cardinals' in the left valve (Boss & Merrill 1965; Yonge & Morton 1980).

The taxonomy of the group is poorly understood. Boss & Merrill (1965) suggested that the family comprises a single nominate genus, *Pandora*. A number of subgenera of *Pandora* have been proposed, but they have not been accepted by all taxonomists; Keen (1969) recognised six subgenera. Iredale (1930) erected the genus *Frenamya* for the southern Australian representative then known as *Coelodon patulus*, and placed it in the family Periplomatidae. A definitive systematic revision is needed of this family which has numerous, temperate species in the Northern Hemisphere, but very few tropical and subtropical species.

The prismatonacreous shell of *Pandora* is strongly inequivalve and inequilateral. The valves are highly compressed, the left valve being convex and the right flat to concave. The anterior part of the shell is much shorter than the posterior, the former being rounded and the latter coming to a blunted point. Well-defined commarginal lines ornament the shell surface. The hinge margin is straight with a low lying umbo. A secondary ligament of fused periostracum unites the valves dorsally. Secondary hinge teeth are present in the form of anterior, central pedunculate and posterior

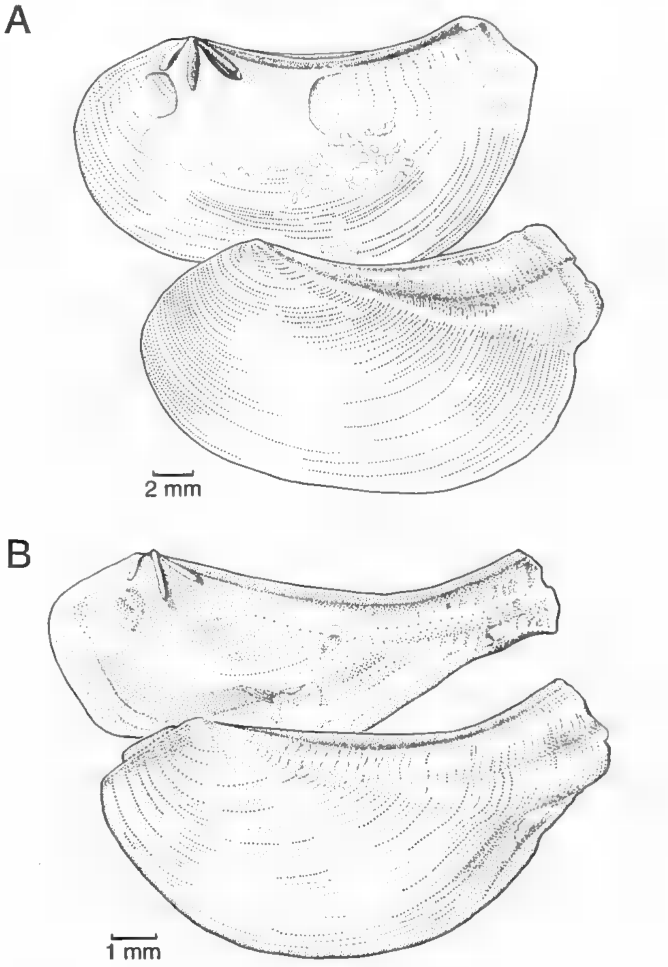

Figure 9.13 Family Pandoridae. Shell valves: A, *Pandora (Frenamya) patula*, right valve in interanl view, left valve in external view; B, *Pandora (Frenamya) elongatus*, right valve in internal view, left valve in external view. [A.J. Hill]

cardinal teeth (Boss & Merrill 1965). The primary ligament is internal and sits in the poorly developed chondrophores. A long lithodesma is present in some members of the family, but appears to be absent from *Pandora (Frenamya) patula*. The adductor scars are subequal with the anterior scar being slightly smaller. The pallial line is punctuated; no pallial sinus is evident.

Pandora patula, a rare species found subtidally in South Australia and southern Western Australia has a thin white, inequilateral and inequivalve shell. The umbones lie low on the shell dorsum. The posterior of the shell is elongate compared to the relatively short anterior region.

Allen (1954), Boss & Merrill (1965) and Morton (1984b) reviewed the biology of some Atlantic pandorids. The mantle margins are fused except for the inhalant and exhalant siphons, and an elongate pedal gape. There is no fourth pallial aperture. The siphons are short, fused along their length and tipped with short papillae (Morton 1984b). The adductor muscles are subequal. Anterior and posterior retractor muscles insert on the bottom of the adductor muscles. The large foot is laterally compressed and has a well-developed byssal gland and groove. There do not, however, appear to be byssi formed in the adults though such attachment threads may be used by juveniles (Allen 1961a).

Characteristic of the subclass, the ctenidia of pandorids are composed of a complete inner demibranch and a reduced outer demibranch reflected upwards. The gills are plicate and heterorhabdic. The mouth is bordered by a pair of medium-sized, bilobed labial palps. The stomach is of Purchon's (1956b) Type IV with conjoined midgut and style sac. The rectum passes above the heart (Allen 1954), but does penetrate the upper reaches of the pericardial chamber (Boss & Merrill 1965). As is typical for the subclass, the anus opens along the postero-dorsal border of the posterior adductor muscle.

A large pericardial chamber encloses the ventricle and paired auricles. Pericardial glands lie dorso-lateral to the pericardium (Boss & Merrill 1965). Kidneys are located posterior to the heart and exit via a common urinogenital aperture into the suprabranchial chamber just below the pericardium. The nervous system is typical of the Anomalodesmata with cerebropleural ganglia located under the anterior adductor muscle and extending long connectives to the visceral ganglia beneath the posterior adductor muscle. Paired statocysts, of Morton's (1985b) Type B_1 are present, abutting the fused pedal ganglia in *Pandora (Frenamya) ceylanica* (Morton 1984b, 1985b).

Pandorids are simultaneous hermaphrodites that have external fertilisation. Cleavage and early development of an eastern Atlantic pandorid have been described by Allen (1961a) (see Fig. 9.4). Development is rapid, occurring in less than 96 hours. Gastrulae are produced in about 9–10 hours and a trochophore is evident after 17–18 hours followed by a short lived (less than 24 hours) veliger. Dispersal is thus restricted and spat probably set close to parental populations.

Pandorids live in sandy to muddy substrata in relatively shallow waters where they lie on their left valve at a slightly oblique angle just below the sediment surface. Collections of *Pandora (Frenamya) patula* are rare, but it has been recorded from southern Australia from Gulf St Vincent, South Australia, to Bunbury, Western Australia, at depths of 5–15 m (Cotton 1961; Ludbrook & Gowlett-Holmes 1989). The paucity of collections could be a result of highly localised populations, reflecting the very short planktonic life of the veligers. Boss & Merrill (1965) noted that this geographic isolation can also result in species pairs, as appears to occur in the western North Atlantic. In Australian waters, both intrinsic and extrinsic barriers may inhibit this speciation phenomenon. The short planktonic period of *Pandora* is a possible intrinsic barrier maintaining species populations within regionalised areas. Allen (1961a) found that the 'active swimming phase' of *P. inaequivalvis* lasted only 18 hours; thus dispersal would be limited. Geographic barriers represent extrinsic barriers maintaining allopatric species pairs.

Because of their poor preservation and the dearth of fossils, little is know of the fossil record of the Pandoridae. Keen (1969) gave a range of Oligocene to Recent for *Pandora sensu stricto*, but recorded *Frenamya* (= *Pandora*) only from the modern fauna.

Family Myochamidae

The Myochamidae, commonly called the false jingle shells, are characterised by having strongly inequivalve, often triangular, shells with prominent umbones (Fig. 9.14B, C). The shells are either free or attached. No shell gape is present. The hinge lacks teeth and the ligament is internal or absent. The mantle edges are fused with only a pedal gape, fourth pallial aperture, and siphonal openings remaining. The siphons are short and separate.

Two genera, *Myadora* and *Myochama*, are usually recorded for the family. Two genera and eight species have been recorded from Australia by Cotton (1961) and Macpherson & Gabriel (1962); Iredale & McMichael (1962) list 14 species from New South Wales (including the thraciid *Phragmorisma watsoni*). In total, there could be as many as 18 myochamid species in Australian waters, since others are known from New Zealand (Powell 1979). *Myadora*, the more speciose of the two genera in the south-western Pacific, has free-living, burrowing forms in sands and muds of mid-energy beaches whereas individuals of *Myochama* species live cemented to other shells, often taking on the superficial appearance of the substratum. Morton (1981a) suggested that ecologically, *Myadora* in the south-western Pacific parallels *Pandora* in the Atlantic.

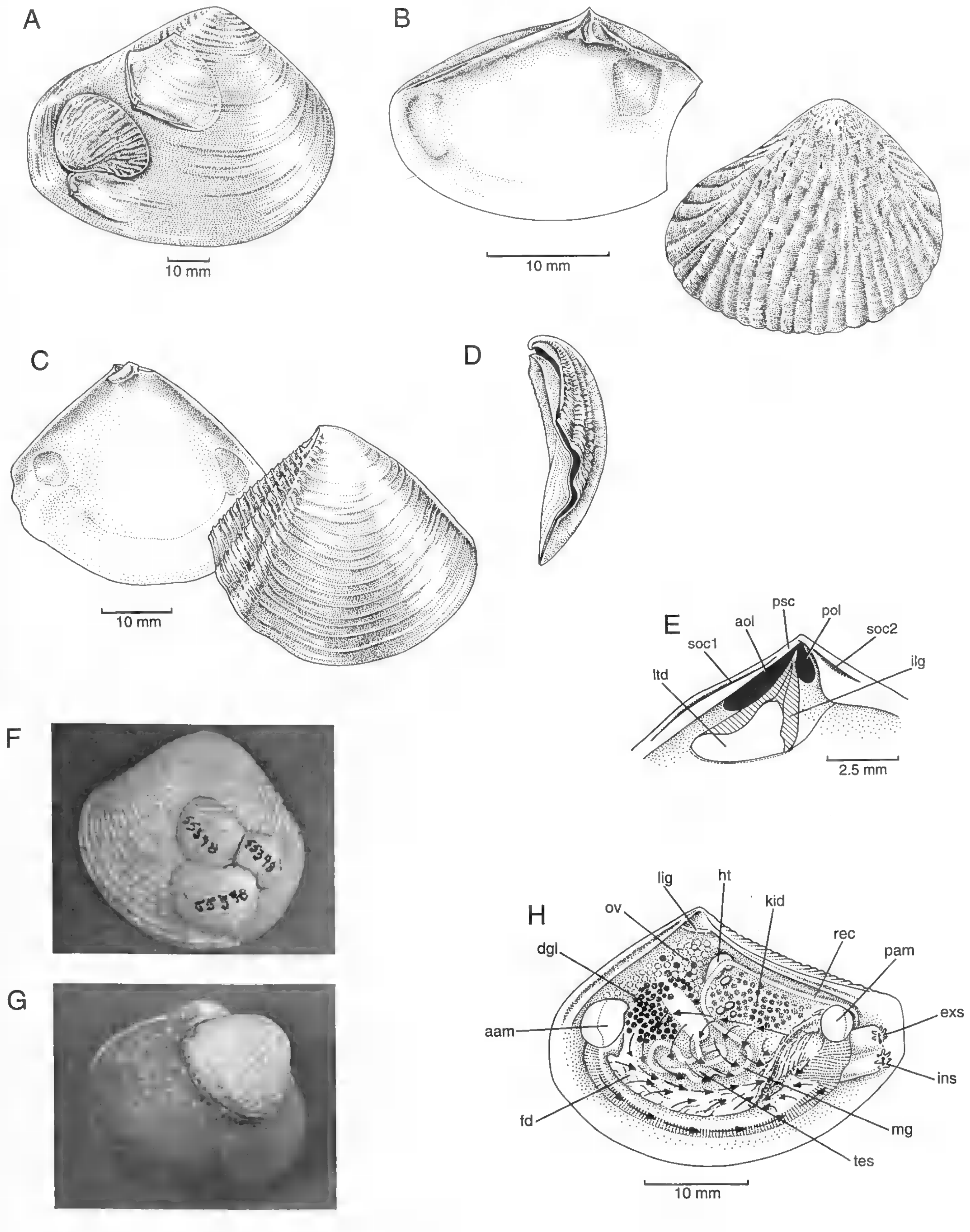

Figure 9.14 Family Myochamidae. **A**, **B**, *Myochama anomioides*: **A**, cemented onto a valve of *Eucrassatella* sp.; **B**, shell valves, right valve in internal view, left valve in external view. **C**, **D**, *Myadora brevis*: **C**, shell valves, left valve in internal view, right valve in external view; **D**, paired shell valves, posterior view, showing the flat left valve and concave right valve. **E**, *Myochama anomioides*, ligament and umbonal region, right lateral view. **F**, *Myochama keppelliana*, three animals on a host bivalve; note modifications to shell shape in response to close neighbours; the bivalves also develop exterior sculpture resembling that of the host. **G**, *Myochama anomioides*, attached near the umbone of a host bivalve. **H**, *Myadora striata*, arrangement of the visceral mass and ciliary currents; left valve, mantle lobe and ctenidium removed. **aam**, anterior adductor muscle; **aol**, anterior outer ligament layer; **dgl**, digestive gland; **exs**, exhalant siphon; **fd**, food; **ht**, heart; **ilg**, inner ligament layer; **ins**, inhalant siphon; **kid**, kidney; **lig**, ligament; **ltd**, lithodesma; **mg**, midgut; **ov**, ovary; **pam**, posterior adductor muscle, **pol**, posterior outer ligament layer; **psc**, fused periostracum; **rec**, rectum; **soc1**, socket 1; **soc2**, socket 2; **tes**, testis. (E, after Yonge & Morton 1980; H, after Morton 1977) [A–E, H, R. Plant; F, G, R.S. Prezant]

The taxonomy of *Myadora* has not been examined carefully. It is quite likely that there are several synonyms among the nominal species listed, and there is some doubt as to the familial placement of some species. *Myochama* closely resembles *Myadora* except for its cemented life style (Morton 1981a). However, except for the work on the functional morphology of *Myadora striata* (Morton 1977), and the brief report on *Myochama anomioides* by Hancock (1853a), little is known of the biology of the family.

The shells of *Myadora* (Fig. 9.14C, D) and *Myochama* (Fig. 9.14A, B, F, G) are readily distinguishable. *Myadora* is very similar in appearance to *Pandora* although it is the left valve that is flat or slightly concave (as in *Myadora alba*). The shell is inequilateral with a longer posterior region sloping down from the prominent and often pointed umbones. The right valve is convex and often has two radial ridges extending from the umbo to the postero-ventral shell margin. The right valve also has a series of commarginal 'growth' ribs, on the left valve, but not as deeply imprinted. The typically worn umbo of the right valve reveals the underlying nacre of the prismatonacreous shell. *Myochama* species are also strongly inequivalve with the thin right valve cemented to a host bivalve. The epibiont often takes on the external shell ornamentation of the host, including radial ribs and beading. The left valve is slightly inflated above the host surface and the animals can form small clumps on the host surface. When this occurs, the external margins of these myochamids are 'moulded' to accommodate crowding, a condition typical of bivalves growing in dense populations. In both genera, the postero-dorsal margin is often concave and the umbones point slightly posteriorly.

The adductor muscle scars are about the same size and are located close to the shell margins (Fig. 9.14B, C). The anterior adductor muscle scar has a posterior depression giving it a kidney-shaped outline. The deeply recessed, but well-formed pallial line forms a narrow pallial sinus just below and extending just beyond the anterior margin of the posterior adductor muscle scar. A large triangular ligament pit, housing a brown internal ligament, is present beneath the umbones. A flat, elongate lithodesma is present ventral to the ligament, and a thin layer of periostracum forms a dorsal secondary ligament above the hinge line. Although typically described as being edentulous, *Myadora* has long secondary teeth on each side of the umbo of the left valve that fit securely into complementary cardinal grooves of the opposite valve. A similar system is present in *Myochama* although the teeth are shorter and extend only a short distance from the ligament pit (Fig. 9.14E).

The mantle lobes are fused along their length except at the short siphons, the small fourth pallial aperture and the slit-like pedal aperture. The fourth pallial aperture is located just beneath the inhalant siphon. The siphons are separate, short and are not ornamented. In *Myochama anomioides*, and other myochamids, the siphons are fully retractable into the shallow pallial sinus. This sinus, deeply recessed beyond the mantle edge and the outer lobes of the mantle totally enclose the siphons when they are withdrawn. The pedal gape is located antero-ventrally beneath the anterior adductor muscle in *Myadora* (Morton 1977). *Myadora* has a large, active foot and is capable of quickly reburrowing. In *Myochama anomioides*, the pedal gape is a narrow slit, located directly in front of the anterior adductor muscle and about one half its height in length. The foot of *Myochama* is small and lacks a byssal groove, reflecting the cemented, sessile habit of this genus. It is unknown if the small foot, located behind the anterior adductor muscle, serves any function associated with the pedal gape although it is unlikely that it can reach the gape. The adductor muscles are nearly isomyarian and easily separated into 'quick' and 'catch' muscles (Morton 1977). Pedal retractor muscles are small, and the pallial muscles are well developed.

The ctenidia of both genera are large and occupy most of the pallial cavity. The gills, heterorhabdic and plicate, are typical of Anomalodesmata and have the outer demibranch reduced and reflected. Morton (1977) has outlined the ciliary currents associated with the gills and labial palps of *Myadora striata*. The palps are small in both genera. The gut is typical of the subclass. A Type IV stomach (Purchon 1958) is present and contains a large gastric shield. The sorting areas and number of primary ducts in the stomach of *Myadora*, are characteristic of bivalves living in areas with high sediment loads (Morton 1977). The rectum penetrates the ventricle and exits behind the posterior adductor muscle. Figure 9.14H shows a view of the internal anatomy of *Myadora striata*.

A typical pericardial system is present. The heart is composed of a single ventricle and two auricles. The kidneys are large and located posterior to the umbones just in front of the posterior adductor muscle. They open by separate nephridiopores into the suprabranchial chamber.

Little is known of the nervous and sensory systems of myochamids. *Myadora* has a Type B statocyst (Morton 1985b). *Myadora boltoni* has a Type B_2 and *Myadora striata* a Type B_3. In the latter species, the statocysts are separate from the pedal ganglia. Each contains a large number of statoconia and a single larger irregular-shaped statolith. Both statolith and statoconia appear to have an inorganic nature (Morton 1985b). In *Myadora boltoni*, the statocysts abut the pedal ganglia and contain fewer statoconia and a more regularly ovoid statolith.

Myochamids are simultaneous hermaphrodites. The large ovaries are located in the antero-dorsal region of the visceral mass, just in front of the kidneys. The testes are located beneath this region, and their tissues are interspersed among the digestive diverticula and down into the foot. The paired gonads open via separate gonopores on each side of the body (Morton 1977). Nothing is known of the embryology of the Myochamidae.

Species of *Myadora* are typical inhabitants of mid-energy sand flats and shallow subtidal waters, environments quite similar to those of *Pandora*. Unlike pandorids, however, several common species of *Myadora* are found in Australian waters (approximately 14 species known). *Myadora* species live buried at an oblique, often 45° angle, in sand (Yonge & Morton 1980), with the left, flattened valve downward. The short, separate siphons project above the sediment surface. Although capable of rapid reburrowing (aided by its large, muscular foot), *Myadora* has reduced pedal retractor muscles, reflecting a more sedentary life style. This trend, towards sedentary modes of life, is perpetuated in the permanently attached *Myochama*. In this bivalve genus, the foot and the pedal retractors are reduced. Cementation to the host surface in *Myochama* species is effected by an adhesive periostracum that forms the template for the outer shell surface which in turn conforms to the substratum surface (Yonge 1979). Yonge (1979) suggested that cementation in *Myochama* evolved from a *Myadora* or *Pandora* type of life style involving pleurothetic habits. *Myochama tabida* is often cemented to *Eucrassatella cumingii*, *Myochama anomioides* to *Glycymeris broadfooti* or *Eucrassatella kingicola* (Fig. 9.14A, F). Typically, single specimens occur on the umbonal region of the host shell; if more, and the specimens are crowded, they may be attached to posterior regions of the host shell (Fig. 9.14G). The host bivalves usually lack siphons and are shallow burrowers or epifaunal.

The family has a wide distribution in the south-western Pacific (Cotton 1961) with primary radiation, according to Morton (1977), stemming from the subgenus *Myadora (Myadora)*.

Myochama anomioides, the type species of the genus, also occurs on species of *Neotrigonia*, *Modiolus*, *Pecten*, *Mimachlamys* and *Exohaliotis* (Cotton 1961); Yonge & Morton (1980) reported it from the right valve of the scallop *Equichlamys bifrons*. Larvae probably settle on any appropriate shell or, possibly, rocky substratum. This relatively common species occurs in much of South Australia, Tasmania, Victoria and New South Wales; *Myochama keppelliana* is almost certainly a junior synonym.

Myochama tasmanica is a rare and poorly known species from south-eastern Australia, its type locality being Long Bay, Tasmania (Cotton 1961; Powell 1979). The small shell is triangular with prominent umbones. In New Zealand this bivalve attaches to *Tawera spissa* or *Paphies australis* (Powell 1979). The newly settled juveniles have a regular form, but later attain an irregular shape with growth conforming to the host. Thus, it remains to be demonstrated that this is a distinct species. Species of *Myochama* (about four known) are restricted to south-eastern Australia, Tasmania and New Zealand.

There are many more species of *Myadora* than *Myochama* in the south-west Pacific. Species of *Myadora* can be collected from shallow coastal waters although some, such as *Myadora delicata*, occur in waters as deep as 540 m. Several species within the Myochamidae may occur sympatrically. *Myadora ovata*, *Myadora brevis*, *Myadora pandoriformis* and *Myochama strangei* have all been collected from Port Jackson, New South Wales.

The Myochamidae are recorded from the Upper Eocene (Darragh 1985). Interestingly, most cemented bivalves have their origins in the Mesozoic (Yonge 1979).

Family Cleidothaeridae

The Cleidothaeridae, represented by the single genus *Cleidothaerus*, are restricted to Australia and New Zealand. They are shallow-water, sessile animals with heavy shells (Fig. 9.15; Pl. 16.4) which are cemented by the right valve to hard substrata. Little is known of this group and accounts by Odhner (1917), Lamy (1936) and Morton (1974, mostly on *C. maorianus*) form the basis of the description of this genus. More recently, Beu *et al.* (1990) have discussed the taxonomy of *Cleidothaerus* species.

The exact number of extant species is uncertain. Cotton (1961), Macpherson & Gabriel (1962), Iredale & McMichael (1962) and Powell (1979) list *Cleidothaerus albidus* as the only valid cleidothaerid species in southern waters. Beu *et al.* (1990) concluded that there are probably only two living species of *Cleidothaerus*, *C. albidus* and *C. pliciferus*. The other names reported in the literature, *C. chamoides*, and *C. maorianus* are probably synonyms of *C. albidus*.

The shell of *Cleidothaerus albidus*, covered by a thin, brown and usually eroded periostracum, is aragonitic and composed of an external simple prismatic layer and a biphasic inner nacre layer (Taylor *et al.* 1973). The markedly inequivalve and inequilateral shell is permanently attached to the substratum by the larger right valve (Fig. 9.15A). The right valve is deeply concave and strongly keeled with the attached anterior portion being flat and the exposed posterior portion being slightly convex though both sides are of approximately equal size. The left valve is flat and fits over the right valve like a cap. The shell is coiled as a result of tangential growth (Yonge 1967). Valves are united by a secondary periostracal ligament, although this is split anteriorly. Irregular growth lines are evident on both valves. The umbones, directed downward in the fixed position of the living animal, are subspiral, this being clearly evident on the left valve and a reflection of the coiled nature of the shell. Internally, the left valve has a prominent peg-like secondary tooth located just anterior to the inner ligament and beneath the umbo. This secondary tooth fits securely in a socket on the opposing right valve (Fig. 9.15B). The anterior adductor muscle scar is elongate and extends from the bottom of the tooth/socket to near the base of the valve. A short pallial line joins this scar with the smaller, ovoid posterior adductor scar. Although reported by Cotton (1961) to lack a pallial sinus, this bivalve has a very shallow and subtle sinus just adjacent to the ventrum of the posterior adductor scar. The primary ligament is attached to a deep curved chondrophore. This ligament is asymmetrical, the right side being broader than the left. A curved lithodesma, reflecting the curved nature of the shell, surrounds the primary ligament (Morton 1974).

The mantle, ventrally pigmented a bright orange, is extensively fused leaving free lobes at the siphons and the fourth pallial aperture. *Cleidothaerus albidus* has a small anterior pedal gape, but Odhner (1917) reported no such gape in *C. pliciferus*. The fourth pallial aperture is located just ventral to the inhalant siphon. The outer mantle fold is divided into two distinct lobes (Morton 1974). The short siphons, formed from the inner mantle folds (Morton 1974), are separate and muscular. The aperture of the inhalant siphon is crowned by papillae.

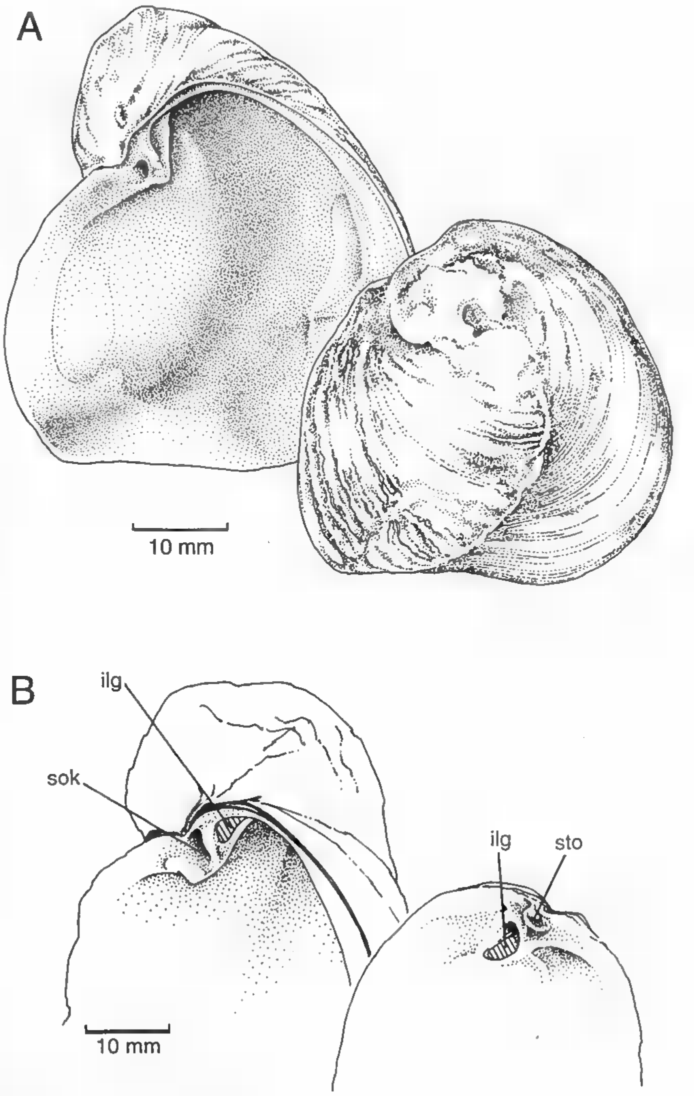

Figure 9.15 Family Cleidothaeridae. *Cleidothaerus albidus*: **A**, shell valves, right valve in internal view, left valve in external view; **B**, details of hinge. **ilg**, inner ligament; **sok**, socket; **sto**, secondary tooth. [R. Plant]

Cleidothaerus is strongly heteromyarian, the anterior adductor being about twice as large as the posterior. Well-developed pallial retractor muscles allow retraction of the mantle edge and siphons. The pedal retractors are reduced (Odhner 1917). The small compressed foot, which reflects the sessile life style, serves no burrowing or locomotory function; however, it may be involved in cleansing of the pallial cavity (Morton 1974).

The ctenidia are large, heterorhabdic and plicate. The left and right gills are asymmetrical, the left ctenidium being smaller than the right. Each gill is composed of two demibranchs, the outer of which is reduced and reflected dorsally. The labial palps are well developed and are almost as long as the ctenidia. As is typical of the Anomalodesmata, *Cleidothaerus* has a Type IV stomach (Purchon 1958) and a conjoined midgut and style sac. The intestine passes above the heart and kidneys.

The renopericardial system of *Cleidothaerus* is described by Morton (1974). The pericardium is located in front of the paired kidneys and is aligned in a dorso-ventral position. Nephrostomes, the apertures that drain the pericardium, exit from the postero-lateral corners of this chamber. Distal kidney limbs exit via nephridiopores located in the posterior suprabranchial chamber.

The nervous system of *Cleidothaerus pliciferus* was described by Odhner (1917). The cerebral ganglia are paired, the right being located higher in the body than the left. The pedal and visceral ganglia are each fused into a single ganglionic mass. Large buccal ganglia are located behind the cerebral ganglia. A pair of statocysts, each with a large statolith and numerous small statoconia (Type B_2), abut the pedal ganglia (Morton 1985b).

As is so for most anomalodesmatans, the Cleidothaeridae are simultaneous hermaphrodites. They have large dorsal ovaries and paired oviducts that open suprabranchially near the nephridiopores (Morton 1974). The testes are located ventrally and the single vas deferens also opens near the nephridiopores.

Morton (1974) was successful in getting *Cleidothaerus albidus* to spawn in the laboratory. The resulting larvae were positively phototactic, a response reflected in the fact that typically specimens are collected from the upper surface of rocks. Morton found no indication of byssal attachment by the larvae. Larvae settle on their right valves and produce large amounts of periostracum that probably serve as the source of initial attachment.

Cleidothaerus species live attached to rocks, empty shells and algal holdfasts on exposed rocky shores and subtidally down to about 40 m. *Cleidothaerus albidus* has been collected from southern Australia and New Zealand, and *C. pliciferus* from northern Western Australia. The heavy shell is often encrusted with fouling organisms, including barnacles, ectoprocts and coralline algae, and is sometimes drilled by boring worms and bivalves. The general morphology of *Cleidothaerus* has been strongly influenced by the sessile life style. Permanently attached by the right valve from the larval stage, these cleidothaerids have taken on a certain level of asymmetry including a coiled lithodesma, a strongly heteromyarian condition, an enlarged right ctenidium and associated palp, an enlarged right ovary, and a dorso-ventral alignment of the heart. The evolution of the genus *Cleidothaerus* has paralleled many of the evolutionary developments in other cemented bivalves (Morton 1974) that exhibit differences in the size of the organs of the right and left as a consequence of the tangential growth.

Cleidothaerus has a fossil record extending back into the Tertiary. A few valves of *Cleidothaerus* have been recovered from the Australian Oligocene and Miocene (Runnegar 1974), but according to Darragh (1985) the earliest record of the genus from Australia is from the Lower Miocene. Runnegar (1974) speculated that the genus evolved from a generalised verticordiid and represents a stage in the trend within the Anomalodesmata towards an epifaunal, sessile lifestyle.

Superfamily VERTICORDIOIDEA

The Verticordioidea, represented by the single family Verticordiidae, is a group of carnivorous, mostly deep-water animals. Unlike the carnivorous Poromyidae and Cuspidariidae, which have true septibranch ctenidia, Verticordiidae have ctenidia that are less muscularised and slightly more like a typical anomalodesmatan ctenidium. The superfamily is diagnosed by a thin white shell that is edentulous with a sunken primary ligament and a well-developed calcareous lithodesma (Fig. 9.1D). Type B mantle margin fusion is present as are arenophilic radial mantle glands, ciliary siphonal sense organs, and a fourth pallial aperture. Verticordioideans are among the least modified of the predatory bivalves. Numerous similarities between the shallow-water Lyonsiidae and the Verticordiidae suggest a phylogenetic linkage. These similarities include features of the arenophilic radial mantle glands (Allen & Turner 1974; Prezant 1979b, 1981b, 1985), byssal, digestive, and ctenidial systems (Allen & Turner 1974; Prezant 1977), and shell microstructure (Taylor *et al.* 1973; Prezant 1981a). Runnegar (1974) suggested that the Mesozoic lyonsiids were the stem group for the deep-sea Anomalodesmata. Morton (1987b), however, produced convincing arguments for a link between the Parilimyidae and the Verticordiidae, stemming from a Mesozoic pholadomyoidean stock.

Comparisons of the four predatory anomalodesmatan families were made by Morton (1987b), especially regarding the siphonal system. Several differences can be recognised between the two verticordiid subfamilies, the Lyonsiellinae and the Verticordiinae. These include variation in siphonal behaviour, presence of taenioid muscles versus standard siphonal retractor muscles, and presence of a pedal opisthopodium in some Lyonsiellinae (Allen & Turner 1974; Morton 1987b). The superfamily and family, nevertheless, are tightly united by characters outlined above. Similarities between the Lyonsiellinae and the Poromyidae, in particular with regard to prey capture, prompted Morton (1987b) to suggest an evolutionary link between these two groups, with a common ancestry in the Parilimyidae.

Family Verticordiidae

Verticordiids form a group of typically thin-shelled, carnivorous bivalves. They are a well-known part of the deep-sea benthos and widely distributed, however, their biology is poorly understood. Atlantic deep-sea verticordiids have been studied extensively by Allen & Turner (1974). Morton (1985c) has discussed prey capture in *Lyonsiella formosa*. They typically live at bathyal or abyssal depths, although shallower-water species are known. Few verticordiids have been reported from Australian waters although this is probably a reflection of their small size and deep-water habits.

The fragile shells (Fig. 9.16A, B) are generally small (in the range 3–6 mm), typically granulose, ornamented with small radially aligned beads or spinules and radial ribs of variable prominence and sculpture. The shells are equivalve, but variably inequilateral. Verticordiid shells are trapezoidal or subcircular in outline with prominent umbones usually directed forwards, and have a smooth rounded or deeply serrate ventral margin and often a concave antero-dorsal margin. They are composed of prismatic, nacreous and myostracal layers and are covered by a very thin periostracum. Shells of most species appear edentulous, although some have a single smooth cardinal and rarely a lateral tooth anterior to the sunken ligament on the right valve (some *Verticordia*) (Allen & Turner 1974). A variable-sized lithodesma (Fig. 9.1D) is present beneath the internal ligament and is similar to that of lyonsiid bivalves (Prezant & Carriker 1983; Morton 1985a). A thin periostracal cover forms a dorsal secondary ligament. The pallial line is evident but usually weakly developed. A pallial sinus is not well developed or is absent.

Aspects of the internal morphology of a verticordiid are illustrated in Figure 9.16C. The mantle margins are fused except at the regions of the siphons and the extensive pedal gape and usually the fourth pallial aperture. *Lyonsiella* in this family lacks a fourth pallial aperture. Well-defined arenophilic radial mantle glands typically line the mantle edge (Allen & Turner 1974), and resemble those of other Anomalodesmata (Prezant 1979b, 1981b; Morton 1981a). With the exception of *Lyonsiella fragilis*, verticordiid siphons typically are short. All are fused at their bases. The inhalant siphon, upon eversion, acts to entrap small prey which are then 'inhaled' for ingestion (Morton 1987b). In all but *L. fragilis*, prey must swim very near the inhalant siphon to be taken; *L. fragilis* has an elongate inhalant siphon and thus can feed at longer distances. The siphonal tentacles of verticordiids are tipped with ciliary sense organs similar to those of other septibranchs (for example, Poromyidae, Cuspidariidae) (Morton 1987b). Taenioid muscles, present only in *Lyonsiella*, retract the well-developed siphons (Morton 1987b). Adductor muscles are isomyarian to slightly heteromyarian. The foot may be large (for example, *Lyonsiella formosa*; Morton 1985c) or small (for example, *Verticordia jaffaensis*; Cotton 1961), and is usually byssate. Pedal retractor muscles are reduced, and the anterior pair may be absent in some species (Morton 1987b).

The ctenidia are modified from the typical anomalodesmatan form. They are reduced and arranged almost horizontally in the pallial chamber. The inner demibranch has reduced ascending and descending lamellae and the outer demibranch has a reduced descending lamella which is reflected upwards. Along the lateral edges of the ctenidium, thin tissue junctions fuse the demibranchs to the mantle and viscera (Allen & Turner 1974). The verticordiid

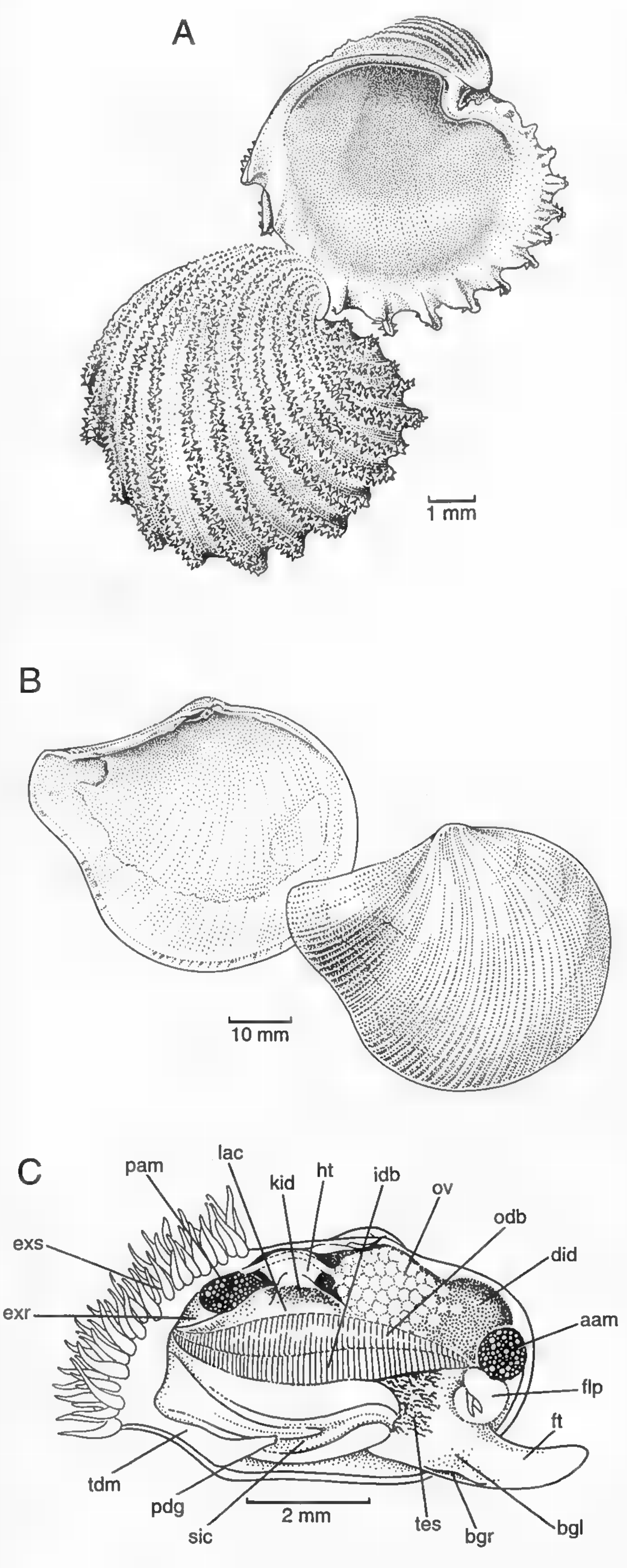

Figure 9.16 Family Verticordiidae. **A**, **B**, shell valves: **A**, *Verticordia ericia*, left valve in internal view, right valve in external view; **B**, *Euciroa galatheae*, left valve in internal view, rigth valve in external view. **C**, *Lyonsiella formosa*, organs of the mantle cavity, right shell valve and mantle lobe removed. **aam**, anterior adductor muscle; **bgl**, byssal gland; **bgr**, byssal groove; **did**, digestive diverticula; **exr**, exhalant siphonal retractor muscle; **exs**, exhalant siphon; **flp**, fused labial palps; **ft**, foot; **ht**, heart; **idb**, inner demibranch; **kid**, kidney; **lac**, lacunal system; **odb**, outer demibranch; **ov**, ovary; **pam**, posterior adductor muscle; **pdg**, posterior limit of pedal gape; **sic**, siphonal cowl; **tdm**, taenioid muscle; **tes**, testis. (C, after Morton 1985c) [A, A.J. Hill; B, C, R. Plant]

digestive system is modified to accommodate a carnivorous diet. Gut contents of verticordiids studied have included Foraminifera (Knudsen 1967), polychaete remnants (Bernard 1974), copepods (Allen & Turner 1974), and other small crustaceans such as amphipods and ostracods (Knudsen 1970). The labial palps are fused and form a trumpet-like structure for the reception of prey items (Morton 1985c, 1987b). Allen & Turner (1974) found that the oesophagus is able to expand considerably to allow prey items to enter the stomach. The large stomach, Purchon Type II, is usually lined with scleroprotein and may assist with 'crushing' of food (Allen & Turner 1974). The primary ducts leaving the stomach are very short. There is a small style sac that leads to a short hind gut; the rectum penetrates the ventricle and is posteriorly inflated. The pericardium is behind the umbones. The heart comprises a single ventricle and a pair of lateral auricles and lies above the large paired kidneys. The kidneys lie just anterior to the posterior adductor muscle. An unusual system of lacunae surrounds the kidneys and extends down the mantle and throughout the suprabranchial chamber (Allen & Turner 1974; Morton 1985c). The lacunal system may be involved in regulation of the hydraulic pressure changes that occur during feeding in some verticordiids (Morton 1985c). Statocysts are present and are of Morton's Type B_1 (Morton 1985b).

Verticordiids have paired testes and ovaries. The ovaries are typically larger than the testes and produce only a few large ova, usually in the order of a few hundred (Allen & Turner 1974). Larvae have short planktonic lives (Knudsen 1979); however, few have been available for detailed reproductive and developmental studies.

Verticordiids are widespread though not abundant members of the deep-sea fauna. With short planktonic lives, the distribution of some species may be limited, but there are species that have a wide distribution in the abyss. Unlike the Cuspidariidae, which have representatives on the continental shelf, the Verticordiidae are almost totally confined to the deep sea, as are the Poromyidae (Allen 1983). The morphology of verticordiids appears to be adaptive for an infaunal, predatory life style (Fig. 9.5D).

Vokes (1980) recorded 15 extant genus-group taxa in the Verticordiidae (16 if *Thracidora* is added). However, Keen (1969) listed eight extant genera and nine were listed in Vaught (1989) including those of Keen, plus an additional genus that was described after Keen's work. Soot-Ryen (1966) and Thiele (1935) also referred *Thracidora*, a genus erected by Iredale (1924), to the family. Although most authors have included it in the Thraciidae, it seems more appropriately placed in the Verticordiidae, probably in the Lyonsiellinae.

The modern Australian verticordiid fauna includes the type species of four genus-group taxa proposed by Iredale (1930). All were accepted by Keen (1969), albeit as subgenera of *Verticordia* (*Spinosipella*, *Vertambitus* and *Vertisphaera*) or *Lyonsiella* (*Proagorina*). Another taxon proposed by Iredale is *Setaliris* which is based on New Zealand species, and is also represented in the south-eastern Australian fauna. At the generic level the Australian fauna is quite diverse. Unfortunately, too little is known of the taxonomy or distribution of verticordiids, living or fossil, to draw many conclusions about their biogeography. One species, however, seems to have a wide distribution in the southern ocean. *Verticordia (Spinosipella) ericia* is widely recorded from southern Australia (Cotton 1961) and is also known from northern New Zealand (Powell 1979) and southern Africa. It can be recognised by its shell which is about 6 mm in length and has deep radial ribs covered with spinules.

There are few, if any, extensive collections of Australian verticordiids. Cotton (1961) recorded only three species from South Australia and Macpherson & Gabriel (1962) noted only two additional species. Iredale & McMichael (1962) recorded four species from New South Wales. Among Australian species, *Verticordia (Verticordia) jaffaensis*, occurs in South Australia at depths between 180 and 540 m, reaching a size of only 3 mm (Cotton 1961). Another South Australian verticordiid, reaching around 6 mm, *V. (Verticordia) bordaensis*, has been collected from water as shallow as 40 m off Backstairs Passage (Cotton 1961). Macpherson & Gabriel (1962) listed *V. (Verticordia) tasmanica* from Bass Strait. This species is similar to *V. bordaensis*, but has more pronounced radial sculpture and a more deeply excavate anterior-dorsal margin (Cotton 1961). *Thracidora flindersi*, distributed from Beachport, South Australia, to Western Australia (Dell 1964), has been taken from 540 m (Cotton 1961). The accuracy of a report of *Thracidora arenosa* off Wilson's Promontory by Macpherson & Gabriel (1962) needs to be examined for taxonomic validity.

The Verticordiidae date back to the Palaeocene (Runnegar 1974) and are among the least specialised of the carnivorous bivalves (Morton 1985a). It is likely that the Verticordiidae, Poromyidae and Cuspidariidae, had their origins in some pholadomyoidean stock (Morton 1985a). Verticordiids appear to be rare in the Australian Tertiary. Only two species (both of Neogene age) have been described to date, and a third has been recorded from the Upper Eocene (Darragh 1970; Darragh & Kendrick 1980).

Superfamily POROMYOIDEA

The Poromyoidea, consisting only of the family Poromyidae, is one of the four known groups of carnivorous bivalves. The superfamily has few extant Australian representatives and most of these are from deep waters, although *Poromya illevis* (= *Poromya granulata*, *Ectorisma granulata*) occurs in relatively shallow waters in South Australia.

Allen & Morgan (1981) and Bernard (1974) examined 'septibranchs' of the Atlantic and Pacific respectively. Their work highlighted the fact that these bivalves are an important component of the deep-sea fauna. Nevertheless, most information we have on the biology of the deep-sea septibranchs stems from dissections of preserved museum material. Observations on living and fresh material are rare. There is no information on the population ecology of these bivalves, owing to their deep-sea habitats and overall collecting difficulties.

Family Poromyidae

Poromyids are infaunal, carnivorous, marine bivalves. They can be distinguished from the closely related Verticordiidae and the Cuspidariidae by the presence of an external primary ligament which does not have a lithodesma. The ctenidia are modified to form a septum, a characteristic that is shared with cuspidariids, and the two families are often called 'septibranchs'. Poromyids, on the basis of structural similarities of their siphons and reproductive systems, were considered by Allen & Morgan (1981) to be more closely related to verticordiids than to cuspidariids (Allen & Morgan 1981). Atlantic deep-sea poromyoideans have been described in detail by Allen & Morgan (1981) and Bernard (1974) has examined species from the Pacific. They suggested that there are only two valid extant genera within the family, *Poromya* and *Cetoconcha*. Dall (1881) gave the first account of poromyid anatomy.

The shells are thin, equivalve, and equilateral to slightly inequilateral, and have a rounded anterior margin and a slightly truncated posterior margin (Fig. 9.17A, B). They are also slightly inflated. Some species have an almost smooth shell surface, but most have fine radial rows of small spinules, granules or beads (Allen & Morgan 1981). Poromyid shell microstructure is similar to that of cuspidariids, and unlike that of most other anomalodesmatans, which have prismatonacreous shells. The shells are aragonitic. *Poromya illevis* has an outer granular homogeneous layer, believed by Taylor *et al.* (1973) to be the remnant of a structural breakdown of a more typical prismatic layer. Some poromyids have a two-layered homogeneous shell (Taylor *et al.* 1973). The ligament and hinge system is considered to be conservative and therefore of great taxonomic importance by Yonge & Morton (1980). On the basis of these characters, parilimyids (Pholadomyoidea) are thought to be closely related to the Poromyoidea, and pholadomyoideans are considered to have been the evolutionary stock for the extant deep-sea predatory bivalves (Morton 1987b). A single secondary hinge tooth may be present on the right valve and interconnects with a socket on the left valve (Fig. 9.1B, C). As in the Pholadomyoidea, the primary ligament is external, and is covered by a secondary ligament of dorsal periostracum; a lithodesma is absent (Morton 1980; Yonge & Morton 1980; Allen & Morgan 1981). The adductor muscle scars and associated pedal retractor muscle scars are located high in the shell. A deeply etched pallial line is present with very little indication of a pallial sinus.

The mantle margins are fused leaving only the siphonal openings and an extensive pedal gape. The large pallial retractor muscles are associated with the well-defined pallial line. Arenophilic radial mantle glands are absent (Allen & Morgan 1981). The siphons are separate and often brightly coloured. The inhalant siphon is much larger than the exhalant siphon. The inhalant siphon has a larger aperture than the exhalant. The siphons are surrounded by 13 to 15 long muscular tentacles that surround the base of the inhalant siphon, each with a prominent tentacular nerve (Morton 1981c; Allen & Morgan 1981). Each tentacle is covered with small papillae and is sensitive to the movement of prey. When everted, the inhalant siphon forms an extensive hood-like cowl that could be used in capturing prey (in *Poromya illevis* Fig. 9.5C) (Morton 1981c).

Features of the internal anatomy are illustrated in Figure 9.17C. The adductor muscles are subequal in size, and anterior and posterior pedal retractor muscles are present. A muscular foot with a byssal groove is present, although it is unknown if byssal threads are produced by adults. The foot is long, tapered and active in burrowing. Well-developed septal retractor muscles attach the ctenidial septum to the dorsal part of the shell.

The ctenidia are reduced to a horizontal septum originally described by Pelseneer (1888b, 1911) and again by Ridewood (1903), Yonge (1928), Bernard (1974), Morton (1981c) and Allen & Morgan (1981). This thin, but strong septum divides the mantle cavity into two chambers, the upper supraseptal and the lower infraseptal. It is pierced by the foot as well as by two paired groups of very short gill filaments producing septal ostia. One group of septal ostia is anterior and one group posterior to the penetration point of the foot. The anterior septal ostia are located very close to the palps. Immediately behind the foot, the septum is modified as a large, muscular compensation sac which assists in controlling hydrostatic pressure changes that occur during feeding in these predatory bivalves (Allen & Morgan 1981; Morton 1987b).

The labial palps may be large, or small (for example, *Poromya illevis*), and the inner and outer surfaces are smooth. Yonge (1928) and Morton (1981c) found that the palps were used in *Poromya* species to pull food to the mouth. The digestive system is adapted to a predatory life style with the presence of a short muscular oesophagus, a thick gastric shield, and large-lumened digestive tubules (Allen & Morgan 1981). A Type II stomach is present (Purchon 1956b). Yonge (1928), Purchon (1956b), Bernard (1974) and Allen & Morgan (1981) have described the digestive system of various poromyids. A wide mouth leads to a short, but muscular oesophagus. The muscular stomach is modified for the digestion of large prey items (Yonge 1928, Bernard 1974) and is associated with a small style sac that is continuous with the midgut. A thick gastric shield is present (Allen & Morgan 1981). A few primary ducts exit from the stomach into the mass of digestive diverticula. The lumina of the digestive diverticula are notable for their large size (Yonge 1928). The short midgut extends over the posterior adductor muscle and empties near the base of the exhalant siphon.

The pericardial chamber, located between the posterior adductor muscle and the ligament, contains a typical bivalve heart of one ventricle and two auricles. The rectum penetrates the ventricle. Fused kidneys are embedded in the septum just beneath the pericardial chamber (Morton 1981c). In *Poromya*, the kidneys

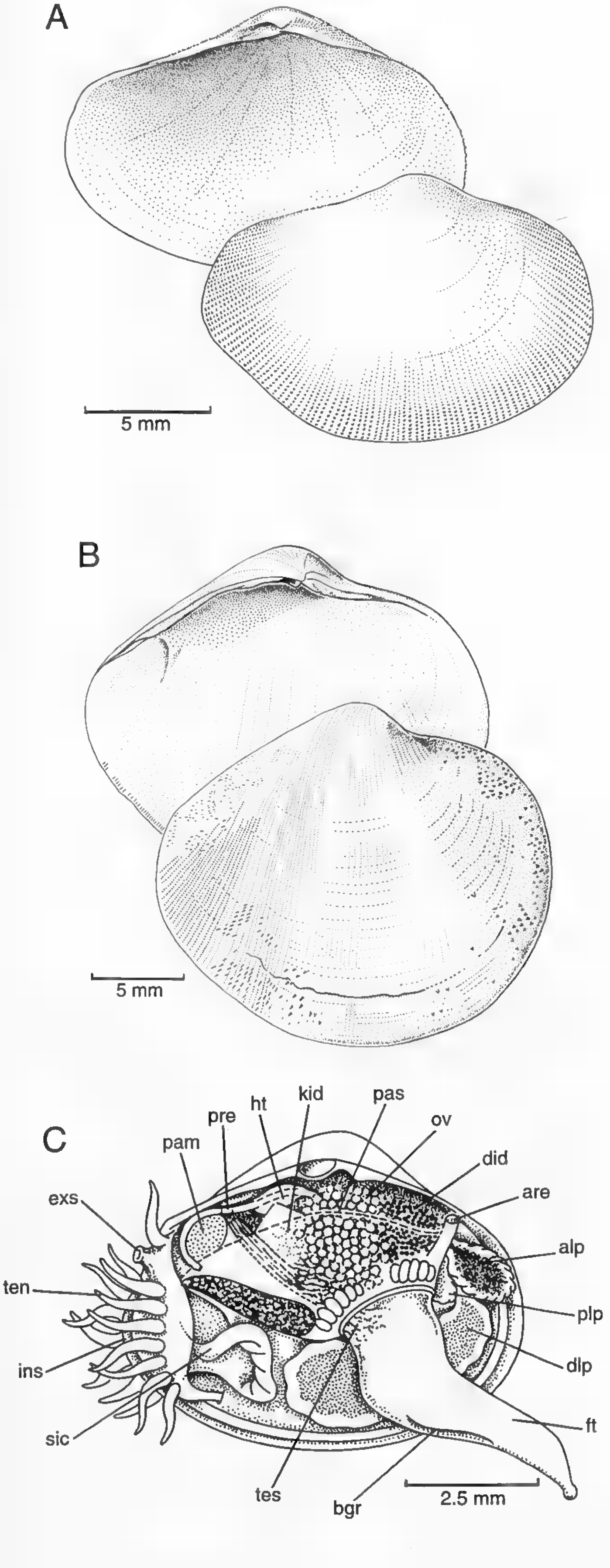

Figure 9.17 Family Poromyidae. A, B, shell valves: A, *Poromya illevis*, left valve in internal view, right valve in external view; B, *Poromya* cf. *buttoni*, left valve in internal view, right valve in external view. C, *Poromya illevis*, organs of the mantle cavity, right shell valve and the mantle lobe removed; the left anterior labial palp is shown distended, the right contracted. **alp**, anterior labial palps; **are**, anterior retractor muscle; **bgr**, byssal groove; **did**, digestive diverticula; **dlp**, distended labial palp; **exs**, exhalant siphon; **ft**, foot; **ht**, heart; **ins**, inhalant siphon; **kid**, kidney; **ov**, ovary; **pam**, posterior adductor muscle; **pas**, posterior adductor muscle; **plp**, posterior labial palp; **pre**, posterior retractor muscle; **sic**, siphonal cowl; **ten**, tentacle; **tes**, testis. (C, after Morton 1981c) [A, C, R. Plant; B, A.J. Hill]

form two lateral sacs that fuse along their anterior region, but are separate posteriorly (Allen & Morgan 1981). The distal limbs, containing large excretory granules (Allen & Morgan 1981; Morton 1981c), exit into large renal apertures at the junction of the kidney and visceral mass (Morton 1981c).

Three pairs of ganglia, visceral, pedal and cerebropleural, are present in poromyids. Visceral and pallial connectives join the visceral and cerebropleural ganglia. A pair of pedal connectives joins the pedal and cerebropleural ganglia. A siphonal nerve ring arises from the pallial connectives (Allen & Morgan 1981). An outer septal nerve runs from the visceral ganglion along the medial portion of the posterior septal muscle and extends anteriorly (Allen & Morgan 1981). *Poromya illevis* has Type B_1 statocysts (Morton 1985b). The siphonal tentacles are sensory and have associated ciliary sense organs (Fig. 9.3C–E; Morton 1981c).

The ovaries of these simultaneous hermaphrodites are situated dorsal to the testes. Often brightly coloured (yellow in *Poromya illevis*; Morton 1981c), the ovaries are situated antero-dorsally; the white testes are found postero-ventrally. The large, yolky eggs lack the thick capsule typical of many other members of the subclass. A pair of oviducts and the vasa deferentia exit the respective gonads and arrive separately, as four thin ducts, female dorsal to male, to merge into a single hermaphroditic duct that exits into a large reproductive papilla. This serves as a cloaca and is located close to the renal aperture. The large supraseptal chamber may serve as a brood chamber (Morton 1981c). The embryology and life history of poromyids remains unknown although it is likely that they have a very short larval period and settle close to the parental populations.

Morton (1981c) described prey capture in some poromyids (see Fig. 9.5C). Presumably they feed on small crustaceans such as copepods, amphipods, isopods, cumaceans, and ostracods, but remains of other organisms have been found in the stomachs of septibranchs including foraminiferans and other protozoans, polychaete setae, sponge spicules, and chaetognaths. Morton (1987b), however, put little credence on the latter as part of the diet of septibranchs, assuming that they are consumed incidentally in the course of feeding on benthic crustaceans. Summaries of potential prey items are found in Bernard (1974) and Morton (1987b). Morton (1987b) speculated that in *Poromya illevis*, the large inhalant siphonal hood is used to capture prey that has been detected by the siphonal tentacles (Fig. 9.5C). The septum, in response, is depressed and the ostia opened. Prey are brought into the infraseptal chamber by contraction of siphonal retractor muscles drawing in the siphonal hood. The compensation sac receives blood that is forced forward by contraction of the siphonal haemocoels. The labial palps then extend back and transfer the food to the mouth.

Some six poromyid species have been reported from Australian waters, but little information is available on their biology and ecology. Checklists and reports have provided the only information on Australian species. The first to be described was *Poromya laevis* from 285 m, east of Cape York, Queensland, a distinctive species that differs from nearly all other poromyids in lacking granules or spicules on the shell exterior. Tate (1892) and Iredale (1930) proposed the genera *Ectorisma* and *Questimya* respectively, for Australian species, but both names were synonymised with *Poromya* by Keen (1969) and Allen & Morgan (1981). (The type species of *Ectorisma* is *E. granulata.* If *Ectorisma* is considered to be a synonym or subgenus of *Poromya*, this species name becomes a secondary homonym of *P. granulata* the type species of the genus, and must thus be referred to by its replacement name *P. illevis*). Apart from *P. illevis*, which has been recorded from waters as shallow as 14–18 m in South Australia (Cotton 1961) as well as New South Wales and Tasmania, all Australian poromyids are from bathyal depths. *Poromya granifera* has been recorded from the deep waters of southern Australia, from 540 m, 190 km west of Eucla (Cotton 1961). Little is known about the relationships of

Australian poromyids, but the presence of *P. laevis* in northernmost New Zealand (Crozier 1966; Powell 1979) and of a species of *Ectorisma*, *E. neozelanica* (referred to *Poromya* by Powell 1979) in southern New Zealand suggests that some taxa may be widely distributed in the south-western Pacific.

Superfamily CUSPIDARIOIDEA

The Cuspidarioidea is the most diverse superfamily of 'septibranch' bivalves recorded from Australian waters. This superfamily is unique within the Anomalodesmata, in that its members are dioecious. Cuspidarioideans are small to medium-sized (size 3–25 mm), thin-shelled bivalves typically inhabiting deep-sea environments. Allen & Morgan (1981) reviewed the functional morphology of Atlantic, and Bernard (1974) that of eastern Pacific cuspidariids, but no comparable work is available for any Australian Cuspidariidae. About 21 species of *Cuspidaria* are found in Australian waters (Hedley 1910; Cotton 1961; Iredale & McMichael 1962; Boyd & Phillips 1985). Another 12 were noted from New Zealand waters by Powell (1979). Several of the latter are probably endemic to New Zealand waters, but it is possible that some of the deep-water 'septibranchs' will be found in Australia.

The oldest cuspidarioideans known are from the Triassic (Runnegar 1974). By the Jurassic, they had the typical dipper-like shape of many extant species and, at least in shell shape, were clearly different from poromyids (Allen & Morgan 1981). The strong similarities between the Poromyoidea and Cuspidarioidea, in terms of shell microstructure, secondary teeth, siphonal sense organs, septum and stomach type (Type II) are possibly a consequence of parallel evolution (Allen & Morgan 1981). The bilayered homogeneous shell microstructure, mode of feeding, and dioecious sexuality, set cuspidarioideans apart. Morton (1980, 1987b) discussed the possible pholadomyoidean origin of the deep-sea septibranchs.

Family Cuspidariidae

Cuspidariid shells are thin, white, and vary in shape from ovate with a strongly rostrate and gaping posterior margin, to trigonal or pyriform (Fig. 9.18). They are usually equivalve to slightly inequivalve, and either strongly inequilateral with a tapered siphonal rostrum and a strongly inflated anterior region or are almost equilateral with a truncate posterior end. There is a thin yellowish periostracum. The shell is aragonitic and composed of two homogeneous layers with an indistinct myostracum (Taylor *et al.* 1973). Some species are smooth, some may have commarginal lines or ribs, and some are granulose, but relatively few have distinct radial sculpture. A slight rostral ridge runs from the umbones to the posterior margins in some species (for example, *Cuspidaria alta*). The anterior shell margin is rounded; posteriorly the narrow siphonal region is truncate or pointed. The latter region is the only portion of the shell where the valves gape during adduction. A simple pallial line is present and has a weak, pallial sinus. Adductor muscle scars are located close to the valve edge. The internal primary ligament is often opisthodetic and may have a small calcareous lithodesma. A small cup-shaped chondrophore holds the rounded ligament. There is, however, wide variation in the form of the hinge and ligament of cuspidariids (Allen & Morgan 1981). The ligament can be opisthodetic (for example, *Cuspidaria parva*) or amphidetic (for example, *C. costellata*). The wide variation in hinge dentition includes presence of lateral and/or cardinal teeth or neither. It is possible that these teeth are secondarily derived (Yonge & Morton 1980).

Hinge and tooth structure can be diagnostic for subgenera of *Cuspidaria*, as outlined by Allen & Morgan (1981). Subgenera *Cuspidaria* and *Cardiomya* have a single postero-lateral hinge tooth in only their right valve; *Myonera* is edentulous; *Rhinoclama* has anterior and posterior lateral teeth in its right valve only; *Luzonia* has no lateral teeth but an anterior cardinal tooth only in its right valve; *Tropidomya* has a single anterior cardinal tooth in each valve; *Plectodon* has long anterior and posterior lateral teeth in its right valve; *Leiomya* has a single pointed cardinal tooth in the left valve but a bifid anterior cardinal as well as anterior and posterior lateral teeth in its right valve; and *Vulcanomya* species lack cardinal teeth but have anterior and posterior lateral tooth in their right valve and an anterior lateral tooth in their left valve. Within the genus *Halonympha* there is a sharp cardinal tooth in the right valve as well as distinct internal shell ridges or clavicles that run along the dorsal margins to the posterior adductor muscle scar.

The genus *Protocuspidaria*, erected by Allen & Morgan (1981), has variable hinge structure, the features forming the basis for three subgenera. *Protocuspidaria* has a single anterior lateral tooth in the right valve; and *Bidentaria* has both valves with an anterior lateral tooth; and *Edentaria* lacks teeth. A long secondary ligament of periostracum helps align the valves dorsally. The ligament and lithodesma of the Cuspidariidae were described by Yonge & Morton (1980).

The thin mantle is fused except for the siphonal apertures and a long pedal gape (running about two thirds the length of the ventral side). There is no fourth pallial aperture. The adductor muscles are slightly heteromyarian with the posterior being slightly smaller. Both muscles are located just inside the valve margins. Well-developed pedal, siphonal and septal retractor muscles are present. The foot is long and tapered and contains a well-developed byssal system though byssal threads are rarely present. The siphons are asymmetrical, the inhalant siphon being long and wide, the exhalant siphon short and narrow. In all species of *Cuspidaria*, seven tentacles surround the siphons basally: four around the inhalant and three above the exhalant siphon. These tentacles, formed from the middle fold of the mantle, contain mechanoreceptors (Reid & Crosby 1980). As in poromyids, the septum controls internal pressure in the septal chamber and assists in prey capture (Reid & Reid 1974).

The cuspidariid gut is adapted for carnivory. The mouth has a wide lumen that tapers to a muscular oesophagus. The muscular labial palps are small. They can be divided into three types that Allen & Morgan (1981) term I, II and III. Type I palps, the most common within the Cuspidariidae are very small and consist of an anterior pair of narrow, triangular palps and a posterior pair of thick pad-like palps. Type II, found only in *Cuspidaria*, are larger than Type I and have elongate posterior palps giving the overall system an antero-posterior symmetrical appearance. Type III palps are larger than both previous palp types and are composed of a 'flap-shaped' anterior pair of palps and enlarged, concave posterior palps. The palps are ciliated, but sorting ridges are absent. The simple stomach is of Purchon's (1956b) Type II and is modified for digestion of larger prey (Yonge 1928; Bernard 1974; Allen & Morgan 1981). Reid (1977) found proteolytic enzymes in the stomach of *Cardiomya* species. A small style sac is present that is continuous with the anterior midgut (Allen & Morgan 1981). The hindgut passes through the ventricle and exits near the exhalant siphon after passing over the posterior adductor muscle. The muscular septum lies horizontally in the mantle cavity, dividing it into supraseptal and infraseptal chambers. The septum is attached to the shell by anterior and posterior septal muscles (Yonge 1928; Allen & Morgan 1981). The foot, as in the Poromyidae, passes through and is fused to the septum. Four pairs of septal pores penetrate the septum on each side of the foot (Allen & Morgan 1981). Sphincter-like muscles allow closure of these pores.

Cuspidariids are infaunal and the apertures of the siphons are positioned almost flush with the sediment surface (Knudsen 1979). Prey are captured by extending the inhalant siphon, to almost twice its relaxed length, towards an identified prey item (Fig. 9.5B; Reid & Reid 1974). The septum is then depressed creating a negative pressure that sucks the prey into the infraseptal chamber. The labial palps extend posteriorly to seize the prey and transfer it to the mouth (Morton 1987b). A reduced lacunal

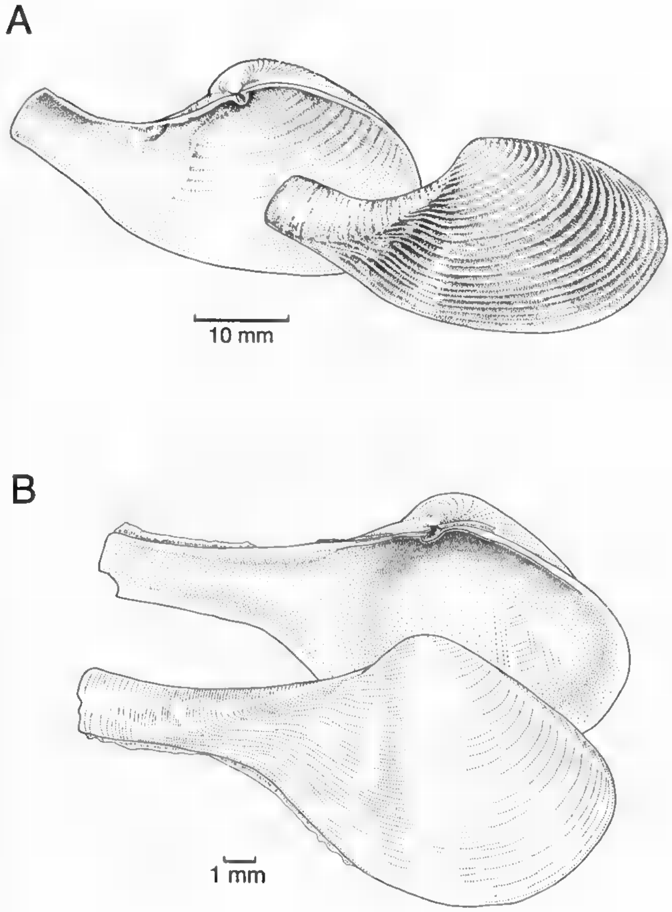

Figure 9.18 Family Cuspidariidae. Shell valves: **A**, *Cuspidaria latesulcata*, left valve in internal view, right valve in external view; **B**, *Cuspidaria angasii*, left valve in internal view, right valve in external view.
[A, R. Plant; B, A.J. Hill]

system, comparable to but not as extensive as that found in verticordiids, may be present (Allen & Morgan 1981) and may similarly function in hydraulic control during feeding.

The pericardial chamber, located just beneath the umbones, contains a tubular ventricle and paired, thin-walled auricles. A complex sinus system opens into the auricles. This system extends over and within the gonads, kidneys, siphons, septum and mantle (Allen & Morgan 1981). Several larger siphonal sinuses are also present. A pair of thin-walled kidneys is found between the gonads and posterior adductor muscles. These empty near the exhalant siphon via paired nephridiopores.

Cerebropleural, visceral and pedal ganglia are present and joined by connectives. Allen & Morgan (1981) did not find a siphonal ganglion as reported by Reid & Reid (1974) in *Cuspidaria*. A septal nerve, originating from the visceral ganglion and running to the cerebral ganglion, and an inner septal nerve, running from the cerebropleural to the pedal ganglion, help to regulate activities of the septum (Allen & Morgan 1981). Cuspidariids have well-defined mechanoreceptors associated with the inhalant siphon (Reid & Reid 1974). They also have Type C statocysts (Morton 1985b) that do not abut the pedal ganglia but are separate from it. Each is composed of only four or five cells fringed by a low microvillar border. A large ovoid statolith is present in each statocyst occupying much of the lumina. Presumably this type of statocyst, found only in the Cuspidariidae, is effective in only very sedentary bivalves (Morton 1985b).

Cuspidariids are predominantly dioecious. Typically, paired ovaries or testes are present dorsal to the posterior region of the stomach. The paired gonads merge behind the stomach and appropriate gonoducts exit near the posterior adductor muscle in the supraseptal chamber (Allen & Morgan 1981). The early development of *Cardiomya pectinata*, an eastern Pacific cuspidariid, has been documented by Gustafson *et al.* (1986). This cuspidariid probably produces non-planktotrophic, direct-developing offspring. The gastrula stage is enclosed in a negatively buoyant capsule that adheres to the substratum. Only prodissoconch I forms prior to deposition of dissoconch shell at a stage when the larva is about 220 µm long.

Development in Cuspidariidae appears to be more like that of other eulamellibranchiate bivalves than that of protobranchiate bivalves (Gustafson *et al.* 1986), but we still have very little information on reproduction and development in this family. Aside from feeding behaviour, much of which is speculative, we know little of their overall behaviour, or indeed, of their physiology.

Cuspidariids typically live buried in sand and mud (Fig. 9.5B) and must be dredged. The powerful septum and long posterior rostrum allow them to bury deep in the sediment, with only the tips of the siphons exposed. Mechanoreceptors allow detection of passing prey, which are quickly entrapped in the predatory suctorial apparatus (Allen & Morgan 1981). The thin shells and typically small size, plus deep-water infaunal habits, make these predatory bivalves difficult to retrieve intact.

The family is represented by about nine genera worldwide. The number of species is probably far more than presently known: most cuspidariids are likely to be small and to live in the deep sea, and many are probably still to be discovered.

Although they are usually assigned to *Cuspidaria* itself, the Australian species vary widely in shape and sculpture, and some are probably assignable to other taxa. Most Australian cuspidariids are from depths greater than 180 m (from the bathyal zone), but the South Australian species *Cuspidaria trigonalis*, which reaches 5 mm in length, lives at depths of only 25–63 m (Cotton 1961). *Cuspidaria trigonalis* in particular differs from typical members of the genus in having a triangular shape as opposed to the typical pyriform shape. Another south-eastern Australian species, *C. dorsirecta*, is smooth and equilateral and has only a very short and wide rostrum; Cotton (1961) suggested that it may belong in *Austroneaera* which was proposed for New Zealand species. Most of the other species have the dipper shape typical of *Cuspidaria*, and many have distinct commarginal sculpture, but *C. ros* is smooth except for faint commarginal ribs. Most cuspidariids are small, but a larger cuspidariid, reaching almost 40 mm in length, *C. latesulcata*, occurs in New South Wales. The most elaborate Australian cuspidariid shell is that of *C. pinna* from waters down to 540 m off Cape Jaffa. This species, which may more appropriately fit into the genus *Cardiomya*, is thin shelled and has about 25 radial ribs crossed by thin and closely spaced commarginal ribs, producing a file like pattern. A similar pattern is present on the posterior half of *Cuspidaria levifrons*, another small deep-water form from off the coast of Eucla, south-eastern Western Australia. *Cuspidaria ros*, also found down to 540 m off the coast of Cape Jaffa, South Australia, has a smooth shell surface with very fine commarginal lines. A few species of *Cuspidaria* have been recovered from Australian Antarctic waters or nearby. These include *C. plicata* and *C. kerguelensis* (Soot-Ryen 1951). Several others have been dredged from the nearby Ross Sea (Dell 1964) and will most probably be collected from adjacent waters in the future.

Cuspidariids are not common in the Australian Tertiary, only three species having been described (Darragh 1970). *Cuspidaria* probably first appeared in the Triassic (Runnegar 1974). *Cuspidaria subrostrata*, a species similar to the extant *C. exarata*, has been recovered from Miocene deposits of Victoria (Cotton 1961).

The origin of the Cuspidariidae, as for the other 'septibranchs' can be sought among pholadomyoideans. The possible relationship of the Cuspidarioidea and the Pholadomyoidea is discussed by Morton (1980).

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CLASS SCAPHOPODA

CHAPTER 10

DEFINITION AND GENERAL DESCRIPTION

Scaphopods are bilaterally symmetrical, burrowing, marine molluscs, commonly called tusk or tooth shells (Fig. 10.1; Pl. 16.5). The external shell is a tapered tube, open at both ends and usually curved. It is smooth or variously sculptured, and ranges in length from 2–50 mm, but may reach 130 mm in the Indo-Pacific *Pictodentalium vernedei.*

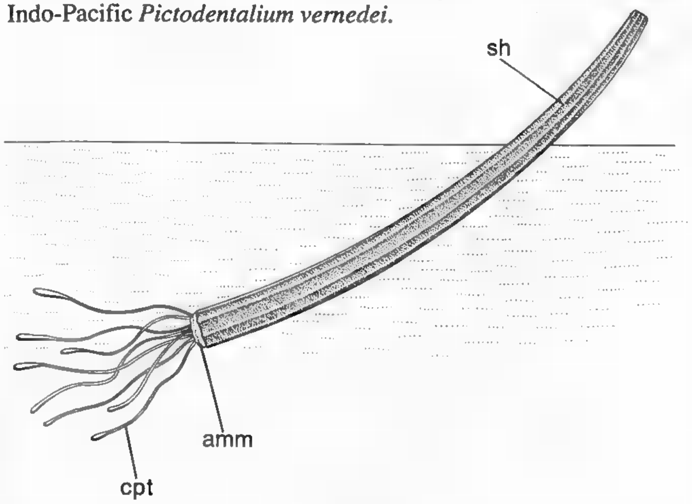

Figure 10.1 *Dentalium* sp. (Dentaliidae) in natural orientation with the captacula extended for feeding. The shell apex does not necessarily protrude from the substratum surface. The foot and captacula are never protruded simultaneously. **amm**, anterior mantle margin; **cpt**, captacula; **sh**, shell. (Modified after Lacaze-Duthiers 1856–1857) [C. Eadie]

A tapered, tubular mantle, fused along the ventral midline and, like the shell, open at both ends, encloses the elongate animal. The foot and feeding organs protrude from the larger, anterior opening of the shell, called the aperture, and the smaller, posterior opening is at the apical end. Through elongation and rotation of the dorso-ventral body axis, the apex is at the posterior end of the shell and the anus lies in the midregion of the body, rather than in a terminal position (Fig. 10.2). In physiological terms and for reasons of convenience, the concave side is referred to as dorsal and the convex side as ventral (Fig. 10.2). Morphologically, only the foot region, between the mouth and the anus, is on the ventral side (Steiner 1992b).

The weakly developed head lacks eyes and is surrounded by clusters of extensible, ciliated filaments, the captacula, which are used to locate and capture food. Osphradia and ctenidia are absent, and respiration takes place via the internal mantle surface. The radula is large, and each row consists of five teeth (Lacaze-Duthiers 1856–1857).

Scaphopods are benthic micro-carnivores inhabiting all types of unconsolidated sediment, at depths from the littoral to the abyssal in euhaline oceans (Shimek 1990). They live completely buried in mud or sand, with only the smaller, posterior end occasionally protruding into the water.

The two major systematic groups in the class Scaphopoda are the orders Dentaliida and Gadilida (Palmer 1974; Starobogatov 1974). Worldwide there are 11 families and 500 to 600 living species. Australia has more than 150 named species (Lamprell & Healy 1997), fossil and extant, from eight families.

HISTORY OF DISCOVERY

Aldrovandi (1642) may have been the first of the pre-Linnaean naturalists to describe a scaphopod. Deshayes (1825) lists him with many others in the synonymy of *Dentalium elephantinum*, though Linnaeus, when he listed four named species in 1758, mentioned only Borani, Lister, Rumphius, Gaultieri and d'Argenville.

In the first scientific monograph on scaphopods, Deshayes (1825) described 42 species, which he distributed between four sections and four sub-sections, all included in his 'Genre Dentale'. Fossil species from the Tertiary deposit of the Paris Basin were also covered, though four of these species were shown subsequently to be serpulid worm tubes. His drawings of the internal anatomy of '*Antalis entalis*' (actually *Antalis vulgaris*) were the first of their kind. Until 1844, when Philippi introduced the genus *Cadulus*, the only generic name available for scaphopods was Linnaeus' *Dentalium. Siphonodentalium* and *Gadila* soon followed.

Lacaze-Duthiers (1856–1857) described the anatomy of *Antalis entalis* in greater detail than Deshayes, accurately elucidating the structure and function of the whole animal. His description of the embryology and larval development, from fertilised ovum to the full-grown larva, were the first, and have hardly been improved on to this day, though valuable contributions were made by Kowalevsky (1883), Fol (1889) and Plate (1892).

Meanwhile, R.B. Watson (1879, 1886) in Britain and W.H. Dall (1881, 1889) in America, were describing scaphopods collected by the *Challenger* and *Blake* expeditions during the 1880s. Pilsbry & Sharp's (1897–1898) magnificent monograph is a bench-mark for taxonomists, and is still the fundamental text for all serious workers on shells and taxonomy of scaphopods. The authors

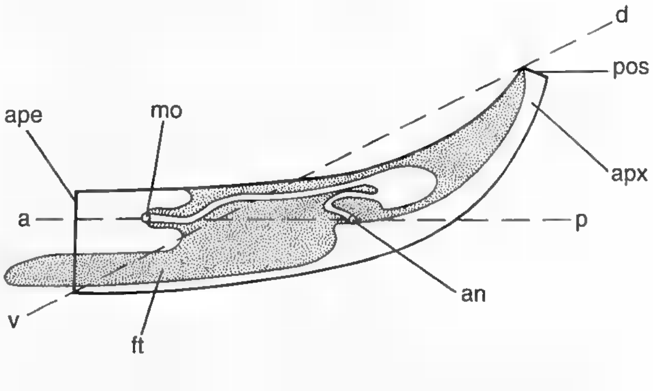

Figure 10.2 Schematic representation of the body axes in Scaphopoda. The captacula are not shown. **an**, anus; **a–p**, antero-posterior axis; **ape**, aperture, anterior opening of shell; **apx**, apex; **d–v**, dorso-ventral axis; **ft**, foot; **mo**, mouth; **pos**, posterior opening of shell. [D. Wahl]

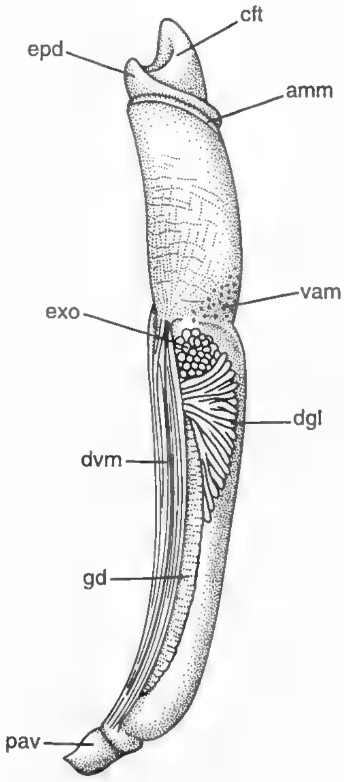

Figure 10.3 *Antalis* sp. (Dentaliidae) removed from its shell, lateral view. **amm**, anterior mantle margin; **cft**, conical tip of foot; **dgl**, digestive gland; **dvm**, dorso-ventral retractor muscle; **epd**, epipodial lobe; **exo**, excretory organ; **gd**, gonad; **pav**, pavilion; **vam**, vascularised part of the mantle. (After Lacaze-Duthiers 1856–1857) [C. Eadie]

described and figured nearly all the known living scaphopods, listed all known fossils, and removed the serpulid polychaetes and other curved, conical-tubed structures, leaving only scaphopods in the class.

Until 1862 when Bronn proposed the class Scaphopoda within the Prosopocephalia, these molluscs always resided among the gastropods, sometimes near the genus *Diodora* on the grounds of having two openings in the shell. Linnaeus placed them between the perforate limpets and serpulids. Pilsbry & Sharp (1897–1898) recognised that they were certainly not gastropods, though undoubtedly molluscs.

Since the late nineteenth century a great deal of work has been done, outstanding among which are Boissevain's (1906) report on the scaphopods from the *Siboga* expedition, Henderson's (1920) monograph of the eastern American scaphopods and Habe's (1964) thorough account of the scaphopods of Japan. Most recently, monographs by Scarabino (1995) and Lamprell & Healy (1997) have greatly expanded knowledge of the diversity and distribution of the scaphopods from the tropical Pacific and Indian Oceans, and Australia respectively.

Ludbrook (1960), Emerson (1962), Palmer (1974), Starobogatov (1974) and Chistikov (1975) provided classifications of the whole class Scaphopoda, and Habe (1977) classified the western Pacific species. Scarabino's (1979) unpublished light microscopy studies on radular morphology provided additional characters for classification. Steiner (1992b) presented the first cladistic analysis of the class using both hard-part and soft-body characters.

Australian scaphopods received some attention for the first time when Brazier (1877) described material from the *Chevert* expedition to tropical Queensland. Tate (1887, 1899), Tate & May (1900), Hedley (1901, 1903) and Verco (1911) added more fossil and extant species. Cotton & Ludbrook (1938) and Cotton & Godfrey (1940) reviewed the previous descriptions and revised the classification. Subsequently, Colman (1958) reviewed the scaphopods of New South Wales, adding six new species and incorporating useful bathymetric and distributional data. Four fossil scaphopods from the Carboniferous of New South Wales were described by Yoo (1988) who also introduced two new laevidentaliid genera (*Scissuradentalium* and *Pipadentalium*). In a comprehensive monograph of the scaphopod fauna of Australia, Lamprell & Healy (1997) recognised 107 extant species from the region, including 46 new species and 28 new records. Their study has clarified the status of several previously named species (some disappearing into synonymy, and leptotypification of others), and has provided photographs and figures of significant type material held in overseas institutions.

MORPHOLOGY AND PHYSIOLOGY

External Features and the Shell

The scaphopod shell is composed of two to four aragonitic layers. A periostracum has been described for two dentaliid species, *Pictodentalium vernedei* (Haas 1972) and *Antalis vulgaris* (Alzuria 1985). This outer organic layer is absent in many gadilid species (Steiner unpublished data). The outer prismatic layer consists of elongate crystals usually arranged perpendicular to the long axis. The glossy surface of many gadilids is the result of a special arrangement of these crystals (Shimek & Steiner in press). The cross-lamellate middle layer is sometimes surrounded by a narrow amorphous layer (Shimek & Steiner in press). The inner layer, if present, has a concentric structure.

The shell is thickest at the posterior end and thinnest at the anterior growing edge. During growth, secretion of new shell material by the anterior mantle margin increases the length of the tube and its anterior diameter. Simultaneously, the outer mantle

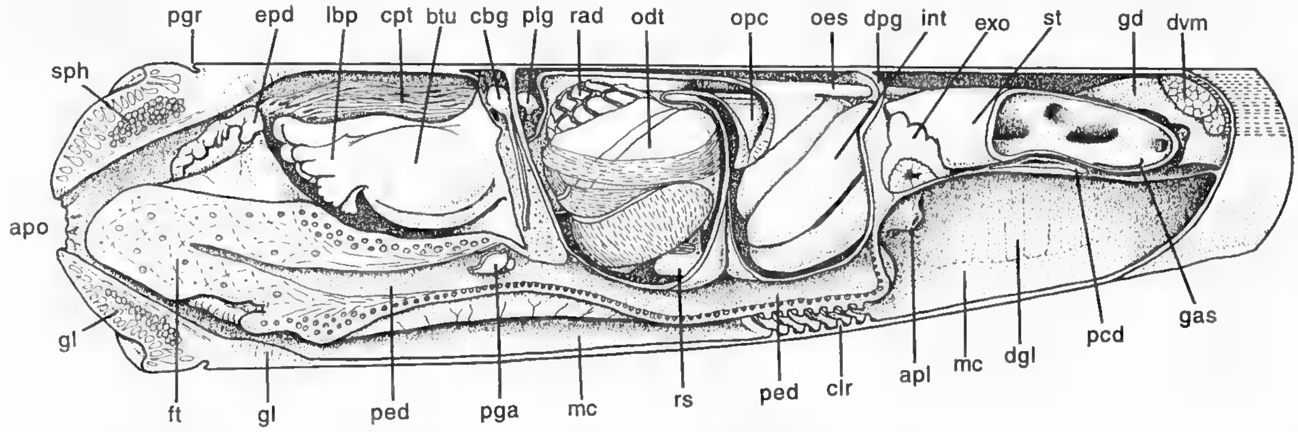

Figure 10.4 *Fissidentalium megathyris* (Dentaliidae), with the mantle and superficial muscle layers partly removed, and foot in longitudinal section, showing internal anatomy. **apl**, anal papilla; **apo**, anterior pallial orifice; **btu**, buccal tube; **cbg**, cerebral ganglia; **clr**, ciliated ridges; **cpt**, captacula; **dgl**, digestive gland; **dpg**, diaphragm; **dvm**, dorso-ventral retractor muscle; **epd**, epipodial lobes; **exo**, excretory organ; **ft**, foot; **gas**, gastric shield; **gd**, gonad; **gl**, glands of anterior mantle margin; **int**, intestine; **lbp**, labial appendages; **mc**, mantle cavity; **odt**, odontophore; **oes**, oesophagus; **opc**, glandular oesophageal pouches; **pcd**, pericardium; **ped**, pedal sinus; **pga**, pedal ganglia with statocysts; **pgr**, periostracal groove; **plg**, pleural ganglia; **rad**, radula; **rs**, radular sac; **sph**, sphincter muscle; **st**, stomach. [G. Steiner]

Figure 10.5 *Fissidentalium* sp. (Dentaliidae), with the foot extended to reburrow after collection from a depth of 300–400 m in the Great Australian Bight. The conical tip of the foot has penetrated the substratum and the right epipodial lobe is extended. **cft**, conical tip of foot; **epd**, epipodial lobe. [K. Gowlett-Holmes]

epithelium adds material to the inner shell surface, increasing shell thickness and decreasing the diameter of the lumen (Lacaze-Duthiers 1856–1857). This is most conspicuous at the posterior end. To prevent complete closure of the posterior opening of the shell, the posterior mantle margin dissolves this surplus shell. A similar decollation is found in the gastropod family Caecidae. Secondary apical shell structures like plugs or pipes are probably secreted by a dorsal extension of the posterior mantle margin, the so-called pavilion (Figs 10.3, 10.10).

Musculature and Locomotion

Pedal morphology differs greatly between the scaphopod orders. The anchoring function of the muscular erectile epipodial lobes in Dentaliida (Figs 10.3, 10.4) is assumed in Gadilida by an inflatable, hydraulic pedal disc which has a crenulated fringe (Steiner 1992a). The common basic pattern of the pedal wall musculature consists of outer circular fibres, two layers of helicoid muscles of opposite handedness, and inner longitudinal muscles. In Dentaliida, in which transverse muscles are also present, the longitudinal muscles are very prominent, allowing only a narrow pedal sinus (Fig. 10.4). In Gadilida, however, the pedal sinus is wide and the longitudinal muscles in the pedal wall are only weakly developed; additionally, there are one to three pairs of central pedal retractor muscles (Steiner 1992a). This arrangement renders the gadilid foot an eversible burrowing organ analogous to the nemertean proboscis.

Scaphopods move through the sediment in a manner similar to bivalves. They extend their burrowing foot, anchor it and drag the shell over it (Fig. 10.5). Trueman (1968) analysed this process in detail in *Antalis inaequicostatum*. Subsequent to some probing movements of its tip, the foot extends by contraction of circular muscles and/or by relocation of haemolymph from other regions into the foot. Then the epipodial lobes are erected, providing anchorage in the sediment. Subsequent contraction of longitudinal muscles pulls the shell forwards over the foot.

The dorso-ventral muscles are the only means by which the animal is fixed to its shell. There is one pair in the Gadilida, and the Dentaliida have two partly fused pairs. These muscles connect the longitudinal pedal muscles with the shell apex. The connection consists of flat muscle sheets in the lateral body walls in Dentaliida and the gadilid suborder Entalimorpha. In the gadilid suborder Gadilimorpha, the central pedal retractors run posteriorly through the pedal and intestinal sinus, where they are continuous with the dorso-ventral muscles (Steiner 1992a).

In addition to forming the pedal musculature, the dorso-ventral muscles give rise to pallial muscles in the anterior part of the mantle. These fibres retract the anterior mantle margin from the shell opening. The only other distinct muscular structures in the scaphopod mantle are the sphincters regulating the width of the anterior (Fig. 10.4) and posterior (Fig. 10.10) mantle openings. In Gadilida, a clasp of vertical muscle fibres draws close the mantle entrance to a vertical slit (Steiner 1991).

Feeding and Digestion

The captacula are the main feeding organs of scaphopods (Fig. 10.1). These thread-like, extensible organs originate from a captacular shield on each side of the buccal tube. Their number ranges, according to the size of the animal, from 30 for *Cadulus subfusiformis* (Steiner unpublished data) to about 300 for *Antalis entalis* (Morton 1959; Sahlmann 1973). Each captaculum consists of a long stalk and a bulbous, ciliated head with a dorsal pit (Fig. 10.6). In Dentaliida, the ciliation extends onto the dorsal side of the stalk for a variable distance before it breaks up into a series of ciliary tufts and finally disappears (Gainey 1972; Shimek 1988). The stalk in Gadilida bears only a few tufts of cilia or lacks ciliation entirely (Shimek & Steiner in press).

Longitudinal muscles only are present in the stalk of each captaculum, 10 in Dentaliida and five to seven in Gadilida (Shimek 1988; Shimek & Steiner in press). Near the head, the muscles split to form a delicate web of fibres that allows the head to change shape and to bend. A cerebral nerve in the centre of the stalk terminates in a small ganglion, the captaculum ganglion, at the base of the captacular head (Fig. 10.6B). The haemolymphatic space in the stalk is extremely narrow. Two types of gland cells occur on the head, one opening into the dorsal pit and producing proteins and cholinesterase, the other secreting base-rich proteins through the lateral epithelium (Sahlmann 1973).

Captacula autotomise frequently and are constantly replaced. Captacular buds arise at the ventral side of the captacular shields. While they are moved dorsally by division of epithelial cells at the shield base, the buds elongate and differentiate the nerve, ciliation and muscles in that order (Plate 1892).

The absence of circular muscles led Morton (1959) to hypothesise that the captacula are extended by hydraulic pressure, analogous to the extension of echinoderm tube feet. The narrow lumen of the stalk, however, does not permit elongation by rising blood pressure. Observations by Davis (1968) that captacula of *Cadulus quadridentatus* move by the beating of cilia on the captacula head have been corroborated by reports on other species (Sahlmann 1973; Poon 1987; Shimek 1988; Steiner 1990). Thus, captacula move over and between sediment particles like interstitial worms, but can also be lifted off the sediment surface. They are retracted by contraction of the longitudinal muscles of the stalk.

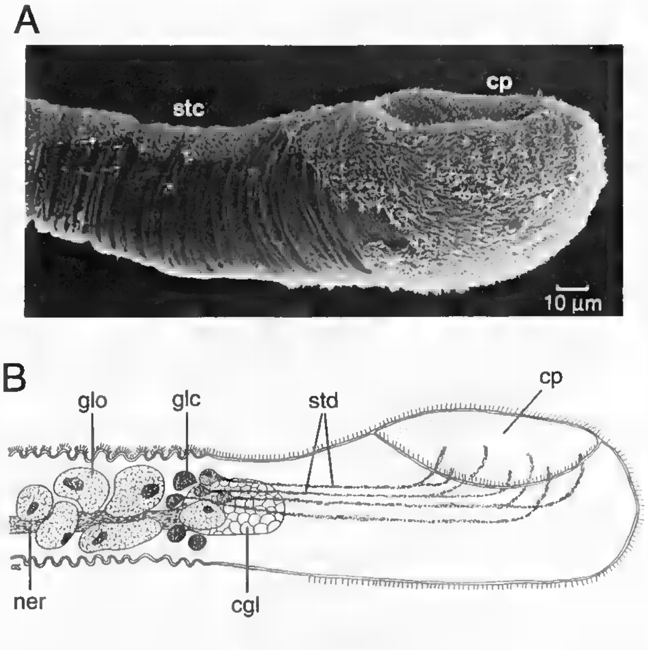

Figure 10.6 Dentaliid captacula, lateral view. A, *Antalis dentalis*, showing the dorsal ciliated pit and stalk ciliation. B, *Antalis* sp., showing glandular and nervous elements; the connective tissue and muscles are omitted. **cgl**, captaculum ganglion; **cp**, ciliated pit; **glc**, gland cells opening into the ciliated pit; **glo**, gland cells opening through the lateral epithelium; **ner**, nerve; **stc**, stalk ciliation; **std**, secretory duct. (B, modified after Plate 1892) [G. Steiner]

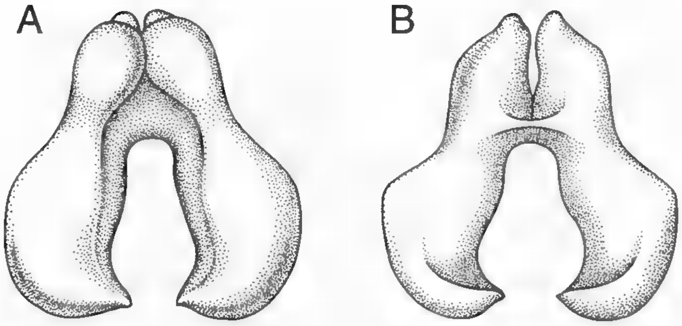

Figure 10.7 Cartilage-like radular bolsters of *Antalis* sp. (Dentaliidae): A, dorsal view; B, ventral view. (After Lacaze-Duthiers 1856–1857) [C. Eadie]

Adhesion to prey is presumably effected by a duo-gland system in the captacular head (Shimek 1988), similar to those found in many invertebrate groups (Hermans 1983). The sucker-like mechanism proposed by Morton (1959) and Bilyard (1974) is unlikely to function in the absence of the necessary musculature (Shimek 1988).

To commence feeding, the foot produces a feeding cavity in the sediment at the anterior shell opening. Exploring the surface of this cavity, the captacula locate and take hold of food items which they withdraw into the mantle cavity. Several captacula may manipulate large prey (Gainey 1972). Dinamani (1964a) and Shimek (1988, 1990) noted transport of sediment particles along the ciliary tracts of captacula in *Dentalium conspicuum* and *Rhabdus rectius*. The foot may also participate in collection of sediment in dentaliids (Dinamani 1964a; Gainey 1972; Poon 1987) and foraminiferans in gadilids (Shimek 1988, 1990). Neither the radula nor the mouth protrudes from the mantle cavity. Food is passed from the captacula to the mouth where final selection seems to be made by the surrounding ciliated and frilled labial appendages.

There is little doubt that scaphopods are, and probably have been for long geological periods, predominantly carnivorous (Lacaze-Duthiers 1856–1857; Fischer-Piette & Franc 1968; Palmer 1975; Steiner 1992b). Dentaliida must be considered generalists in their diets (Shimek 1990). Foraminiferans, bivalve spat, ostracods, diatoms, small gastropods, marine mites and invertebrate eggs, as well as sediment particles, have been found in the buccal pouches of certain Dentaliida (Dinamani 1964a; Gainey 1972; Sahlmann 1973; Bilyard 1974; Poon 1987; Shimek 1990). Members of the order Gadilida are more specialised in their diets than the Dentaliida and feed almost exclusively on foraminiferans. Certain foraminiferan species are selectively ingested whereas others are neglected. Deposit-feeding has not been observed in the species investigated (Poon 1987; Shimek 1988, 1990).

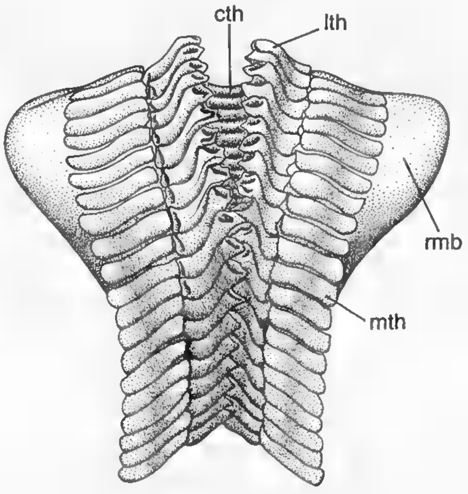

Figure 10.8 Radula of *Antalis* sp. (Dentaliidae), dorsal view. **cth**, central tooth; **lth**, lateral tooth; **mth**, marginal tooth; **rmb**, radula membrane. (After Lacaze-Duthiers 1856–1857) [C. Eadie]

The mouth is at the tip of the buccal tube or proboscis, which is probably formed by fusion of the postoral tentacles (Steiner 1992b). Laterally, the central lumen communicates with a pair of buccal pouches. Prey are stored here before being masticated by the radula. A single jaw marks the transition to the buccal cavity which contains the radula (Fig. 10.4) and subradular sense organ.

The radular apparatus is enormous relative to body size (Morton 1959). It serves for trituration, but is not used to collect food, as in gastropods. The radula is supported by a large pair of cartilage-like radular bolsters where the buccal muscles attach. The bolsters are somewhat horseshoe-shaped (Fig. 10.7) with the radular sac descending between them (Fig. 10.4). Each row of five teeth consists of a simple, oblong central tooth, flanked on each side by a complex lateral and a plate-like marginal tooth, resting on the radular membrane (Fig. 10.8; Lacaze-Duthiers 1856–1857). The radular sac epithelium secretes the teeth and impregnates them with phosphates and iron salts (Shimek & Steiner in press). Radular function is not well understood. Lamprell & Healy (1997) have presented radular scanning electron micrographs of several Australian species of Dentaliida and Gadilida.

The oesophagus shows the basic pattern typical of chitons and conchiferans (Salvini-Plawen 1988). The anterior part has a tripartite lumen with a central ciliated food groove and large, lateral glandular oesophageal pouches. Posterior to the glands, the oesophagus is a simple tube opening dorso-laterally into the stomach, where the food is rolled into a simple protostyle (Salvini-Plawen 1988; Steiner unpublished data) and exposed to extracellular digestion. The ventral side of the stomach is differentiated into ciliated sorting areas and a gastric shield; a vestigial caecum is present at the posterior end.

In the Dentaliida, the digestive gland is arranged symmetrically on each side of the stomach (Figs 10.3, 10.4), but in the Gadilida it is asymmetrical, extending only along the left side of the body. The tubules extend finger-like between the inner and outer mantle epithelia. In both orders, a pair of posterior diverticula stretch out between the gonad tissues (Salvini-Plawen 1988). Enzymes from the oesophageal pouches and the digestive gland digest food extracellularly in the stomach. Dissolved and particulate matter is processed within amoebocytes and resorptive cells of the digestive gland after phagocytosis (Taib 1981) and pinocytosis (Sahlmann 1973).

Posterior to the stomach, the digestive tract changes direction from posterior to anterior where it forms a convoluted intestine. Three intestinal loops are generally present, but species of *Bathoxiphus* (Entalinidae) have four or five, and *Cadulus aberrans* (Gadilidae) have only two (Steiner 1994). The rectum receives the duct of the rectal gland that probably excretes lipid substances (Sahlmann 1973). The anus opens as an oblique slit on a small papilla on the ventral midline just posterior to the foot (Fig. 10.4).

Respiration and Circulatory System

Scaphopods lack ctenidia. The delicate inner mantle epithelium is the site of gas exchange. The ventilatory function of ctenidia is performed by cilia on a series of pre-anal ridges (Fig. 10.4), these generate the respiratory current. Dentaliida have a higher number of ridges than Gadilida. In the Gadilida the movement of cilia on the apical valve organ also contributes to water flow. Contrary to Yonge's (1937) opinion, the direction of the current is from the posterior to the anterior mantle opening (Steiner 1991). However, at regular intervals piston-like movements of the foot cause vigorous expulsions of water through the posterior opening of the shell. This behaviour expels faeces and gametes from the mantle cavity (Steiner 1990).

The haemolymph is a transparent fluid containing three types of blood cells: leucoblasts, leucocytes and amoebocytes (Arvy & Gabe 1951). It is circulated by the heart, which is a simple, dorsal invagination of the pericardium, situated ventral to the stomach (Fig. 10.4). Other organs contributing to circulation are the foot and the musculature of the perianal sinus and the abdominal region

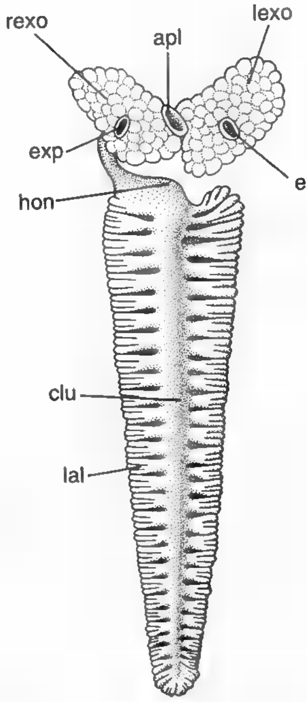

Figure 10.9 The gonad and excretory organs of *Antalis* sp. (Dentaliidae), ventral view with stomach removed. **apl**, anal papilla; **clu**, central lumen; **exp**, excretory pore; **hon**, anterior horn of gonad connected to right excretory organ; **lal**, lateral lobes of gonad; **lexo**, left excretory organ; **rexo**, right excretory organ. (After Lacaze-Duthiers 1856–1857) [C. Eadie]

(Steiner 1992a; Shimek & Steiner in press). There are no vessels, but there are several distinct sinuses. These interconnected spaces are named the pedal, perianal, abdominal, intestinal, buccal and cerebral sinuses (Lacaze-Duthiers 1856–1857).

Excretion

The paired excretory organs lie laterally in the perianal sinus and do not communicate with each other (Figs 10.4, 10.9). Each excretory organ empties into the mantle cavity through a large excretory pore lateral to the anus (Fig. 10.9). There are no consistent reports of a renopericardial connection, and the duct reported by Distaso (1906) between the pericardium and the left excretory organ has not been confirmed. Reynolds (1990a) reported a connection to the right excretory organ in only one of his sections from several specimens of *Rhabdus rectius*. The highly vacuolated excretory epithelium is identical in both excretory organs and is composed of two types of gland cells (Reynolds 1990b).

Lipid substances are excreted by the densely ciliated tubules of the rectal gland (Sahlmann 1973). During the reproductive season gametes are shed via the right excretory pore (Plate 1892; Boissevain 1904).

Nervous System

The nervous system Scaphopoda is, except for the presence of a buccal system, similar to that of protobranch bivalves (Lacaze-Duthiers 1856–1857) and has been described by Plate (1892) in minute detail. The neurones concentrate mainly in the large cerebral, pleural, visceral and pedal ganglia (Fig. 10.11). Collagenous connective tissue sheaths all ganglia and their connectives and commissures (Gabe & Prenant 1950).

The cerebral ganglia are connected by a short cerebral commissure. Pleural and pedal connectives extend to the respective ganglia. Paired nerves extend into the dorsal part of the anterior mantle region and into the buccal tube. The latter have a common root with the buccal system. Buccal connectives descend to paired subradular ganglia and continue posteriorly to the buccal ganglia between the oesophagus and radular sac. Nerves from the individual captacular ganglia enter the cerebral system via thick captacula nerve trunks. The statocyst nerves run parallel with the pedal connectives.

The large pedal ganglia lie in the pedal sinus with the statocysts closely attached. The cerebropedal and pleuropedal connectives are fused along almost their entire length. In the Gadilida, three pairs of pedal nerves innervate the pedal musculature, and there are six or seven pairs in the Dentaliida (Shimek & Steiner in press).

The elongate pleural ganglia are separated from the cerebral ganglia only by a muscular septum (Fig. 10.4). A single nerve pair extends into the ventral anterior mantle region. The ganglia taper into the visceral connectives that run posteriorly lateral to the bundles of dorso-ventral muscles (Steiner 1992b). The connectives may be cord-like in their posterior part (Steiner 1990).

The visceral ganglia are triangular in shape and communicate by a long commissure. A pair of abdominal nerves extend from their posterior ends. They form small ganglia at the posterior mantle margin from whence nerves enter the pavilion (Fig. 10.10).

Gabe (1949) described acidophilic neurosecretory cells in the cerebral, pleural, and subradular ganglia of *Antalis entalis*.

Sense Organs

The totally infaunal mode of life of scaphopods at depths where little or no light penetrates has resulted in a shift of emphasis from a photosensory system to a chemotactile system. Distaso's (1906) report of an osphradium has never been confirmed (Steiner 1991). Thus, the captacula and the epithelia of the mantle margins presumably are the only sources of information on the environment. The selective uptake of food by the captacula (Shimek 1988, 1990), their coordinated movements and presence of a ganglion in each filament indicate the highly developed sensory capability of these feeding organs. However, Sahlmann (1973) found no discrete sensory structures and ascribed perceptive qualities to the entire epithelium of the captacular head.

The statocysts, filled with numerous statoliths, are attached to the posterior side of the pedal ganglia (Fig. 10.4), but their nerves are supplied by the cerebral ganglia.

The subradular organ assumes an unusual position in the buccal cavity. Unlike the situation in other conchiferan molluscs, it rests on the floor of the subradular pouch. The sensory epithelium of the cup-shaped structure is surrounded by mucoid gland cells (Boissevain 1904). It is innervated by the subradular ganglia, and presumably is a 'taste' organ.

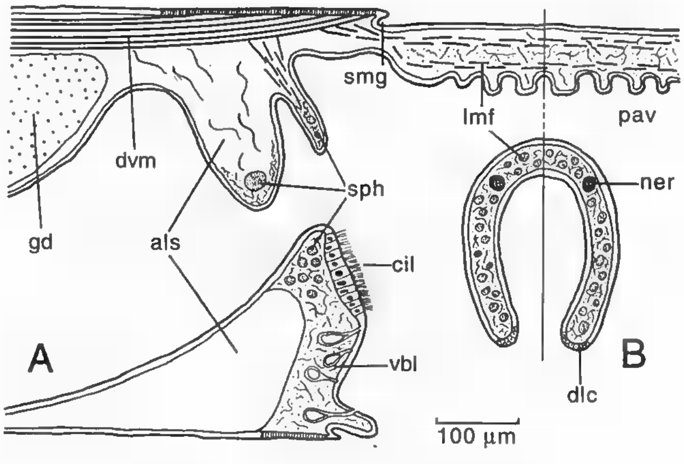

Figure 10.10 **A**, posterior mantle margin of a generalised dentaliid scaphopod, in longitudinal section. **B**, a cross-section through the pavilion at the position indicated in A. **als**, annular sinus; **cil**, ciliated area; **dlc**, differentiated ledge cells; **dvm**, dorso-ventral retractor muscle; **gd**, gonad; **lmf**, longitudinal muscles; **ner**, nerve; **pav**, pavilion; **sph**, sphincter muscle; **smg**, supramarginal groove; **vbl**, ventral bolster of connective tissue. [G. Steiner]

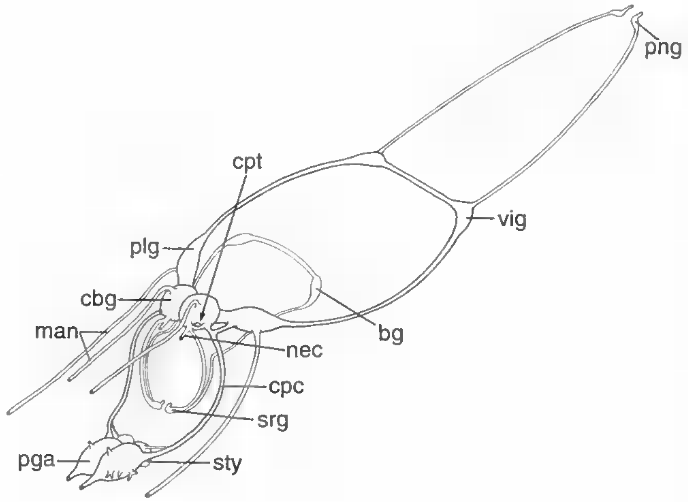

Figure 10.11 The scaphopod nervous system, schematic representation. **bg**, buccal ganglion; **cbg**, cerebral ganglion; **cpc**, fused cerebropedal and pleuropedal connectives; **cpt**, captacula nerve, indicated by arrowhead; **man**, mantle nerves; **nec**, nerve of the oral cone; **png**, pavilion ganglion; **pga**, pedal ganglion; **plg**, pleural ganglion; **srg**, subradular ganglion; **sty**, statocyst with nerve; **vig**, visceral ganglion. [G. Steiner]

The mantle margins are the only tissues that are in constant contact with the environment. Although there are no distinct sense organs, unicellular ciliary receptors are abundant (Reynolds 1988; Steiner 1991). At the anterior mantle margin in the Gadilida, there are collar receptors on papillae on the frontal epithelium. A common feature of the Dentaliida is an annular ciliary organ at the anterior mantle opening; it may function to ventilate the sensory epithelium. This organ is replaced in *Rhabdus rectius* by paired slit-like invaginations of unknown function (Steiner 1991).

Reproduction

In scaphopods, sexes are separate, and only a single example of hermaphroditism is known, in *Antalis entalis* (d'Anna 1974). The unpaired, elongate gonad lies posterior to the stomach and embraces the posterior diverticula of the digestive gland (Figs 10.3, 10.4). In both sexes, the gonad consists of numerous lobes (Fig. 10.9) which are embedded between the mantle epithelia, like those of the digestive gland. At spawning, the gonad fuses with the right excretory organ, and gametes exit by the right excretory pore into the mantle cavity (Boissevain 1904).

The testes produce sperm of a primitive type (Franzén 1956). Mature spermatozoa have a simple, apical acrosome and an elongate midpiece with four or five mitochondria surrounding the base of the axoneme (Dufresne-Dube, Picheral & Guerrier 1983). The formation of the acrosome from a single golgi complex is unique among molluscs (Hou & Maxwell 1991).

Oogonia and, during vitellogenesis, oocytes, are surrounded by follicle cells before they detach from the ovary wall (Steiner unpublished data). Vitellogenesis occurs in the postpachytene stage of meiosis (Raven 1966). Two different types of yolk granules are accumulated in the ooplasm of *Antalis dentalis* (Reverberi 1972), *Cadulus subfusiformis* and *Pulsellum lofotensis* (Steiner unpublished data). In living specimens, yolk may appear white, yellow or pink (Reverberi 1972). At the vegetal pole, the ooplasm is devoid of yolk, but mitochondria are abundant (Reverberi 1972). Detachment from the ovary wall is correlated with the appearance of long microvilli, which secrete a thick jelly layer in *C. subfusiformis* and *P. lofotensis* (Steiner unpublished data). The eggs of *A. dentalis* and *A. antillarum* have symbiotic bacteria of unknown significance attached to the vegetal pole (Timmermans, Geilenkirchen & Verdonk 1970; Geilenkirchen, Timmermans, van Dongen & Arnolds 1971). The jelly layer is the only layer which envelops the egg.

Embryology and Development

Spawning in Dentaliida under laboratory conditions has been documented for *Antalis entalis* (Lacaze-Duthiers 1856–1857) and for a female *Dentalium conspicuum* (Dinamani 1964b). In each species eggs or sperm were expelled from the mantle cavity through the posterior opening of the shell by repeated retractions of the foot. The gadilids *Pulsellum lofotensis* and *Cadulus subfusiformis* shed their eggs through the anterior mantle opening. In members of this order, sperm also leave the mantle cavity anteriorly (Steiner 1993). Fertilisation takes place externally or within the mantle cavity. The interaction of spermatozoa and eggs has been analysed by Dufresne-Dube *et al.* (1983).

The early studies by Lacaze-Duthiers (1856–1857) and Kowalevsky (1883) remain the only references for larval development. Several generations of scientists elaborated on *Dentalium* as one of the classic cases of polar lobe formation (Verdonk 1968a, 1968b; Geilenkirchen *et al.* 1971; van Dongen & Geilenkirchen 1974a, 1974b, 1974c, 1975; van Dongen 1976a, 1976b, 1976c). Raven (1966), McFadian-Carter (1979) and Moor (1983) provide detailed reviews and references. Apart from the early development of *Antalis*, however, little is known about scaphopod ontogeny.

Cleavage is unequal and follows the general molluscan pattern of spiral cleavage (Raven 1966). The formation of polar lobes occurs during the first three cleavages (Wilson 1904). At gastrulation, the large, yolk-rich macromeres are invaginated to form the archenteron. The blastopore remains open and shifts ventrally, but the anus does not form before metamorphosis (Kowalevsky 1883).

Eventually, cilia appear and the larva starts to swim. The larva is lecithotrophic and short-lived. The preoral region forms the larval locomotory organ, a transient testa (or calymma) comprising three or more rings of large ciliated cells (Fig. 10.12; Lacaze-Duthiers 1856–1857; Kowalevsky 1883). During growth the postoral region elongates, while the calymma is pushed forwards. This larval organisation is intermediate between the pericalymma larvae of Neomeniomorpha (Aplacophora) and trochophores of conchiferans and is referred to as a stenocalymma (Salvini-Plawen 1990).

The postoral region of the larva gives rise to most of the adult organs (Moor 1983). The mantle and larval shell form on the dorsal side. Their margins grow ventrally, and fuse in an anterior direction along the ventral median line (Fig. 10.12), and thus shape the tubular mantle cavity and shell (Lacaze-Duthiers 1856–1857). During elongation of the postoral region, the primordia of the foot with a transitory pedal gland, the stomodeum, and the captacula shields appear (Kowalevsky 1883). Gill rudiments have not been reported. The mesoblast is formed by descendants of the 4d cell, but mesenchymatic tissues are also produced by the ectenchymatic cells of the second quartet (van Dongen 1977).

The larvae metamorphose after 3–5 days (Lacaze-Duthiers 1856–1857) and have never been found in plankton hauls. They are slow swimmers and, in the laboratory, often rest at the bottom of their dish (G. Steiner personal observation). At metamorphosis the preoral region with the locomotory prototroch is abandoned (Lacaze-Duthiers 1856–1857; Kowalevsky 1883).

Unlike the larval shells of planktotrophic bivalves and gastropods, those of scaphopods are dissolved or broken away during growth. Only rarely are complete series of shells from juvenile to adult growth stages available for study. Henderson (1920) found such a growth series and published a figure of the larval shell of *Dentalium laqueatum* still attached to the apex of the juvenile shell. It resembled a swollen bulb with two annular constrictions at the posterior opening and about twelve annulations in the anterior part, which give way to the longitudinal ribbing of the adult form. Illustrations or descriptions of larval shells other than *Antalis* are found in Henderson (1920), Cotton & Godfrey (1940), Scarabino (1979), Burch & Burch (1989) and Steiner (1995). Engeser, Riedel & Bandel (1993) discovered similar structures in fossil scaphopods.

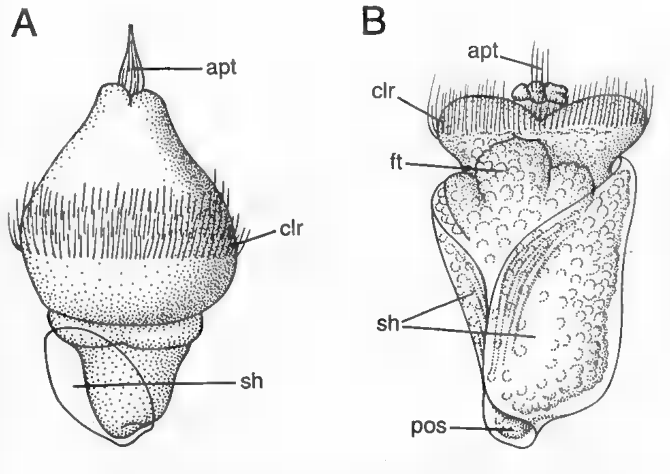

Figure 10.12 Larval stages of *Antalis* sp. (Dentaliidae): A, at appearance of larval shell; B, at commencement of ventral shell fusion. **apt**, apical tuft; **clr**, locomotive ciliary rings; **ft**, foot anlage; **sh**, larval shell; **pos**, posterior opening of shell. (After Lacaze-Duthiers 1856–1857) [C. Eadie]

The larval shells are always bulbous at the tip with a distinct fusion scar along the ventral midline. The younger parts are conical, showing one (in Gadilida) or several (in Dentaliida) transverse annulations (Scarabino 1979). There is a sharp transition in surface texture between the larval/juvenile and the adult shell (G. Steiner personal observation).

NATURAL HISTORY

Ecology

Scaphopods are benthic marine infaunal micro-carnivores inhabiting all types of sediment from soft mud and silts to coarse muddy shell gravels. They are found in euhaline waters in all latitudes and in depths from the littoral fringe to the abyssal. Though they are not normally littoral, an exceptionally low tide may uncover sediments which contain living scaphopods. On the other hand *Siphonodentalium galatheae* is recorded from 7000 m depth. Many species, including several Australian species, are found over a wide depth range. For example, *Cadulus vincentianus* is recorded from 3–2780 m (Lamprell & Healy 1997) and *Laevidentalium erectum* is recorded from 11–2569 m.

Feeding ecology of a few species has been investigated. Bilyard (1974), Poon (1987) and Shimek (1990) found that most scaphopods are highly selective predators on certain foraminiferan species, bivalve spat and other small metazoa. *Rhabdus rectius*, however, is reported to be more of a generalist, also ingesting detritus (Shimek 1990).

Scaphopoda are preyed upon by demersal fish, naticid gastropods, decapod crustaceans and certain asteroids (Fankboner 1969; Shimek 1989; Kropp 1992). Empty shells are frequently inhabited by hermit crabs or sipunculids.

Reproduction, as far as known, is strictly seasonal in coastal waters of the northern Atlantic and eastern Pacific (Steiner 1993; R.L. Shimek personal communication), but seasonality has been reported also in the deep-sea species, *Cadulus californicus* (Rokop 1977).

Economic Significance

No records are available of scaphopods being eaten by humans, the majority being, perhaps, too small. They undoubtedly form part of the diet of bottom-feeding fish, since scaphopod shells have been recovered from the stomachs of these fish (Shimek 1989).

Indians from the north-west of America once used shells of *Antalis pretiosum* for decoration as well as a form of currency. Scaphopod shells, when available, have always figured in shell art – necklaces, pictures and shell-covered boxes – forming part of the economy of coastal resorts (Clark 1963).

FOSSIL RECORD AND PHYLOGENY

The earliest unequivocal scaphopod is *Rhytiodentalium kentuckyensis*, a presumably smooth dentaliid from the Middle Ordovician of Kentucky, United States of America. In the Devonian there are smooth, but obscure, forms which continue into the succeeding Carboniferous period when the first longitudinally ribbed scaphopod makes it appearance. This is *Prodentalium*, a multi-costate form, some specimens of which attain a length of up to 305 mm.

The Palaeozoic–Mesozoic transition witnessed the appearance of scaphopods with concentric annulations now grouped in the genus *Plagioglypta*. This genus has a doubtful record in the Ordovician (Emerson 1962), but appears more frequently, although intermittently, in Mesozoic to Recent faunas (see Scarabino 1995). It is not certain, however, whether the concentric annulations are uniquely derived or are of polyphyletic origin. Throughout the Mesozoic and Cainozoic, two distinct types of scaphopods co-existed. These were smooth laevidentaliids, apparently present continuously from Middle Ordovician times to the present day, and longitudinally ribbed multi-costate forms grouped in *Prodentalium*. These parallel successions are accompanied by sporadic appearances of annulated forms in the Middle Triassic, Lower Jurassic, Lower Cretaceous and early Cainozoic.

It is easy to argue on the evidence of occurrence, that smooth and ribbed multi-costate dentaliids were represented continuously from the Palaeozoic to the present day, but not so easy to make the same case for annulated forms.

In the Cainozoic, during the Miocene period, the first symmetrical, pauci-costate forms (with fewer than about 10 ribs) appear, culminating in the numerous forms of *Dentalium sexangulum* in the Pliocene period. *Dentalium elephantinum*, the scaphopod type species, has no fossil history before the Pleistocene.

The history of the Scaphopoda appears to be quite complex. The earliest member of the Gadilidae is the Lower Cretaceous *Gadila gaultina*. This is a true *Gadila* which is succeeded by *Polyschides* in the Eocene of the Paris Basin. The barrel-shaped *Cadulus* does not occur before the Miocene period. A smooth, thin scaphopod from the Permian of Nevada, United States of America, named *Calstevenus* by Yancey (1973), was placed by him in the family Siphonodentaliidae, based on the strong curvature of the shell and rapid expansion rate. If this is correct, then the very long time gap between *Calstevenus* in the Permian and *Gadila gaultina* in the Lower Cretaceous, requires some explanation. A simpler explanation is that *Calstevenus* was a novel Permian offshoot of the Laevidentaliidae with no special affinities with the Siphonodentaliidae. However, the matter will not be easily settled.

The Dentaliida is an ancient and conservative lineage, showing little anatomical variation. The derived Gadilida are more diverse in their anatomy, which makes it easier to deduce family relationships (Steiner 1992b).

Allowing that we know nothing of the geological history of the Aplacophora, the Scaphopoda is the youngest class of the Mollusca known. By the Middle Ordovician, all other classes of Mollusca had earlier representatives. The rather poor Palaeozoic fossil record Scaphopoda suggests that the ancestral stock of all scaphopods was the smooth Laevidentaliidae, first appearing in the Middle Ordovician, giving rise to ribbed *Prodentalium* in the Carboniferous, annulated *Plagioglypta* in the Permian–Triassic, and the Gadilidae, beginning with *Gadila*, in the Lower Cretaceous. The distribution of shell sculpture in Recent scaphopods, however, renders a longitudinally striated form equally probable as a common ancestor (Steiner 1992b).

A widely accepted theory places scaphopods, bivalves and the fossil rostroconchs in the clade Loboconcha (Salvini-Plawen 1990) or Diasoma (Pojeta & Runnegar 1976), based on the comparable development of mantle and shell and on similarities in the burrowing foot and the nervous system (Steiner 1992b).

CLASSIFICATION

Scaphopoda are classified into two orders, Dentaliida and Gadilida (Palmer 1974; Starobogatov 1974), the latter being subdivided into the suborders Entalimorpha and Gadilimorpha (Steiner 1992b). Compilations and many original descriptions of Australian species are given by Cotton & Ludbrook (1938), Cotton & Godfrey (1940), Colman (1958), Powell (1960), Zeidler & McPhail (1978) and Lamprell & Healy (1997). Scarabino (1995) described 42 new species from the tropical waters of the Indian and Pacific Oceans; some of them from Australian waters.

Family groupings are based mainly on shell and radular characters as very little is known of the variations in soft-part anatomy. Only a few mantle characters are available for classification (Steiner 1991). The shell apices may show slits, notches, plugs or pipes which are still used for classification. Because of the continuous modification of the tip of the shell by the mantle tissue (Shimek 1989; Steiner 1991; Reynolds 1992), these features are neither constant nor reliable enough to be used as diagnostic characters. They may, however, be of help for the identification of the animal and are, therefore, included in the family descriptions, and in the key to the families in one instance. For identification of genera consult Palmer (1974). The family Omniglytidae has been recorded recently from Australia (Lamprell & Healy 1997).

Table 10.1 Classification of the Scaphopoda. Families marked with an asterisk are not represented in Australia.

Class SCAPHOPODA
- Order DENTALIIDA
  - Family Dentaliidae
  - Family Fustiariidae
  - Family Rhabdidae*
  - Family Laevidentaliidae
  - Family Gadilinidae
  - Family Omniglyptidae
- Order GADILIDA
  - Suborder ENTALIMORPHA
    - Family Entalinidae
  - Suborder GADILIMORPHA
    - Family Pulsellidae
    - Family Wemersoniellidae*
    - Family Gadilidae

Key to the families and subfamilies of the class Scaphopoda

1 (a)	Maximum diameter of shell at the aperture	2
(b)	Maximum diameter of shell not at the aperture	Gadilidae (Gadilinae)
2 (a)	Central tooth wider than high; epipodial lobes of foot interrupted dorsally; two pairs of dorso-ventral muscles; digestive gland paired	3
(b)	Central tooth higher than wide; foot eversible with terminal disc; one pair of dorso-ventral muscles; left digestive gland only	9
3 (a)	Shell surface with longitudinal striae or at least four ribs, at least in the apical region	Dentaliidae
(b)	Shell surface smooth or with three ribs	4
4 (a)	Shell surface with three ribs	Gadilinidae (part)
(b)	Shell surface smooth	5
5 (a)	Superior border of central tooth smooth; marginal teeth recurved; apex often with a deep, straight, ventral slit	Fustiariidae
(b)	Superior border of central tooth not smooth; marginal teeth not recurved; apical slit irregular or absent	6
6 (a)	Shell surface always smooth, sometimes eroded; marginal teeth almost straight	7
(b)	Shell surface smooth or with apical transverse annulations; marginal teeth curved	8
7 (a)	Shell weakly tapered, slender, aperture less than five times as wide as posterior opening of the shell; central tooth tricuspidate; anterior mantle margin with two dorso-lateral slits	Rhabdidae
(b)	Shell strongly tapered, aperture at least five times as wide as posterior opening of the shell; central tooth rectangular to polygonal	Laevidentaliidae
8 (a)	Shell with apical annulations or smooth, triangular to circular in cross-section; central tooth tricuspidate	Gadilinidae (part)
(b)	Shell always with apical annulation, always circular in cross-section; central tooth with irregular denticles	Omniglyptidae
9 (a)	Shell surface with four to 13 more or less prominent ribs, often eroded; apical cross-section polygonal or laterally compressed; central tooth with smooth superior edge; lateral teeth bear five to nine denticles; marginal teeth not keeled	Entalinidae
(b)	Shell surface smooth, sometimes with fine striae; apical cross-section circular; central tooth with at least one cusp; lateral teeth tricuspidate; marginal teeth keeled	10
10 (a)	Shell circular in cross-section throughout	Pulsellidae
(b)	Shell dorso-ventrally depressed in cross-section, at least at the aperture	11
11 (a)	Shell strongly curved	Gadilidae (Siphonodentaliinae)
(b)	Shell weakly curved to straight	Wemersoniellidae

Order DENTALIIDA

The shell of members of this order tapers posteriorly with the widest diameter always at the aperture. Longitudinal sculpture, such as ribs or striae, is usually present, but may be lacking. The central tooth of the radula is wider than it is high. The marginal teeth are not carinate (Scarabino 1979).

Two pairs of dorso-ventral retractor muscles are present. The foot is a thick-walled, contractile burrowing organ with its longitudinal musculature associated with the pedal body wall (Steiner 1992a). The conical tip of the foot is separated from the proximal parts by a collar of epipodial lobes which are interrupted dorsally (Steiner 1992a).

The anterior mantle margin bears an outer gland region, a ciliary organ and an inner gland region of epithelial gland cells (Steiner 1991). The posterior mantle opening closes to form a horizontal slit. Its dorsal part is a moveable flap, the ventral one forms a bolster of connective tissue (Fig. 10.10). Both portions of the mantle opening are supported by an annular haemolymph sinus. On average, there are 12 to 15 pre-anal ciliary ridges (Steiner 1991). Each captacular stalk contains 10 longitudinal muscles (Steiner 1992b). Paired digestive glands are present. The ultrastructure of the heart, pericardium and the excretory organs of *Rhabdus rectius* has been investigated by Reynolds (1990a, 1990b).

Few ultrastructural studies of dentaliid reproductive organs are available. Reverberi (1970, 1972) analysed oogenesis, and Hou & Maxwell (1991) described spermatogenesis in *Antalis entalis*. *Dentalium conspicuum* (Dinamani 1964b), *A. entalis* and *A. dentalis* (Lacaze-Duthiers 1856–1857; Kowalevsky 1883) are broadcast-spawners, and the yolk-rich eggs become fertilised outside the pallial cavity. This also holds true for *A. vulgaris*, the only species for which the ultrastructure of egg-sperm interaction has been studied (Dufresne-Dube *et al.* 1983). Knowledge of development is poor, especially of organogenesis, and is restricted to the above-mentioned species of *Antalis*. Development includes a modified spiral cleavage and a demersal, lecithotrophic larva of the stenocalymma type (Lacaze-Duthiers 1856–1857; Kowalevsky 1883; Salvini-Plawen 1980).

Six families can be distinguished: Dentaliidae, Fustiariidae, Laevidentaliidae, Gadilinidae, Omniglyptidae and Rhabdidae. All but the last are represented in Australian waters. The distribution of this order is worldwide, and at all depths from the upper sublittoral to the deep sea. The greatest diversity, however, is found in shallow tropical waters. The oldest known scaphopod, from the Ordovician, belongs to the order Dentaliida (Ludbrook 1960).

Family Dentaliidae

Dentaliid shells are usually robust, almost straight to strongly curved and may reach up to 300 mm in length in fossil forms and about 140 mm in extant species. Longitudinal sculpture varies from four prominent ribs to numerous, fine striae that may be restricted to the apical portion of the shell. Accordingly, the cross-section may be polygonal, circular, or rarely, slightly oval (Figs 10.13, 10.14). The number of ribs may be increased by intercalation or division (Simroth 1894; Pilsbry & Sharp 1897–1898). The apex shows great diversity of form. In species of *Dentalium* (Fig. 10.13B) and *Graptacme* (Fig. 10.14N), it is simple or has a shallow notch on the concave side. A deep slit or a series of perforations is typical for the genus *Fissidentalium* (Fig. 10.14F) whereas in the genera *Antalis* (Fig. 10.14J) and *Pictodentalium* (Fig. 10.13J) the posterior opening of the shell is narrowed by a calcareous plug, sometimes with a short pipe attached to it. The family includes the only brightly coloured scaphopods, which may show greenish (for example, *Dentalium elephantinum*), yellow or pink (for example, *Pictodentalium formosum hirasei*) pigmentation.

The central tooth of the radula has an entire, arched surface, which may be smooth or granulated. Similarly, the working area of the lateral teeth can be smooth, granulated or striated (Scarabino 1979). The marginal teeth are curved. In the pavilion, which is a posterior dorsal extension of the mantle, only a few, scattered subepithelial gland cells can be found (Steiner 1991).

The greatest diversity of Dentaliidae occurs in tropical and subtropical waters from the upper subtidal to depths of about 1000 m (Scarabino 1979). In higher latitudes and deeper water the number of taxa decreases.

Lamprell & Healy (1997) have identified 59 extant dentaliid species in the Australian fauna. Genera represented are (the number of species per genus is indicated in brackets): *Dentalium sensu stricto* (38, including 16 new); *Dentalium (Pictodentalium)* (one); *Dentalium (Lentigodentalium)* (three, including two new); *Graptacme* (three, including one new); *Fissidentalium* (11, including six new); and *Tesseracme* (three, including one new).

The names *Antalis* and *Paradentalium* have not been used for the Australian fauna by Lamprell & Healy (1997) because of inadequate delineation from *Dentalium sensu stricto*. Similarly, they consider *Pictodentalium* and *Lentigodentalium* to be, at best, subgenera of *Dentalium* and not worthy of full generic status. Within the genus *Dentalium*, Lamprell & Healy have utilised a species-group approach similar to that of Pilsbry & Sharp (1897–1898) and Boissevain (1906), in preference to the establishment of further, probably unjustified, subgeneric taxa.

The genus *Dentalium* is not only the most speciose within the family Dentaliidae, but also clearly the largest genus within the class Scaphopoda. Within the Australian fauna, *Dentalium* species constitute almost two thirds of the represented Dentaliidae and over one third of the Scaphopoda (Lamprell & Healy 1997). In shallow-water species (0–50 m) sandy sediments are preferred, whereas in deeper water (50 m and beyond) sand/mud or fine mud are more typical substrata (Lamprell & Healy 1997). Many species of *Dentalium* recorded from Australia have broad geographic and bathymetric ranges and may be locally common.

The first appearance of the Dentaliidae in the fossil record (genus *Prodentalium*) is from the early Devonian (Pilsbry & Sharp 1897–1898). In Australia 12 fossil dentaliid species have been described in the literature, mostly Tertiary in age (Tate 1887, 1899; Cotton & Ludbrook 1938; Ludbrook 1956), but also one species of *Fissidentalium* from the Carboniferous of New South Wales (Yoo 1988).

Family Fustiariidae

Fustiaria is the sole genus in the Fustiariidae. The gradually tapered shell is thin and slender, and moderate in length and curvature (Fig. 10.15). It is circular in cross-section. Except for faintly visible growth lines, the surface is polished, transparent and lacks sculpture. On the convex side, the apex usually has a long and narrow slit which is continuous with a shallow groove in the internal surface of the shell (Fig. 10.15B). Within a population, however, specimens with and without the slit can be found and are reported repeatedly (for example, Pilsbry & Sharp 1897–1898; Ludbrook 1954). A small notch may also be developed on the concave side, giving the apex a slightly bilobed appearance. These observations demonstrate the problem of defining scaphopod species by their apical features.

The lateral and marginal teeth of the radula resemble those of the genus *Antalis* (Dentaliidae) (Scarabino 1979), but the central tooth is not arched and shows an almost flat surface.

The posterior mantle margin differs from that of other Dentaliida in the absence of the sphincter muscle, the ventral bolster of connective tissue and the ring sinus. Instead, the dorsal flap is enlarged and is the only structure which regulates the width of the posterior mantle opening. Large subepithelial gland cells occur in the pavilion in great abundance and fill the space between the epidermal layers (Steiner 1991).

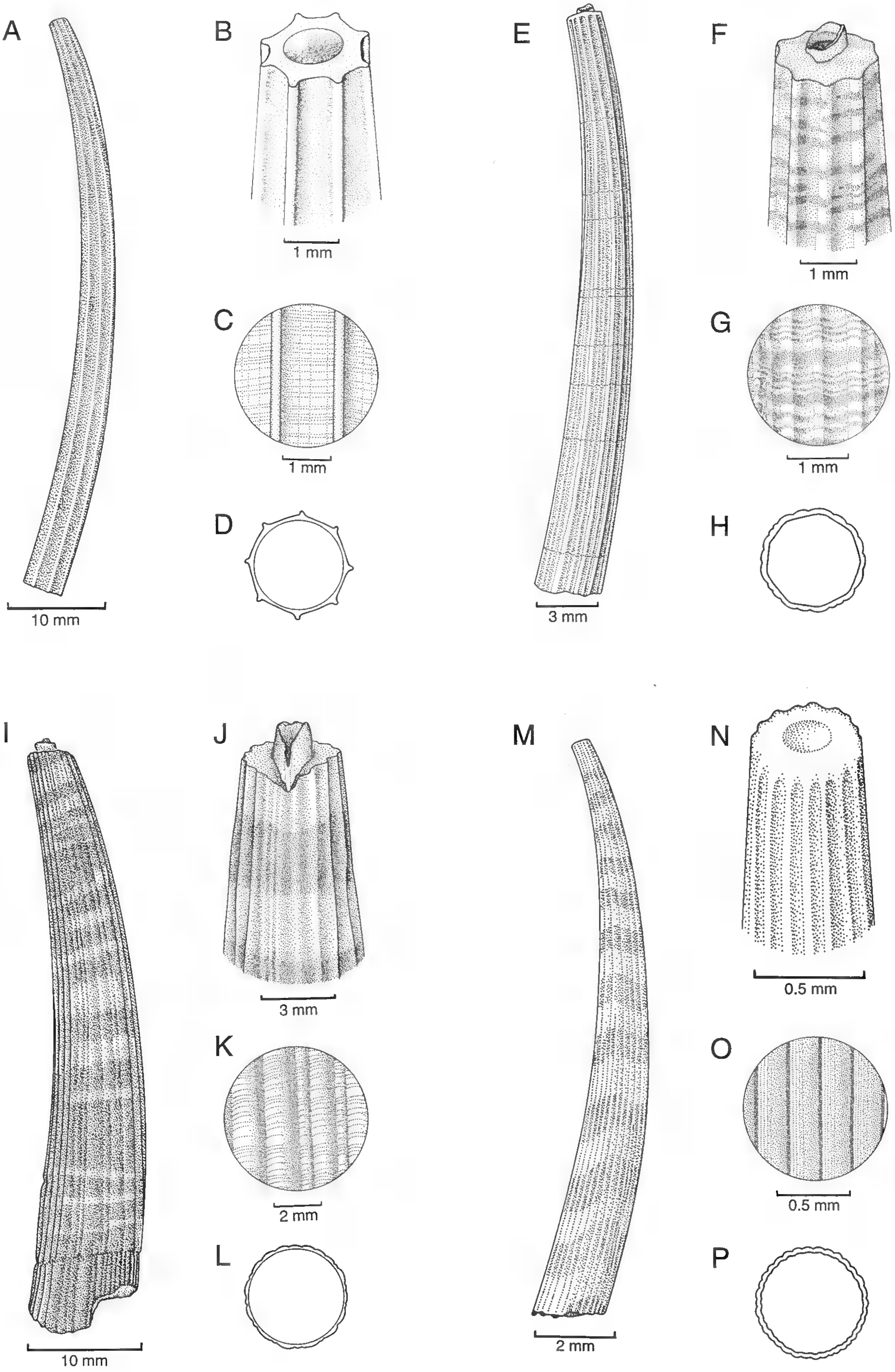

Figure 10.13 Australian Dentaliidae. Shell characters: **A–D**, *Dentalium javanum*; **E–H**, *Paradentalium intercalatum*; **I–L**, *Pictodentalium fomosum* **M–P**, *Lentigodentalium* sp. **A**, **E**, **I**, **M**, profile; **B**, **F**, **J**, **N**, apex; **C**, **G**, **K**, **O**, sculpture; **D**, **H**, **L**, **P**, cross-sectional shape at aperture. [C. Eadie]

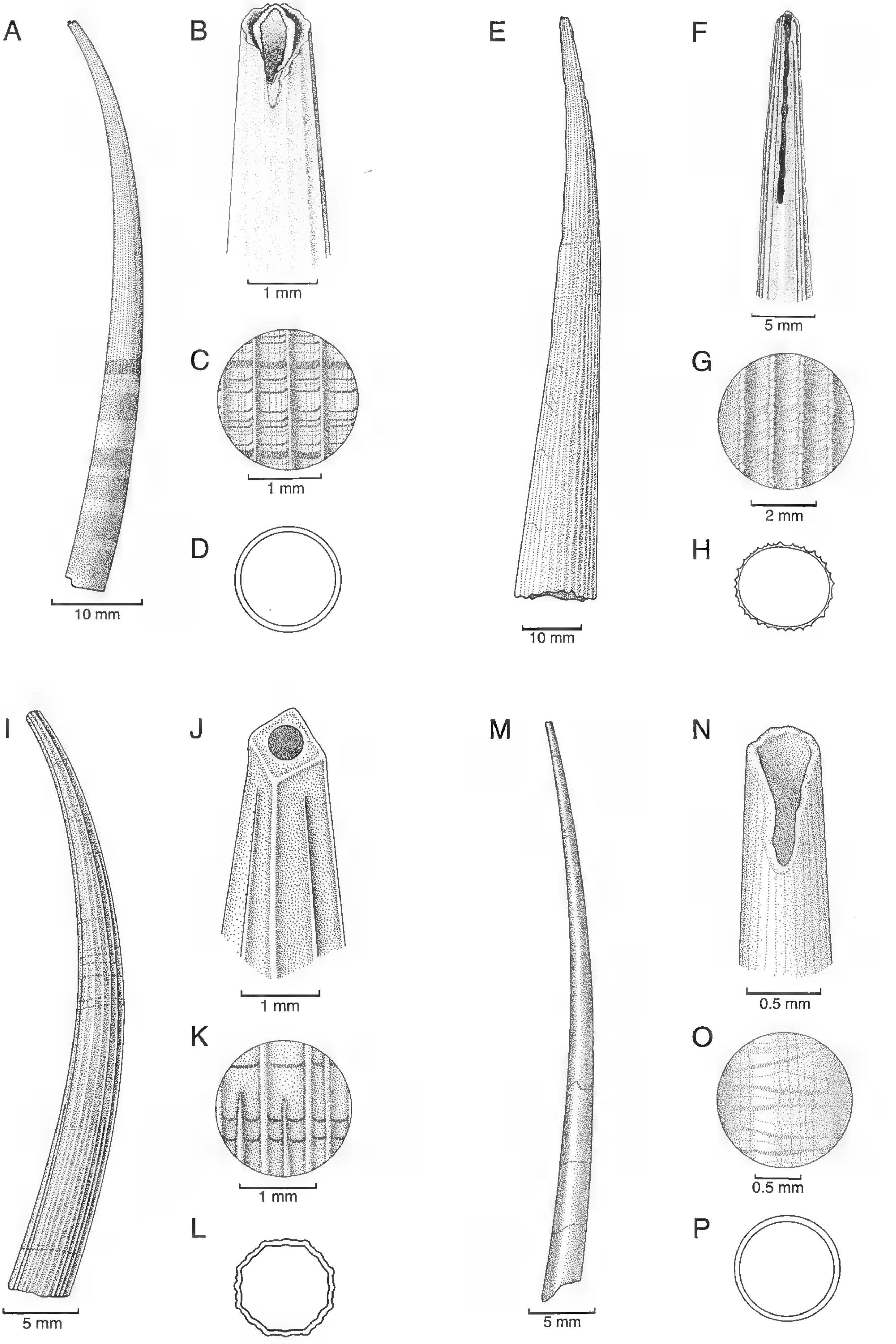

Figure 10.14 Australian Dentaliidae. Shell characters: **A–D**, *Tesseracme quadrapicale*; **E–H**, *Fissidentalium yokoyamai*; **I–L**, *Antalis* sp.; **M–P**, *Graptacme aciculum*. **A, E, I, M**, profile; **B, F, J, N**, apex; **C, G, K, O**, sculpture; **D, H, L, P**, cross-sectional shape at aperture. [C. Eadie]

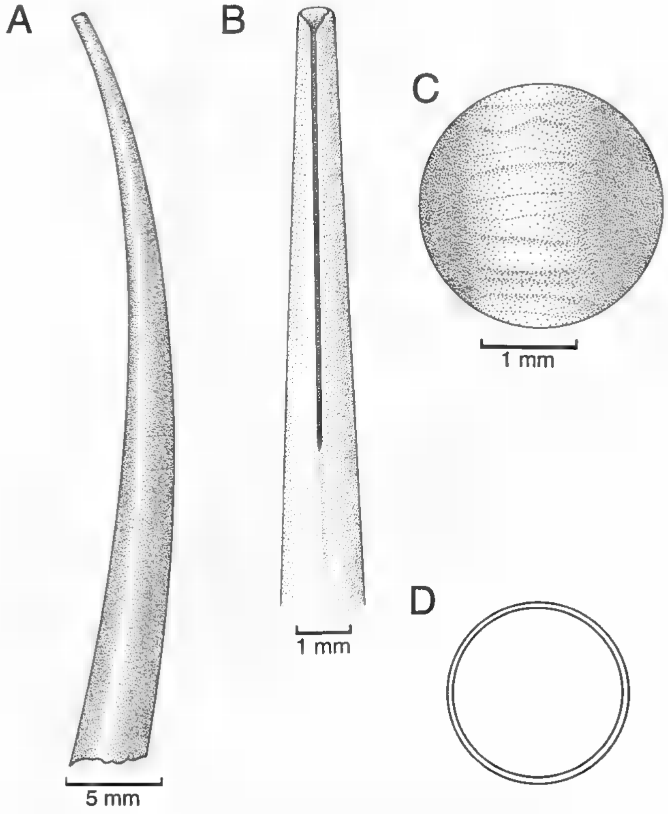

Figure 10.15 Australian Fustiariidae. Shell characters of *Fustiaria caesura*: **A**, profile; **B**, apex; **C**, sculpture; **D**, cross-sectional shape at aperture. [C. Eadie]

Fustiariids are reported from warm waters only. They occur mainly in sublittoral waters of the Caribbean, the equatorial Atlantic, the Mediterranean Sea and the western Indo-Pacific Ocean. Lamprell & Healy (1997) recognise only two species within the Australian fauna, *Fustiaria caesura* (Fig. 10.15), an endemic, occurring at depths of 60–399 m off the eastern, southern and western coasts, and *F. stenoschizum*, a species known also from the Philippines and West Indies, and recorded from Western Australia and Queensland at depths from 2–163 m.

The oldest member of the group was found in Cretaceous sediments (Emerson 1962).

Family Rhabdidae

Shells of this monogeneric family are nearly straight, and taper very gradually towards the apex. The shell is thin and fragile, and semi-transparent, except for whitish, eroded areas. No sculpture is present; the surface is smooth and polished. The apex is simple or extended by a fragile tube, which is continuous with the shell. The surface of the central tooth of the radula is distinctly trilobed, whereas the lateral teeth are massive and strongly sculptured, and the marginals are straight and bear small annulations on the anterior edge (Steiner 1991).

The family is distributed from the north-eastern Pacific and the south-western Atlantic to the Southern Ocean, and is yet to be reported from Australian waters. The oldest genus, *Rhabdus*, is recorded from the Miocene (Emerson 1962).

Family Laevidentaliidae

The shell is moderately curved, and is medium to large in size, reaching up to 100 mm in *Laevidentalium caudani* (Pilsbry & Sharp 1897–1898). It tapers rapidly, so that the diameter of the circular aperture is more than five times that of the posterior opening of the shell (Fig. 10.16). Apart from clearly visible growth lines or longitudinal undulations the shell surface is smooth and polished. However, Lamprell & Healy (1997) found that in *L. lubricatum*, fine longitudinal striae are present posteriorly in the shells of juvenile and uneroded larger specimens, and consequently have emended the diagnosis of the family Laevidentaliidae (and genus *Laevidentalium*) accordingly. The apex can be notched on the convex side, but is usually simple.

The central radular tooth is subrectangular or subpolygonal in shape (Scarabino 1979). The long lateral teeth have flat, almost straight apical portions, with the surface smooth or striated. The marginal teeth are also slender and only slightly curved.

Laevidentalium is the only Recent genus in this family, following the separation of the genus *Rhabdus* to its own family (Rhabdidae). *Laevidentalium* is found mainly in tropical to temperate waters from shallow to bathyal depths. The record depth for this order is for *Laevidentalium leptoskeles* collected from 4760 m depth south of Australia (Watson 1879).

Twelve species of *Laevidentalium* were recorded by Lamprell & Healy (1997) in the Australian fauna, four of which were described as new. One species *L. largicrescens*, previously known only as a fossil from Victoria (Upper Miocene to Pliocene) was shown to be still extant in deep water off the eastern coast (depth range 284–3058m). Some Australian laevidentaliids such as *L. erectum* and *L. lubricatum* not only have considerable bathymetric ranges (from approximately 15 m to over 1300 m or deeper), but occur essentially around the entire coastline, often in large numbers (Lamprell & Healy 1997).

Rhytiodentalium kentuckyensis (Pojeta & Runnegar 1979) and *Plagioglypta iowaensis* (Bretsky & Bermingham 1970), the oldest known scaphopods from the Ordovician, may belong to this group.

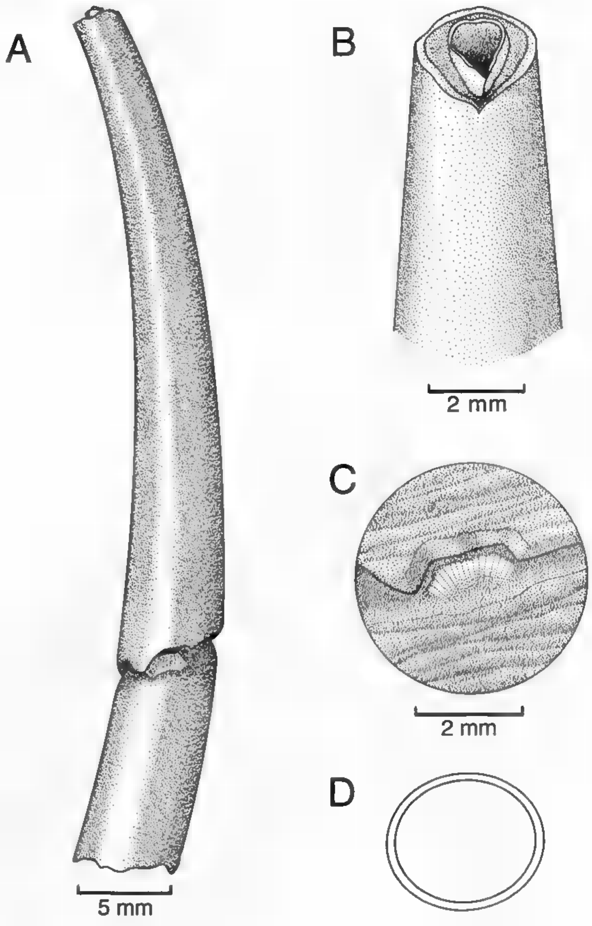

Figure 10.16 Australian Laevidentaliidae. Shell characters of *Laevidentalium crocinum*: **A**, profile; **B**, apex; **C**, sculpture, on each side of a healed fracture; **D**, cross-sectional shape at aperture. [C. Eadie]

Family Gadilinidae

The shell is small to moderate in size, sometimes fragile, and varies considerably in curvature. Its cross-section is subcircular or nearly triangular. The sculpture consists of apical annulations, three longitudinal ribs, or is lacking (Fig. 10.17). Frequently, the apex is truncate, plugged, and a tube usually arises near the ventral rim of the plug (Fig. 10.17B, F). In juveniles, and sometimes in adult specimens, the apex is simple and not notched.

The central radular tooth has a somewhat triangular shape with a tricuspid surface. The bases of the lateral teeth are slender in relation to their crowns and the marginal teeth are curved (Scarabino 1979).

Scarabino (1979) united *Episiphon*, *Gadilina*, *Anulidentalium* and the fossil genus *Lobantale* in this family. Extant species occur worldwide in all depths.

According to Lamprell & Healy (1997) *Episiphon* is the only gadilinid genus known from Australian waters. They recorded four species, *E. virgula* (Fig. 10.17A–D), *E. bordaensis* (both largely southern in distribution) and two new species (both largely northern in distribution; see Fig. 10.17E–H). All four show a wide bathymetric range, but are commonest at depths of over 100 m, chiefly in sand and mud sediments (see Lamprell & Healy 1997).

The fossil record dates back to the Jurassic (Emerson 1962).

Family Omniglyptidae

The shell in this monogeneric family is small to medium-sized with a moderate curvature (Chistikov 1975). The sculpture of dense annulations is confined to the apical portion. The aperture is circular in cross-section (Fig. 10.18). The apex has a simple rim or features a small notch on the convex side.

The radula is characterised by a central tooth with an irregular surface, tricuspidate lateral teeth, and curved marginal teeth (Scarabino 1979).

The occurrence of the single, Recent genus, *Omniglypta*, is limited to depths less than 1800 m in the western Indo-Pacific and the south-western Atlantic Ocean. Two Australian species are known (Lamprell & Healy 1997): *O. anulosum* (Fig. 10.18) and *O. cerina*, both previously classified as species of *Dentalium*.

Order GADILIDA

In members of the Gadilida, the largest diameter of the shell is around the mid-point, at the aperture, or immediately behind it. In this order, the Entalinidae (suborder Entalimorpha) are the only family with thick, longitudinally ribbed shells. Generally, the other families have thin shells with glossy surfaces. Apical, longitudinal striae are known in a few genera, for example, *Striopulsellum* (Scarabino 1979). On the inner shell surface, a pre-apical callus marks the site of insertion of the retractor muscles. The height of the central tooth of the radula exceeds its width.

The single pair of dorso-ventral retractor muscles extend almost directly into the foot. There, the major part of the longitudinal musculature is detached from the pedal body wall and is continuous with large portions of the dorso-ventral retractor muscles. The foot is a thin-walled, retractile and eversible organ (Steiner 1992a). The tip is formed by a crenulate terminal disc, with or without a terminal filament.

The outer gland region and ciliary organ of the anterior mantle margin as found in the Dentaliida are not present. The inner gland region comprises both epithelial and subepithelial gland cells. The posterior mantle opening can be narrowed to a vertical slit by a dorso-ventral muscle clasp, where an annular ciliary organ for generating an inhalant water current is present. The ledges of the pavilion are covered by a ciliated epithelium. Usually there are four to eight pre-anal ciliated ridges (Steiner 1991).

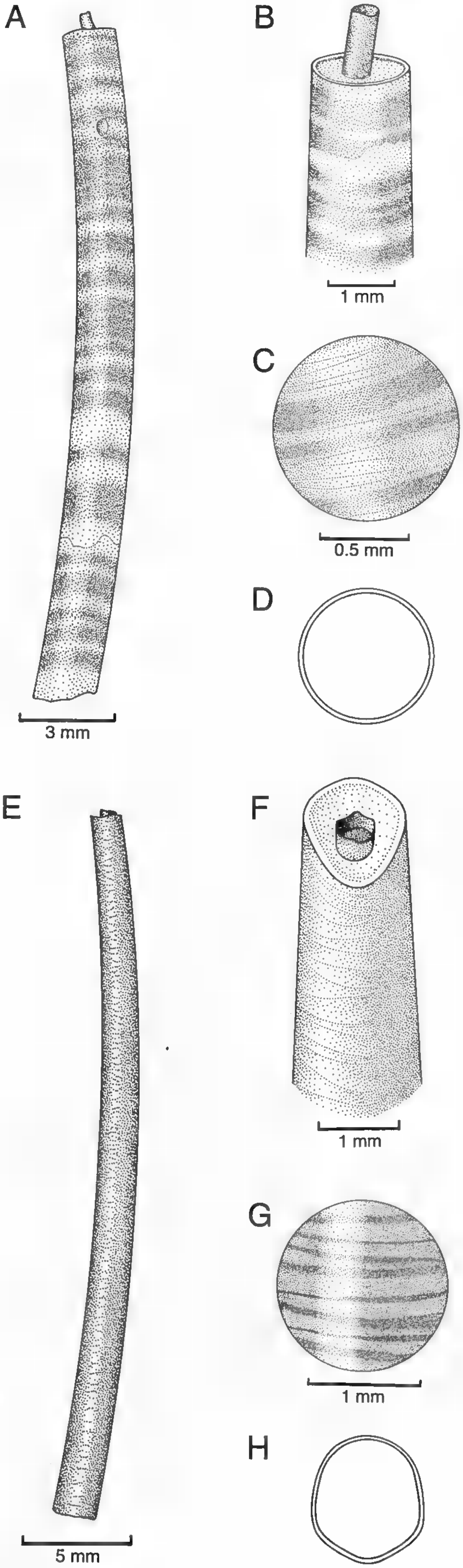

Figure 10.17 Australian Gadilinidae. Shell characters: **A–D**, *Episiphon virgula*; **E–H**, *Episiphon* sp. **A**, **E**, profile; **B**, **F**, apex; **C**, **G**, sculpture; **D**, **H**, cross-sectional shape at aperture. [C. Eadie]

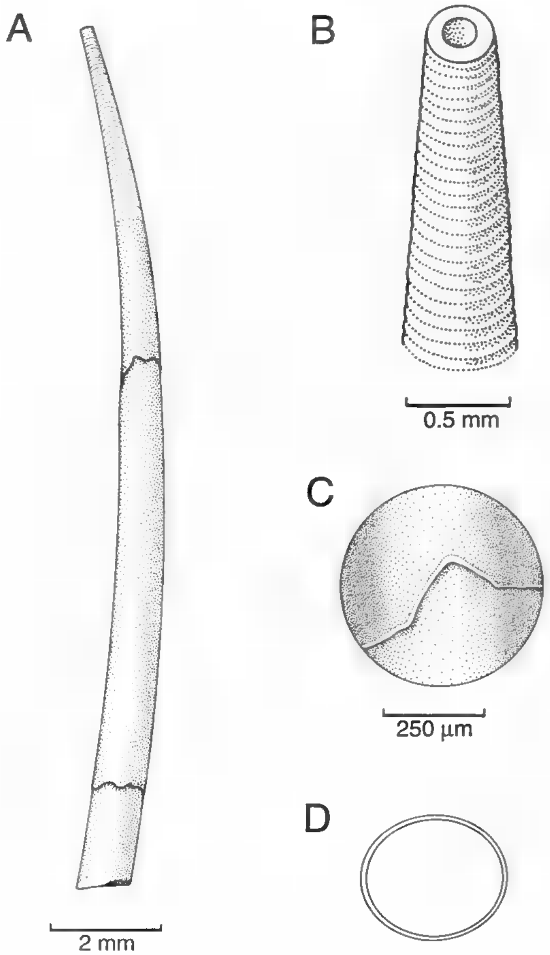

Figure 10.18 Australian Omniglyptidae. Shell characters of *Omniglypta anulosum*: **A**, profile; **B**, apex; **C**, sculpture; **D**, cross-sectional shape at aperture. [C. Eadie]

The captacula are retracted by five to seven longitudinal muscles; most gadilid scaphopods have six such muscles. Only the left digestive gland is present. Nothing is known about the ontogeny of any member of the Gadilida.

Representatives of one family in the suborder Entalimorpha and four families in the suborder Gadilimorpha occur in the marine sediments around the Australian continent. Though Yancey (1973) described the genus *Calstevenus* from Lower Permian deposits, and assigned it to the Gadilida, members of this order are not well documented before the Cretaceous (Emerson 1962).

Suborder ENTALIMORPHA

The shell is relatively large and thick-walled (similar to dentaliid shells) compared to that in other Gadilida, moderately to strongly curved, with the largest diameter always at the anterior end (Fig. 10.19). There are four to 13 primary longitudinal ribs, and secondary longitudinal or transverse striae may fill the intercostal spaces, which are otherwise smooth. In cross-section, the shell is polygonal, oval, or laterally compressed and only rarely circular. A simple apex is usual, but in some species a fissure or a short line of perforations is present on the concave side.

The anterior margin of the slender central tooth is entire. Five to nine denticles, approximately equal in size, arm the lateral teeth. The marginals are simple and lack a keel (Scarabino 1979).

The organisation of the pedal musculature is intermediate between that observed in the Dentaliida and in the Gadilimorpha. The longitudinal muscles are detached from the body wall in the foot only. Four to six muscle strands in the pedal sinus join the body wall at the base of the foot (Steiner 1992a). The pedal disc carries a terminal filament. Six or seven longitudinal muscles are present in the captacula (Steiner 1992b). Numerous epidermal papillae rise from the frontal epithelium of the anterior mantle margin (Steiner 1991).

Family Entalinidae

The diagnosis is the same as for the suborder. The family includes the genera *Bathoxiphus*, *Contentalina*, *Entalina*, *Entalinopsis* (= *Heteroschismoides*) and *Pertusiconcha*. Chistikov (1982) has reviewed some of the species of this family. The family is cosmopolitan from shallow to abyssal depths.

Lamprell & Healy (1997) recorded six species of Entalinidae in their monograph: two species of *Entalina* (*E. mirifica* plus one new species, Fig. 10.19A–D) and four species of *Bathoxiphus* – *B. tricarinatum* (Fig. 10.19E–H), *B. colmani* and two new species. Their study shows that Australian entalinids occur in only small numbers and at depths of 150 m to over 3600 m in sediments ranging from rubble to fine mud.

The oldest fossil recorded is from the Triassic (Emerson 1962). Three fossil gadilinid species are known from Australia: *Gadilina tatei*, *G. triquetum* (both from the Lower Miocene of South Australia) and *Episiphon tornatissimum* from the Victorian Pliocene (Tate 1887, 1899; Pilsbry & Sharp 1897–1898).

Suborder GADILIMORPHA

The shells of this suborder are predominantly smooth and glossy and only seldom bear striae. In cross-section they are circular or slightly depressed (Figs 10.20, 10.21). There is at least one cusp on the central tooth of the radula and the lateral teeth always have three denticles. The marginal teeth are keeled (Scarabino 1979). A pair of large dorso-ventral retractor muscles descend directly into the foot and insert on the pedal disc. The central area of the pedal disc is covered by a mucoid epithelium (Steiner 1992a).

Family Pulsellidae

Pusellids are characterised by small to medium-sized shells, with moderate to weak curvature. The aperture is the site of the largest diameter. Sculpture is either lacking or consists of striae or dense annulations. Frequently, the circular or dorso-ventrally compressed aperture is oblique, and the apex is simple (Fig. 10.20; Boss 1982).

The lateral edges of the central radular tooth are parallel or convergent towards the top. The upper edge is roof-like and terminates in a more or less pointed cusp. Although the shape of the lateral teeth shows considerable variation between the genera, three cusps are usually developed (Scarabino 1979).

There is a terminal filament on the pedal disc. Six longitudinal muscle strands are present in each captaculum. As in the Entalinidae, papillae are abundant on the frontal epithelium (Steiner 1991).

The family comprises five genera, *Pulsellum*, *Fissipulsellum*, *Striopulsellum*, *Annulipulsellum* and *Compressidens*, and is worldwide from the sublittoral to depths of 3900 m (Scarabino 1979). Three pulsellid species have been recorded from Australian waters (Lamprell & Healy 1997): two in the genus *Pulsellum* (*P. eboracense*, Fig. 10.20A–D, and one new species) and one species of *Compressidens* (*Compressidens platyceras*, Fig. 10.20E–H). They live in sand and/or mud, in depths from 2 m to over 300 m (occasionally to depths of 2900 m; Lamprell & Healy 1997).

The oldest fossil pulsellid species is from the Palaeocene (Emerson 1962). *Pulsellum adelaidense* is a Late Pliocene species from South Australia (Ludbrook 1956).

Family Wemersoniellidae

The shell of the sole wemersoniellid genus, *Wemersoniella*, is virtually straight and lacks surface sculpture. It tapers slightly towards a blunt apex. The largest diameter is at the aperture, which is depressed in cross-section. The apex bears a conspicuous pre-apical callus and two lateral lobes at the posterior opening of the shell (Scarabino 1986).

The central tooth is subpyramidal. Two granulated areas, separated by a smooth gap, are present on the upper surface of each lateral tooth. The marginal teeth have a pointed inner margin (Scarabino 1986). The pedal disc has a terminal filament and papillae are present on the frontal epithelium. Species of *Wemersoniella* are found in abyssal depths of the Atlantic Ocean.

Family Gadilidae

The shell is small to medium-sized, and circular or dorso-ventrally depressed in cross-section. It is moderately curved to almost straight. The largest diameter is at the aperture in some species only. The shell surface may have a smooth and polished surface or show fine longitudinal or annular striation. The apex may be simple or bear between two and 10 lobes or shallow sinuses.

The central tooth of the radula is complex and varies considerably in structure. One postero-lateral and two antero-lateral cusps are a prominent and common feature of the lateral teeth. The space in between is filled with smaller denticles. The upper surface may also show some granulation. The marginal teeth have curved keels (Scarabino 1979).

The foot is typical of the Gadilida. The pedal disc may lack a terminal filament. Only a few papillae are developed on the frontal epithelium (Steiner 1991).

The family Gadilidae is divided into the two subfamilies, Gadilinae and Siphonodentaliinae; only Gadilinae is represented in the extant Australian fauna.

Subfamily Gadilinae

The shell has a very slight curvature (Fig. 10.21; Pl. 16.5). The aperture is constricted, and some species are almost cylindrical or barrel-shaped. The shell is circular or slightly depressed in cross-section. The apex is either simple or indented by shallow sinuses. The surface is usually smooth and glossy; sculpture, if present, consists of annular striae in the apical quarter of the shell.

The genera in this subfamily are *Gadila*, *Cadulus*, *Dischides*, *Polyschides*, *Platyschides*, *Sagamicadulus* and *Striocadulus*. The assignment of species to these genera is somewhat confusing, because of the doubtful reliability of apical characters and problems in diagnosing these taxa. The subfamily is cosmopolitan and occurs at all depths from sublittoral to abyssal.

Lamprell & Healy (1997) have recorded 19 gadiline species within the Australian fauna, these being distributed between the genera *Gadila* (nine, including four new; Fig. 10.21A–D), *Cadulus* (five, including three new; Fig. 10.21E–G), *Dischides* (two, including one new; Fig. 10.21K–N) and *Polyschides* (three including two new; Fig. 10.21H–J). In addition, these authors relocated *Cadulus ludbrookae*, *C. spretus*, *C. occiduus*, *C. angustior* and *C. bordaensis* to the genus *Gadila*. To date, no species of *Platyschides*, *Sagamicadulus* or *Striocadulus* have been reported from Australia. A number of Australian gadilids have extensive geographical and bathymetric ranges, for example *Cadulus vincentianus*, *C. simillimus* and *Gadila spretus* occur off the coastlines of most states at depths ranging from 10 m to over 2700 m living in sand or mud sediments (Lamprell & Healy 1997).

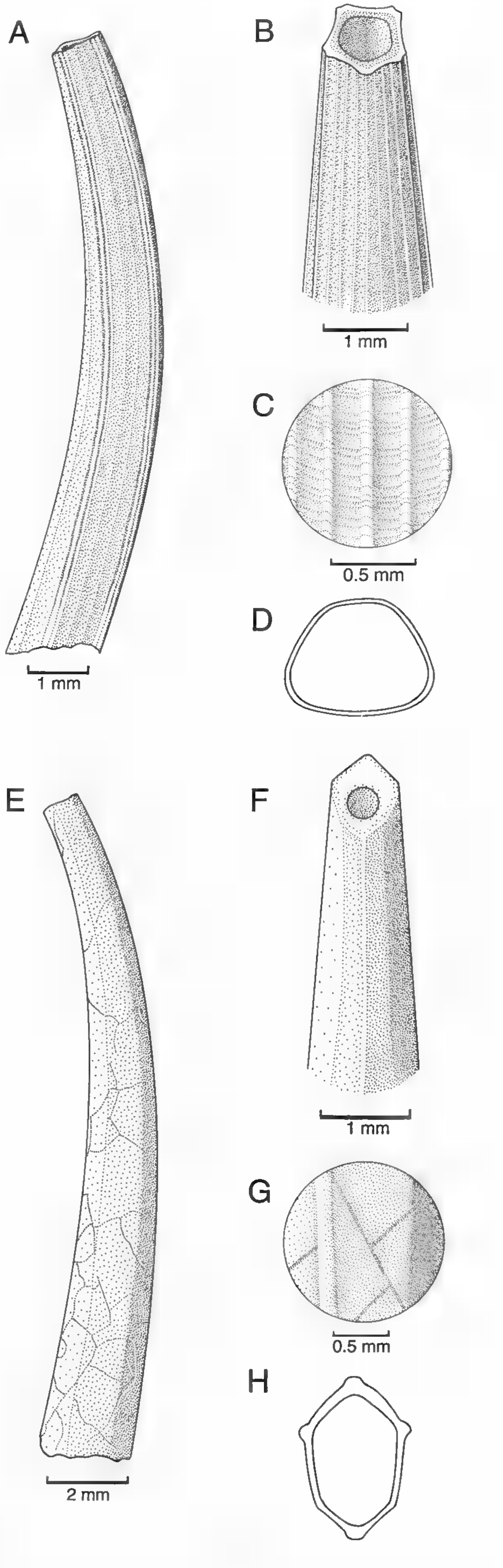

Figure 10.19 Australian Entalinidae. Shell characters: **A–D**, *Entalina* sp.; **E–H**, *Bathoxiphus tricarinatum*. **A**, **E**, profile; **B**, **F**, apex; **C**, **G**, sculpture; **D**, **H**, cross-sectional shape at aperture. [C. Eadie]

Four Australian fossil species have been described: *Cadulus infans* (Pliocene of Victoria), *C. yatalensis* (Late Pliocene of South Australia), *Gadila acuminatus* (Pliocene of South Australia) and *G. mucronatus* (Lower Miocene of Victoria) (Tate 1887, 1899; Ludbrook 1956). The oldest known fossil in the subfamily is from the lower Cretaceous (Emerson 1962).

Subfamily Siphonodentaliinae

The shells are small to medium-sized and curved. The largest diameter is at the aperture. The apical rim has two to 10 lobes separated by slits of various depth. The only genus in this subfamily is *Siphonodentalium*, thought to be represented in Australia by *S. eboracense*. However, this species has recently been transferred to the genus *Pulsellum*, in the family Pulsellidae. The subfamily is distributed worldwide, from shallow waters to depths of 7000 m (*S. galatheae*; Knudsen 1964). In the fossil record, *Siphonodentalium* appears in the Eocene (Emerson 1962).

ACKNOWLEDGEMENTS

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REFERENCE MATERIAL

The material illustrated in Figs 10.13 to 10.21 is held at either the Australian Museum, the Queensland Museum or in the private collection of K. Lamprell. Information detailing each specimen is as follows:

10.13A–D – Arafura Sea 11°09'S 134°03'E, Lamprell Colln; 10.13 E–G – Port Lincoln South Australia, Aust. Mus. Colln; 10.13 I–L – north Western Australia, Lamprell Colln; 10.13 M–P – Lady Musgrave Island, Qld Mus. Colln; 10.14 A–D – 12°36.23'S 141°39.62'E, Qld Mus. Colln; 10.14E–H – north Western Australia, Lamprell Colln; 10.14I–L – Clarence River New South Wales, Aust. Mus. Colln; 10.14M–P – 10°01'S 145°01'E, Qld Mus. Colln; 10.15A–D – Lady Musgrave Island Queensland, Aust. Mus. Colln c.172434; 10.16A–D – Cape Moreton south Queensland, Lamprell Colln; 10.17A–D – Cape Howe Lakes Entrance Victoria 30°13's 149°06'E, Aust. Mus. Colln; 10.17E–H – 17°50.67'S 147°18.2'E, Qld Mus. Colln; 10.18A–D – off Bowen, Queensland 19°44'S 148°14'E, Aust. Mus. Colln c.169939; 10.19A–D – Wollongong New South Wales, Aust. Mus. Colln c.169989; 10.19E–H – NE Sandy Cape Queensland 24°28.2'S 153°31.2'E, Lamprell Colln; 10.20A–D – Gladstone Power Station, Aust. Mus. Colln; 10.20E–H – Challenger Head, Broken Bay, New South Wales, Aust. Mus. Colln c.172625; 10.21A–D – Port Kembla New South Wales, Aust. Mus. Colln; 10.21E–G – 17°22'S 146°48'E, Aust. Mus. Colln; 10.21H–J – 30°45'S 114°51'E, Aust. Mus. Colln; 10.21K–N – Masthead Reef, north Queensland, Aust. Mus. Colln.

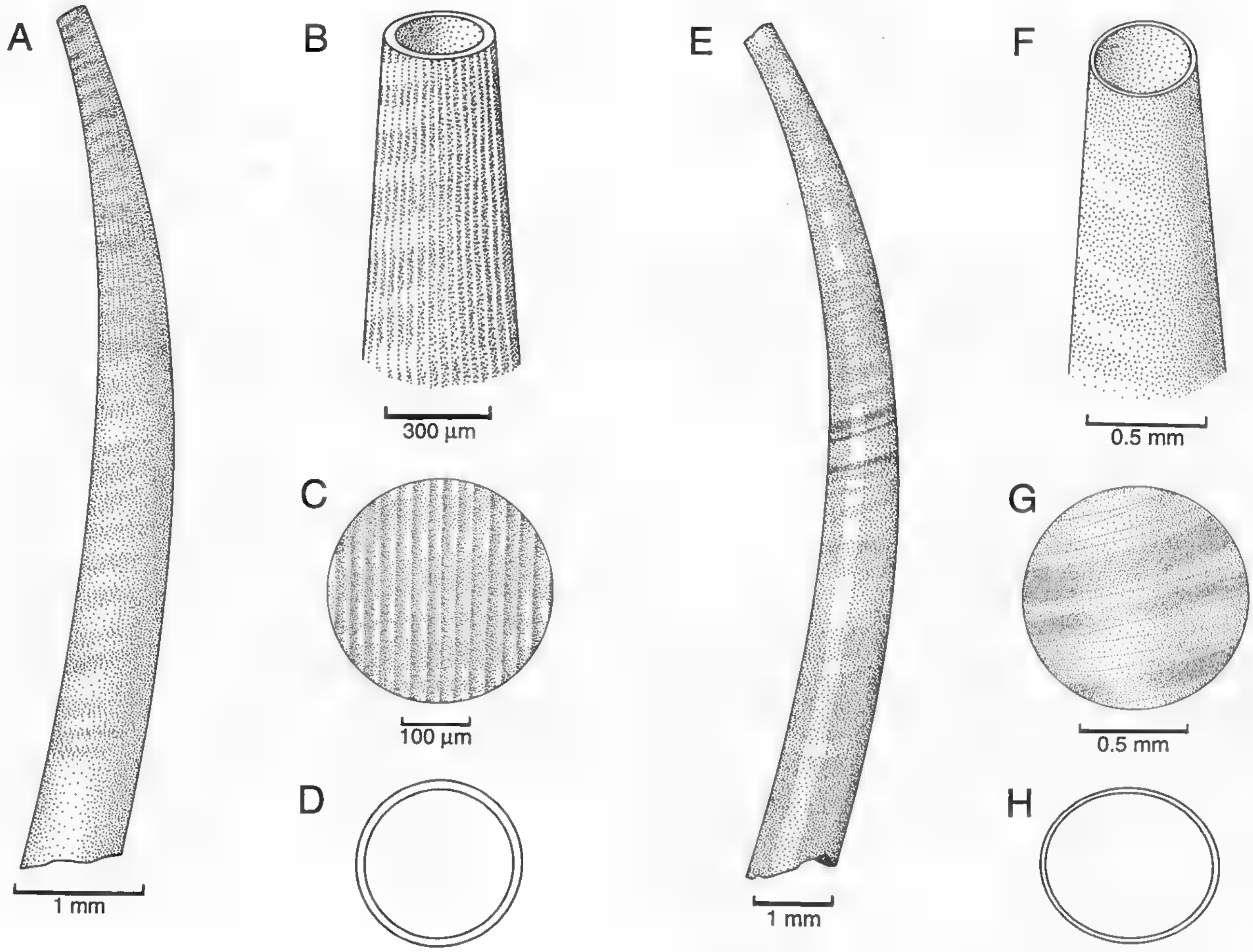

Figure 10.20 Australian Pulsellidae. Shell characters: A–D, *Pulsellum eboracense*; E–H, *Compressidens platyceras*. A, E, profile; B, F, apex; C, G, shell sculpture; D, H, cross-sectional shape at aperture. [C. Eadie]

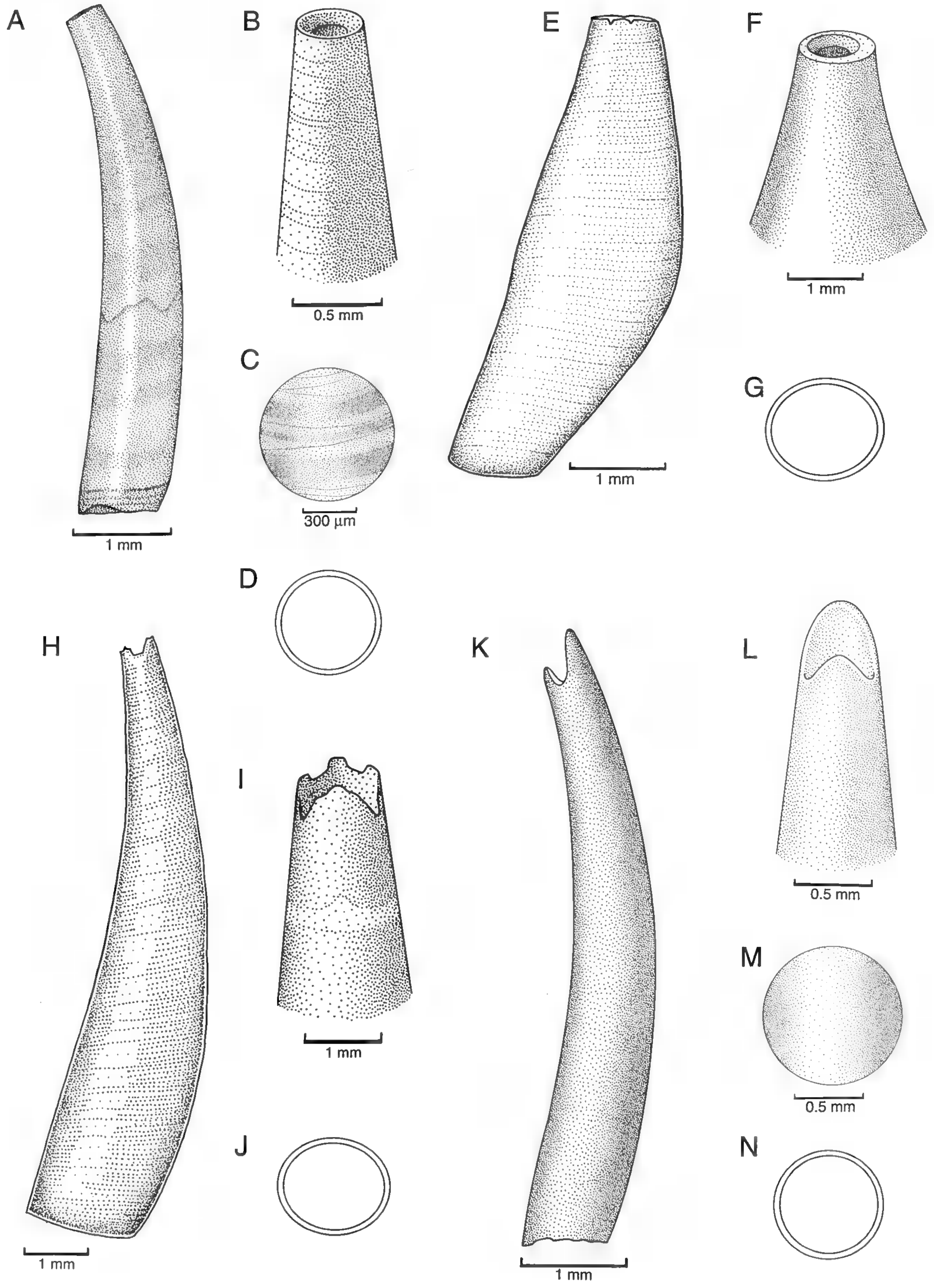

Figure 10.21 Australian Gadilidae, subfamily Gadilinae. Shell characters: **A–D**, *Gadila spretus*; **E–G**, *Cadulus simillimus*; **H–J**, *Polychides gibbosus*; **K–N**, *Dischides prionotus*. **A, E, H, K**, profile; **B, F, I, L**, apex; **C, M**, sculpture; **D, G, J, N**, cross-sectional shape at aperture. [A–D, F, G, I–N, C. Eadie; E, H, L. Newman]

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CLASS CEPHALOPODA

CHAPTER 11

DEFINITION AND GENERAL DESCRIPTION

Cephalopods are the most highly evolved group in the phylum. Their way of life more closely resembles that of fishes than those of the other classes of molluscs (Mangold & Fioroni 1970; Packard 1972; but see O'Dor & Webber 1986). Cephalopods are exclusively marine animals and live in all oceans from the Arctic basin to Antarctica. Although they have a long fossil record, including over 10 000 species, the living fauna comprises only about 650 to 700 species (Voss 1977a). The only surviving cephalopod genus with an external shell is *Nautilus* (Fig. 11.1C; Pl. 21.2), with five extant species (Saunders 1987). All other extant species, in the subclass Coleoidea, have a highly modified internal shell or no shell (Fig. 11.1 A, B, D; Pls 17–20, 21.1, 21.3–21.5).

Cephalopods have retained the bilateral symmetry of their molluscan ancestors. The evolutionary development along the secondary, dorso-ventral axis resulted in the formation of two body parts, the anterior cephalopodium and the posterior visceropallium. The cephalopodium includes the head with its circumoral appendages and the funnel, and the visceropallium consists of the mantle, the mantle cavity with its organs, and the shell and fins, when present. Thus the functional body axes have shifted completely from the ancestral molluscan form: the head and its appendages are anterior, the funnel is ventral and the apex of the body is posterior.

Two major evolutionary trends characterise the Recent coleoid cephalopods. Firstly, the loss of the bulky external shell allowed the development of a powerful muscular mantle which became the main locomotive organ for fast swimming by jet propulsion. Secondly, the nervous centres became concentrated in the head and formed a highly developed brain or central nervous system enclosed in cranial cartilage. The main sensory organs are also located on the head.

The Coleoidea are able to change colour using a complex chromatophore system under nervous, not hormonal, control. This system dominates the animal's behaviour and response to its surroundings and is critical for survival, especially for shallow water benthic and epibenthic forms. With the exception of *Nautilus*, Recent cephalopods have an ink sac, but this is secondarily lost in several deep sea or highly specialised species.

The circulatory system of cephalopods is distinctive in the Mollusca. It is closed and maintains a high blood pressure, as in vertebrates.

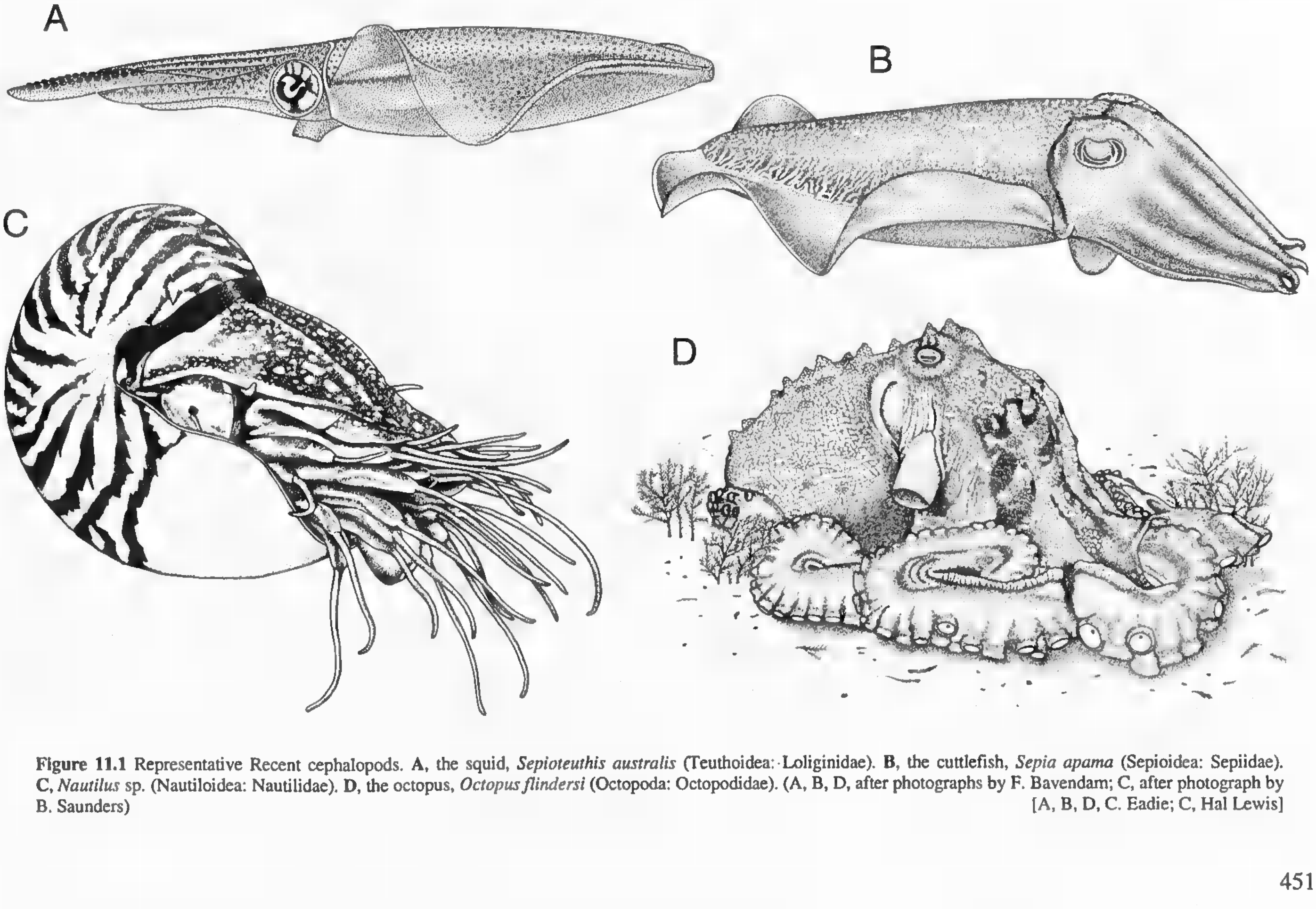

Figure 11.1 Representative Recent cephalopods. **A**, the squid, *Sepioteuthis australis* (Teuthoidea: Loliginidae). **B**, the cuttlefish, *Sepia apama* (Sepioidea: Sepiidae). **C**, *Nautilus* sp. (Nautiloidea: Nautilidae). **D**, the octopus, *Octopus flindersi* (Octopoda: Octopodidae). (A, B, D, after photographs by F. Bavendam; C, after photograph by B. Saunders) [A, B, D, C. Eadie; C, Hal Lewis]

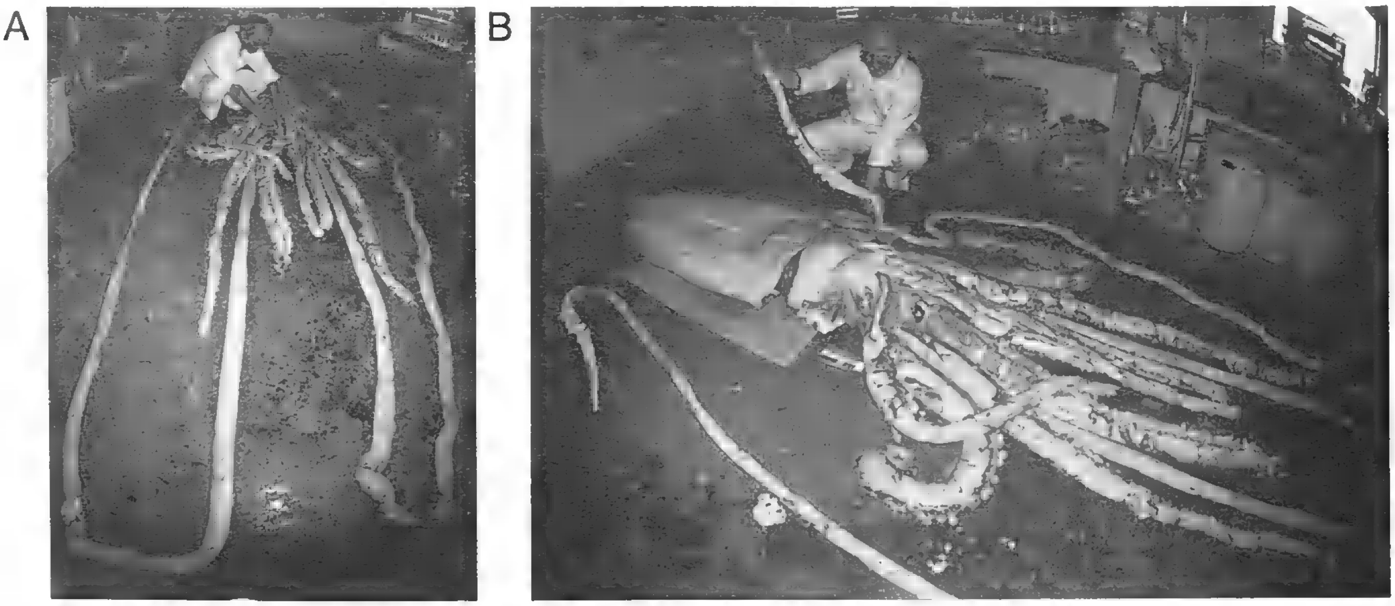

Figure 11.2 An immature female giant squid, *Architeuthis* species (Architeuthidae), netted on 10 January 1996 about 80 nm south of Cape Otway, Victoria, at a depth of 900 m; weight 145 kg. A, the very long tentacles, 7.8 m long, make up most of the total length of 9.8 m. B, the triangular mantle, 1.6 m long, is small compared to the head and the arms, the longest of which was 1.7 m. [F. Coffa/courtesy Museum of Victoria]

Cephalopods are carnivorous and have powerful beak-like jaws (see Fig. 11.25) that enable them to deal with large, live prey. The digestive organs retain their primarily molluscan character, although the primitive molluscan stomach has evolved into two distinct organs, the stomach proper and the caecum.

Cephalopods are dioecious and they exhibit varying degrees of external sexual dimorphism. Males generally have one or more modified arms for the transfer of spermatophores to the females.

Cephalopod eggs are telolecithal, the rich yolk being concentrated at the vegetal pole. Cleavage is meroblastic, not total as in other molluscs. The postembryonic development is direct, so the larval stages and metamorphosis, characteristic of other molluscs, do not occur in cephalopods.

CLASSIFICATION

The class Cephalopoda is divided into two subclasses, namely the Nautiloidea and the Coleoidea. Both occur in Australian waters.

Extant nautiloids are all species of a single genus, *Nautilus*. These have a chambered, coiled, external shell, more than 10 circumoral appendages and four gills; suckers are absent.

In coleoids the shell is internal and reduced or absent, there are eight to 10 circumoral appendages, two gills and suckers are present.

In 1994, Doyle, Donovan & Nixon proposed a new classification for the Coleoidea that has found general agreement. The Recent coleoids are placed in the superorders Debrachia Böttger, 1852 and Octobrachia Fioroni, 1981. The former contains four orders: Spirulida Stolley, 1919; Sepiida Zittel, 1895; Sepiolida Fioroni, 1981; and Teuthoidea Naef, 1916. The Teuthoidea comprises the suborders Oegopsida and Myopsida. The superorder Octobrachia contains the orders Vampyromorpha Robson, 1829; Octopoda Leach, 1817; and Cirroctopoda Young, 1989. In this volume, the subclass Coleoidea is treated in the more traditional classification of four orders: Sepioidea, Teuthoidea, Vampyromorpha and Octopoda.

HISTORY OF DISCOVERY

So far as the written record is concerned, the Cephalopoda was 'discovered' in the Mediterranean Sea. Indeed, through the writings of Aristotle, we know that the ancient Greeks were familiar with this group. Aristotle's Mollusca comprised only cephalopods. He correctly distinguished several Mediterranean species, described their differences and provided accurate information on their anatomy and biology. Very probably he also recognised *Nautilus* as a distinct species (Davis 1987). The Cephalopoda was named as such by Schneider in 1784. However, by that time, the group included the Bellerophontida (Gastropoda) and the Foraminifera. These were removed from the Cephalopoda about three decades later. Linnaeus did not recognise the class as an entity.

The first major monograph on the systematics of the Cephalopoda was that of d'Orbigny (Férussac & d'Orbigny 1834–1848). In 1832, Owen established two subclasses for cephalopods, based on the number of gills, and named the Tetrabranchiata for *Nautilus* and the Dibranchiata for all other living forms. In 1888, Bather introduced the neutral name of Coleoidea for the old Dibranchiata. *Nautilus*, a Linnaean genus, was included in the suborder Nautiloidea, together with its fossil relatives. Leach (1817) divided the Coleoidea into two orders, the Decapoda and the Octopoda. Since d'Orbigny, the Decapoda has been subdivided into the Myopsida, in which the eyes have a protective cornea, for example, *Loligo* and *Sepia*, and the Oegopsida, the non-loliginid squids, which lack a cornea. Naef (1912) recognised the artificial division based on the presence or absence of a cornea, separated *Sepia* from *Loligo*, and established the suborder Sepioidea including also *Spirula*. He united the Loliginidae and the Oegopsida in the suborder Teuthoidea.

The major division of the Coleoidea into two orders, Decapoda and Octopoda, lasted until 1939 when Pickford established a new order, the Vampyromorpha, with one species, included previously in the Octopoda. The division by Voss (1977b) of the Recent Coleoidea, into the four orders Sepioidea, Teuthoidea, Vampyromorpha and Octopoda, is widely accepted (for example, Nesis 1987; Mangold & Portmann 1989). However, several changes have been proposed at the ordinal level, as well as the establishment of subclasses (Fioroni 1981; Clarke 1988; Young, J.Z. 1989; Guerra 1992; Doyle, Donovan & Nixon 1994).

Research in the 19th Century and at the beginning of the 20th Century concentrated on species descriptions and systematics, during the period of the great oceanographic cruises, including the *Challenger* (Hoyle 1885), *Valdivia* (Chun 1910, 1915), *Plankton-Expedition* (Pfeffer 1912) and *Prince Albert I, de Monaco* (Joubin 1900, 1902, 1918). In the first decades of the 20th Century, important monographs were published on areas such as the Gulf of Naples (Naef 1923) or taxa such as the Octopoda (Robson 1929, 1932). According to Sweeney & Roper (1991), this was the golden age of cephalopod research.

Research on systematics has continued. Indeed, many lower taxa (families, subfamilies, genera) are badly in need of critical revision (Voss 1977a; Roper 1983). In recent decades, however, the gradual awareness of the importance of cephalopods in the marine ecosystem (Clarke 1980) and the increasing interest in their fisheries (Voss 1973, 1983; Okutani 1977; Rathjen 1983; Roper, Sweeney & Nauen 1984; Rathjen & Voss 1987; IREP-FAO) has stimulated research, primarily on life histories. Since the late 1930s, cephalopods have been the focus of basic research in their own right, and for biomedical interest.

The history of discovery of the Australian fauna is given in subsequent chapters on the two subclasses.

MORPHOLOGY AND PHYSIOLOGY

External Features and Shells

Cephalopods are bilaterally symmetrical and have a mantle with either an external or an internal shell. A large mantle cavity contains one or two pairs of gills and, in some species, light-emitting photophores. It receives the openings of ducts from the kidneys, rectum and ink sac and from the gonad – one in males, one or two in females. Water is drawn into the mantle cavity at the sides of the large head and forced out of the mantle cavity through the funnel below the head. The head bears appendages, of which the eight shorter ones are called arms, the longer ones tentacles. In the mouth are two large, protrusible, chitinous jaws and a radula. The eyes, on each side of the head, are very large, and may be unequal in size in some species. They may be covered by a cornea or have the lens exposed to the sea. The pupil is either horizontal, a W-shaped slit or round. The funnel, lying ventral to the head, consists of a medial fused muscular tube and two collar folds. In coleoids, the tube is usually long and mobile, and able to direct the water flow in any direction. In *Nautilus*, two free flaps overlap to form a tube.

Cephalopod size spans four orders of magnitude. Adults can measure as little as 20 mm or as much as 20 m in total length (Fig. 11.2).

Externally, cephalopods have two general forms (Fig. 11.1; Pls 17–21). In *Nautilus*, the external shape is dominated by a planispiral, calcareous shell in which the body is sheltered and into which the head can be withdrawn and covered by the hard fleshy hood (Fig. 11.1C; Pl. 21.2). Chambers within the shell provide for buoyancy control (Denton & Gilpin-Brown 1966; Ward 1988) and also protection against predators. In all other Recent cephalopods, skin and muscle enclose the shell. Among the coleoids only *Sepia* and *Spirula* have calcareous shells with chambers used for buoyancy control (Denton, Gilpin-Brown & Howarth 1961; Denton, Gilpin-Brown & Howarth 1967; Denton & Gilpin-Brown 1971). In teuthoids and some sepioids, the shell is a thin, chitinous, feather-shaped shaft called a gladius or pen (for review see Toll 1988). *Ancistrocheirus* however, has a thick, stiff pen of cartilage with chitin dorsally. The shell is cartilaginous and saddle-shaped in the cirrate octopods, and reduced to two small, slender rods in the benthic incirrate octopods. No vestige of the shell occurs in some sepioids and the pelagic incirrate octopods. The secondary shell of the epipelagic octopod, *Argonauta*, serves as brooding chamber.

Other skeletal elements in cephalopods include the cartilages that surround the brain and statocysts, the nuchal and funnel cartilages which interlock the cephalopodium and visceropallium in decapod cephalopods (Fig. 11.3), and the fin supports.

The entire external surface of cephalopods with an internal shell, or no shell, is covered by skin elements that fulfil a variety of functions (Fig. 11.1A, B, D). The epidermis comprises cylindrical epithelial cells, most of which are mucous cells, which render the cephalopod skin slippery. Some special structures in the skin, such as the hatching or Hoyle's organ, and Kölliker bristles, disappear shortly after hatching. The dermal layer contains muscular fibres,

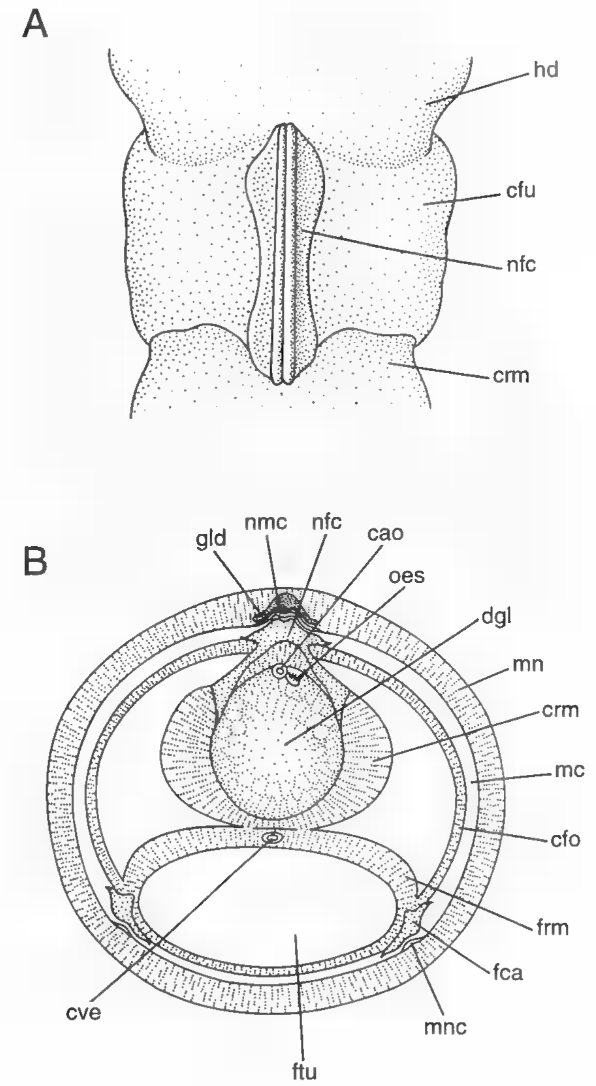

Figure 11.3 Nuchal and funnel cartilages in squid. **A**, nuchal cartilage of the funnel. **B**, transverse section of a decapod at the level of the funnel cartilages. **cao**, cephalic aorta; **cfo**, collar fold; **cfu**, collar of funnel; **crm**, cephalic retractor muscle; **cve**, cephalic vein; **dgl**, digestive gland; **fca**, funnel cartilage; **frm**, funnel retractor muscle; **ftu**, funnel tube; **gld**, gladius; **hd**, head; **mc**, mantle cavity; **mn**, mantle; **mnc**, mantle cartilage; **nfc**, nuchal funnel cartilage; **nmc**, nuchal mantle cartilage; **oes**, oesophagus. (After Grassé & Mangold 1989) [C. Eadie]

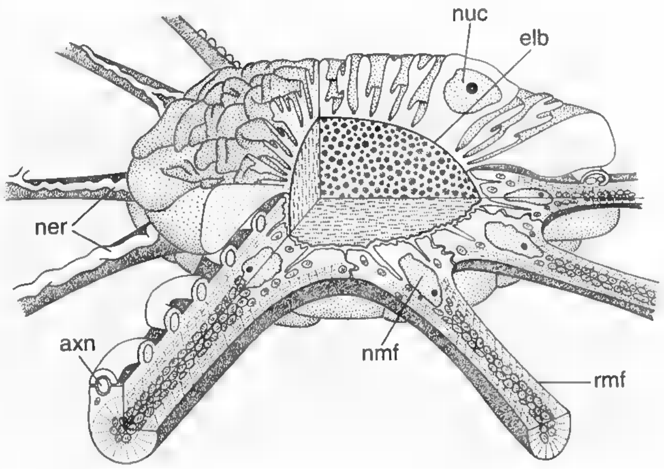

Figure 11.4 Chromatophore of *Loligo opalescens* (Loliginidae). **axn**, axon; **elb**, elastic bag (contracted) containing the pigments; **ner**, nerves; **nmf**, nucleus of muscle fibre; **nuc**, nucleus of main cell; **rmf**, radiating muscle fibre. (After Cloney & Florey 1968) [C. Eadie]

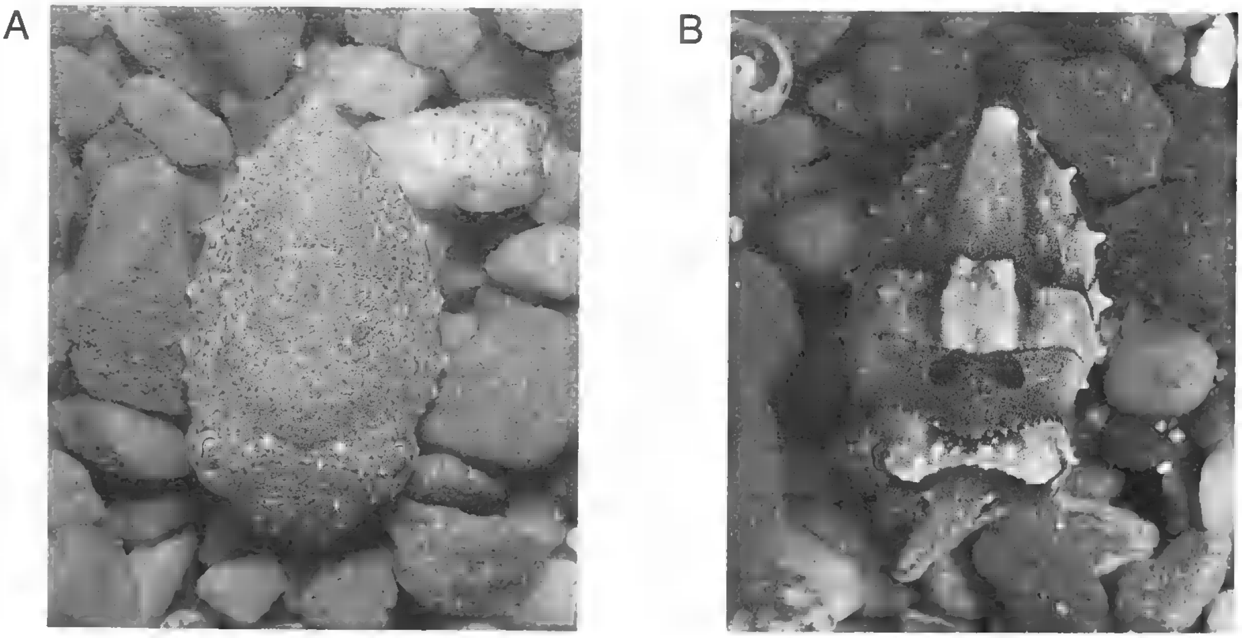

Figure 11.5 Camouflage shown by a newly hatched *Sepia officinalis* (Sepiidae) resting on a background of pebbles. **A**, uniform colouration, with slight mottling, which resembles larger pebbles nearby. **B**, 'white square' pattern, in which enhanced contrast by expansion of chromatophores at the edges of the squares mimics the shadows between the pebbles. (After Hanlon & Messenger 1988)
[courtesy Roger T. Hanlon]

connective tissue matrix and the elements of the chromatic system: chromatophores, iridophores and, in some species, leucophores.

Chromatophores are small, thin-walled, pigment-filled elastic sacs (Fig. 11.4) which can expand to change the transparent skin immediately to a yellow, deep red or brown colour, by contraction of surrounding radiating muscle fibres. Iridocytes reflect the light very efficiently to produce silvering and iridescence. The combination and proportion of pigment varieties are species specific (Packard & Hochberg 1977; Packard 1988). The chromatophoric system allows both visual communication and near perfect background-matching capabilities (Fig. 11.5). Moreover, in many octopods, and in *Sepia* species, superficial dermal musculature can produce wrinkles, warty bumps or even papillate structures in place of the sometimes smooth skin (Pl. 17.5). Such breaks in outline, together with colour background matching, are of great value to all coleoid cephalopods that live in coastal waters. Some oceanic species have permanent cartilaginous skin structures such as scales, papillae and tubercles (Roper & Lu 1990).

In many species, the skin also contains photophores which fulfil similar functions to the chromatophores and iridophores, but in different habitats. In mid-water, photophores, ranging in structure from very simple to highly sophisticated (Arnold & Young 1974; Young, R.E. & Bennett 1988), produce ventrally directed, bioluminescent light to eliminate the silhouette of a squid against the highly directional daylight welling downwards from the surface (Herring 1977, 1988; Young, R.E. 1977). Photophores are best developed in the teuthoids (Fig. 11.6).

Appendages surround the mouth of all cephalopods. In *Nautilus*, numerous pairs of digital tentacles are disposed in three irregular concentric rings. These are sheathed, sensory and adhesive tentacles, with grooves down their inner surfaces and transverse constrictions that resemble segments (Griffin 1900; Fukuda 1987). There are no suckers. Immediately surrounding the mouth is a series of shorter, buccal tentacles some of which exhibit strong sexual dimorphism in males (spadix).

Sepioids and teuthoids have eight short arms and two longer tentacles positioned between the third and fourth arms. *Vampyroteuthis* has eight arms and two small sensory filaments that represent the highly specialised second arm pair. Octopods have eight arms, usually longer in relation to the body length than those of the sepioids and teuthoids, and they have no tentacles. The arms are connected at the bases by a membranous web. The oral surface of the arms of sepioids and teuthoids is attached by the buccal membrane to the outer lip that surrounds the mouth. The latter contains muscular attachments which are often extended to form lappets.

The arms and tentacles are muscular organs, with muscular fibres tightly packed in a three-dimensional arrangement. In the absence of fluid-filled cavities and hardened skeletal elements, the musculature itself both creates movement and provides skeletal support (Kier 1982, 1985, 1991). There are important differences in the musculature of arms and tentacles. For example, the cross-striated transverse muscles present in tentacles facilitate the incredibly rapid extension required to catch prey.

The oral surface of the arms of coleoids bears one to eight rows of suckers. Octopods and *Vampyroteuthis* have sessile suckers without chitinous rings. Teuthoid and sepioid suckers are stalked and have chitinous rings, which may be modified into chitinous hooks in some oceanic squid. In finned octopods and *Vampyroteuthis*, the single row of suckers is bordered on each side by a row of cirri. The two long tentacles of decapod cephalopods are usually longer than the arms. The stalk is mostly bare, and a terminal expanded club bears from four to many rows of suckers or hooks. Species of a few oceanic teuthoid families lose their tentacles early in life.

The ontogenetic changes in shape and body proportions may be considerable, although not as dramatic as in other molluscs (Sweeney, Roper, Mangold, Clarke & Boletzky 1992). Planktonic hatchlings are tiny with a round, rather stout body and short arms (Fig. 11.7A). In some species, the juveniles are so different from the adults that they were described as a different species. Benthic hatchlings most closely resemble the adults. Males and females of some species differ markedly in size and shape; males are dwarfs in *Argonauta* and related genera.

Musculature and Locomotion

Development of a siphuncle and a transverse partition which formed a buoyancy chamber in the shell enabled the first cephalopods to move off the sea bottom. Such shelled cephalopods flourished until the end of the Cretaceous (Teichert 1988). All had a calcareous shell from which they could pump out fluid and ions through the siphuncle to create a low-pressure gas-filled chamber. This enabled them to control their density and

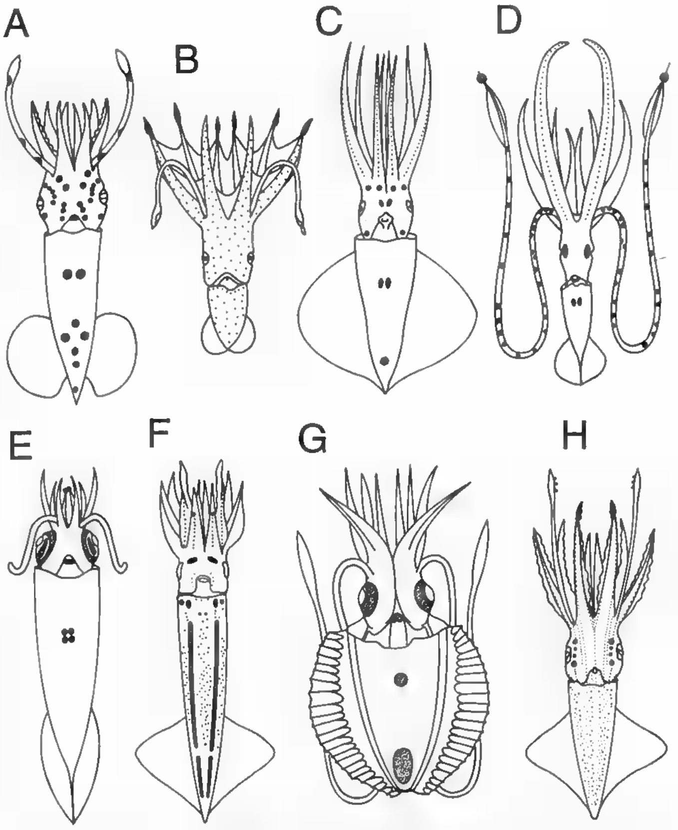

Figure 11.6 Arrangement of photophores in some teuthoid genera. **A**, *Pterygioteuthis*. **B**, *Histioteuthis*. **C**, *Octopoteuthis*. **D**, *Chiroteuthis*. **E**, *Phasmatopsis*. **F**, *Sthenoteuthis*. **G**, *Ctenopteryx*, male. **H**, *Abraliopsis*. (After Herring 1977) [C. Eadie]

hence their depth (Denton 1974). Such relatively slow-moving animals, often with large external and non-streamlined shells, proved no match for the predatory fishes which appeared in the Ordovician, and only the genus *Nautilus* survived (Packard 1972).

In *Nautilus*, jet propulsion is more primitive than in coleoids. Locomotion is brought about by the flaps of the funnel held into a tube shape and by retraction of the hood and head into the shell. Fluid and ions are pumped out of the chambers to keep the shell buoyant as the animal grows. The swimming and buoyancy mechanisms of *Nautilus* are described in detail by Chamberlain (1987), Greenwald & Ward (1987) and Ward (1988).

The calcareous shells of cuttlefishes became flattened and incorporated into the mantle. The animal retains the capacity to maintain a stable depth by adjusting the amount of fluid inside the shell, and fins and jet propulsion provide for manoeuvrability and rapid escape.

Possibly some time before the fishes evolved, some cephalopods lost their shells and thus abandoned this form of buoyancy control altogether. Either they adopted a bottom living habit, as in the near-shore octopuses of today, or found ways of attaining neutral buoyancy in mid-water, other than a chambered shell. These mechanisms freed cephalopods from the depth restriction imposed by thickening of the shell to resist ambient pressure at depth.

An alternative method for staying off the bottom probably was to perfect the method of jet propulsion already employed by the shelled cephalopods. Loss of the mineral component (calcium carbonate) and main bulk of the shell allowed the development of a streamlined body and the ability to contract the body muscles around the water-filled mantle cavity. The resultant powerful jet of water from the head end of these elongate animals enabled them to stay off the bottom by rapid and energetic swimming. Such active animals could compete successfully with fish. The development of high-speed muscle contraction, sensory organs and a brain enabled these animals to capture sufficient prey to maintain the necessary high metabolic rate.

These morphological features are best developed in several families of squids, most notably the neritic Loliginidae and many of the oceanic families, such as the Ommastrephidae and Onychoteuthidae (Figs 11.1A, 13.8, 13.12, 13.20; Pl. 18.6). To improve swimming, not only were more highly developed mantle muscles required, but large adductor and collar muscles were necessary to stop the higher pressures from forcing the head away from the opening of the mantle. Such changes have permitted a piston-like action to bring about even greater pressure for the jet force. These muscular squids are denser than seawater and must swim continually in order not to sink. Some of these squids take advantage of water currents, gliding on them with their fins barely moving (O'Dor *et al.* 1994).

The mantle is the primary organ of locomotion in these fast swimming animals. Beneath the skin, the muscular layer is sandwiched between the internal and external tunics. The tunics consist of elastic collagen tissue, connective tissue and fine longitudinal muscle fibres (Fig. 11.8). The bulk of the muscular layer comprises obliquely-striated, circular muscles, divided in portions by radial fibres (Ward & Wainwright 1972). The radial and circular muscles alternately dilate and constrict the mantle to circulate a flow of water through the mantle cavity. Contraction of the circular muscles increases water pressure and seals the collar against the head and mantle opening, forcing the water to pass through the funnel. When the circular muscles relax and the radial fibres contract, the collar relaxes and water enters the mantle cavity through the mantle opening. The elastic fibres prevent the deformation of the mantle after contraction. These fibres store part of the energy produced by the circular muscles during contraction and release it when the mantle cavity is refilled with water.

The efficiency of jet propulsion depends primarily on the volume of the mantle cavity and the mass of the mantle musculature (Wells 1990; Wells & O'Dor 1991). In coleoids the mantle has a ventilatory function as well as a locomotive one, functions which have incompatible requirements. For efficient jet propulsion the

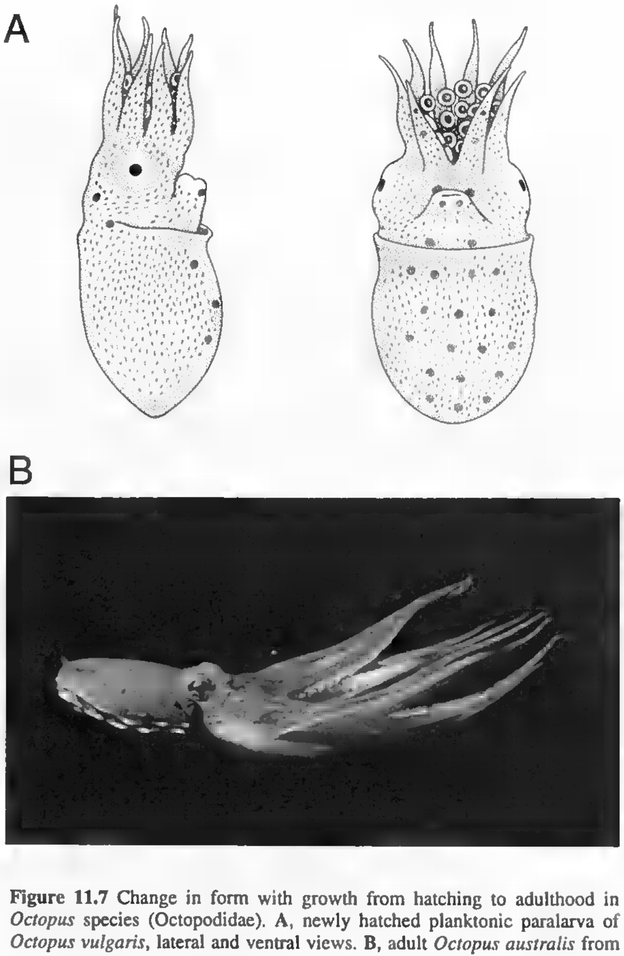

Figure 11.7 Change in form with growth from hatching to adulthood in *Octopus* species (Octopodidae). A, newly hatched planktonic paralarva of *Octopus vulgaris*, lateral and ventral views. B, adult *Octopus australis* from South Australia. (A, modified after Fioroni 1962) [A, C. Eadie; B, F. Bavendam]

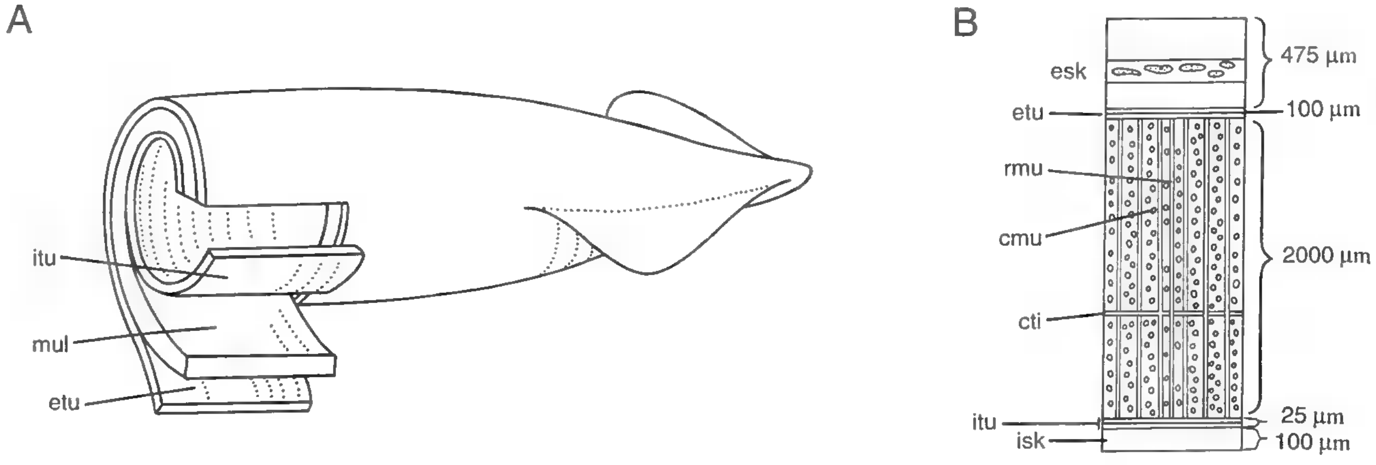

Figure 11.8 Arrangement of the mantle muscles in the squid genus *Lolliguncula* (Loliginidae). **A**, general arrangement. **B**, transverse section through the mantle wall. **cmu**, circular muscles; **cti**, connective tissue containing nerves and blood vessels; **esk**, external skin; **etu**, external tunic; **isk**, inner skin; **itu**, internal tunic; **mul**, muscle layer; **rmu**, radial muscle fibres. (After Ward & Wainwright 1972) [C. Eadie]

stream volume should be maximised, while efficient oxygen uptake requires a slower flow (Wells & O'Dor 1991). *Octopus* and *Sepia* have optimised on oxygen extraction (Wells & Wells 1991), whereas the squids generally are specialised for jet propulsion. The latter may be the most spectacular way of locomotion in cephalopods, but it is not the only one. Many species have additional means of locomotion. Decapods and cirrate octopods use the fins for swimming, octopuses crawl, and several other groups have become neutrally buoyant and drift. There is no doubt that fish swim better and, more importantly, at lower energetic cost than jetting cephalopods (O'Dor & Webber 1986; Wells & O'Dor 1991), but cephalopods are nevertheless very effective swimmers.

Many families of oceanic squids have reverted to low energy lifestyles. Some hover effortlessly in mid-water, by using methods which have distinct advantages over the partial-vacuum, heavy,

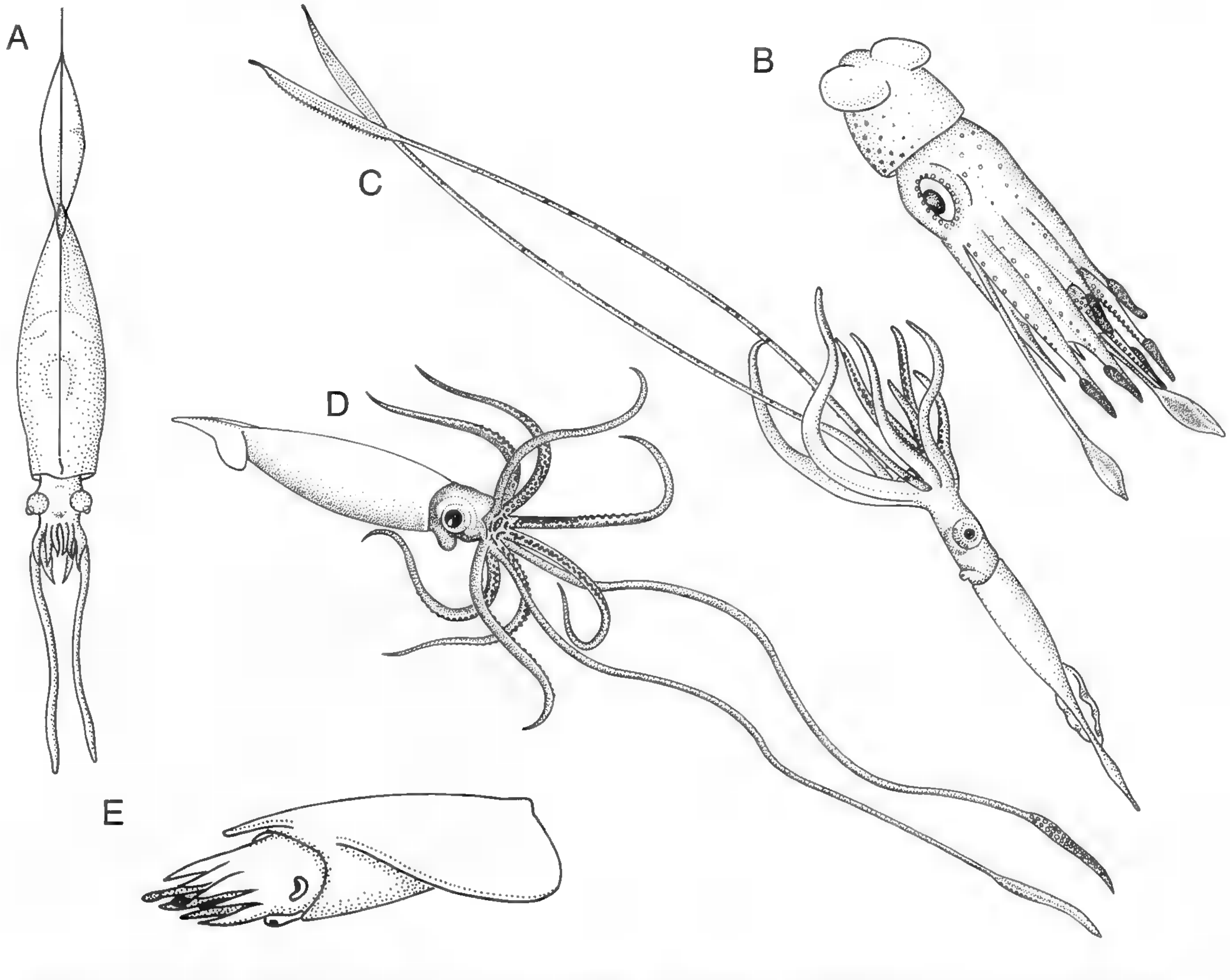

Figure 11.9 Body shapes of neutrally buoyant squids. **A**, *Taonius* sp. (Cranchiidae). **B**, *Histioteuthis* sp. (Histioteuthidae). **C**, *Chiroteuthis* sp. (Chiroteuthidae). **D**, *Architeuthis* sp. (Architeuthidae). **E**, *Taningia* sp. (Octopoteuthidae). (After original by M.R. Clarke) [C. Eadie]

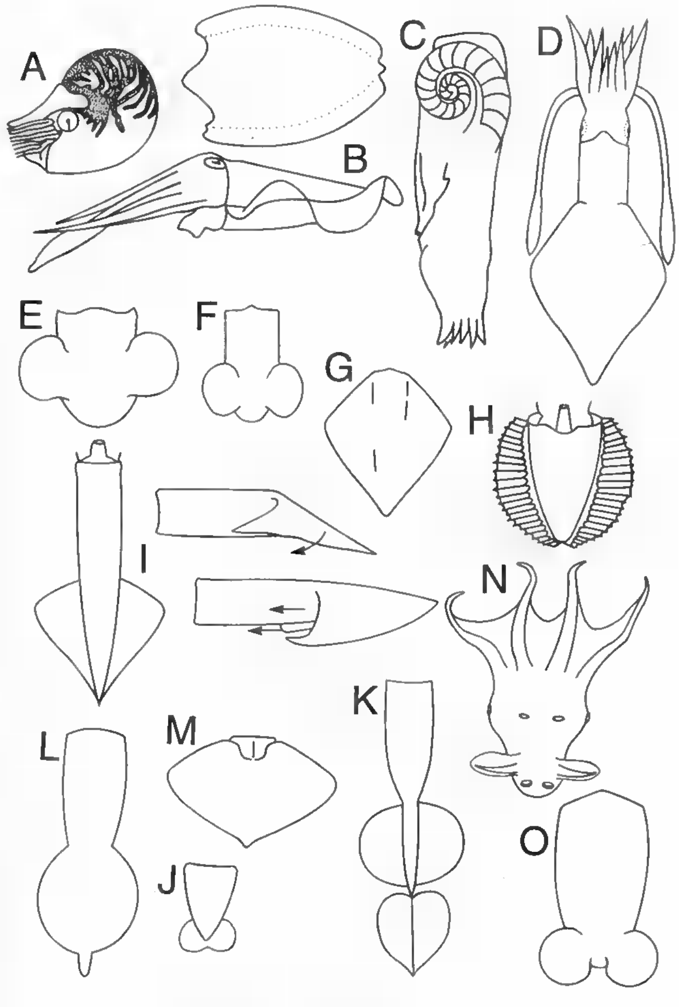

Figure 11.10 Body shapes and fin types in cephalopod genera. **A**, *Nautilus*. **B**, *Sepia*. **C**, *Spirula*. **D**, *Loligo*. **E**, *Sepiola*. **F**, *Pickfordiateuthis*. **G**, *Thysanoteuthis*. **H**, *Ctenopteryx*. **I**, *Ommastrephes*, showing actions to move backward and forward and to produce secondary jet over body. **J**, *Histioteuthis*. **K**, *Grimalditeuthis*. **L**, *Lepidoteuthis*. **M**, *Octopoteuthis*. **N**, *Vampyroteuthis*. **O**, *Bathyteuthis*. (After Clarke 1988) [C. Eadie]

calcareous shell. The Bathyteuthidae and the Gonatidae, widely spread throughout the higher latitudes, achieve neutral buoyancy by producing oil which is stored in their digestive glands. In a further 12 families, ammonium ions converted from nitrogenous waste are used to displace heavier metallic ions in the body fluids, making the squids neutrally buoyant (Clarke, Denton & Gilpin-Brown 1979; Voight, Portner & O'Dor 1994). This mechanism is used in two ways. In the Cranchiidae, all the low density fluid is held in a voluminous coelom, sometimes so large as to make the animal spherical (Pl. 18.10; Clarke 1962). In other ammoniacal families, the low density ions are stored in vacuoles in the tissues of the head, arms and mantle. Respiration in these neutrally buoyant groups has been uncoupled from their locomotion, and the fins provide their main method of propulsion. The body no longer has to be streamlined and the diversity of shapes ranges from excessively elongate to nearly spherical (Fig. 11.9; Pls 18.10, 18.12). Jetting is required only for occasional escape reactions or rapid manoeuvring, the normal, slow gill aeration is by weak mantle pulses.

The fins of all cephalopods, other than incirrate octopods, vary in size and shape (Fig. 11.10). By undulating its narrow, fringe-like fins along the mantle, a cuttlefish can manoeuvre forward, backward or rotate on its axis, although funnel jets assist in these movements. The fins of teuthoids, such as loliginids and ommastrephids, give stability during the glide after each powerful jet pulse. Gentle swimming to and fro is achieved by fin movements coupled with alternate backward and forward direction of the funnel (Pl. 18.6). The fins of many squids can give additional lift, allowing the animals to hover motionless (Zuev 1966; see also Mangold & Bidder 1989a for a review). The benthic sepiolids have large fins used for subtle manoeuvring and stabilisation. In non-actively swimming coleoids, such as the cirrate octopods, the mantle musculature is reduced and saturated with a jelly-like substance. These animals move by opening and closing the deep web which connects the arms like an umbrella, in the way that a jellyfish pulsates (Roper & Brundage 1972; Aldred, Nixon & Young 1983; Vecchione & Roper 1992). The fins act as rudder and stabilisers. *Vampyroteuthis* swims by strong fin movements. The members of the family Octopodidae, although perfectly able to swim by jet propulsion (Pl. 19.3), most often move by crawling over the bottom using their arms and suckers (Pls 19.2, 19.4).

The development of various buoyancy methods has enabled coleoid cephalopods to inhabit every part of the ocean, including its greatest depths. As a result, a huge volume of living space is available to cephalopods, since 76% of the area of the ocean includes depths of 3000–6000 m.

As in all molluscs, the mantle epithelium of cephalopods secretes the shell, and the pallial or mantle fold delimits the pallial cavities. The dorsal part of the mantle cavity is small, and the spacious ventral part forms a protective housing for the organs of the mantle cavity. In *Nautilus*, with its external shell, the fine mantle lines the living chamber and takes no part in locomotion (Fig. 11.11A). The coleoid mantle is external, and encloses the shell when present, the viscera and the mantle cavity organs. It is the major locomotive organ for jet swimming. The mantle cavity complex is illustrated in Figure 11.11B. In decapod cephalopods the dorsal mantle space has no connection with the ventral cavity, but in octopods with their shell vestige, the two cavities communicate. The muscular connections between head, funnel and mantle are shown also in Figure 11.11B, C. The pallial adductor muscle is present in octopods only. The organs of the mantle cavity are shown in Figure 11.11D, E. Further information on the mantle and mantle cavity will be given in the section on respiration.

Body Cavities

The coelomic cavities of the Cephalopoda are more spacious than those of all other molluscs. They comprise renal, pericardial and genital cavities. The four renal sacs are ventral coelomic cavities in *Nautilus*, each opening to the mantle cavity and enclosing one renal appendage. The dorsal pericardial appendages project into four coelomic areas that connect with each other and with the central pericardial coelom. In turn, the latter communicates with the widespread gonocoel through paired openings in the genital septum.

The sepioids and teuthoids have a large, perivisceral coelom that encloses gonad, systemic heart, branchial hearts and a large part of the stomach. The sepioids have two ventral renal sacs, and a spacious dorsal renal sac not present in teuthoids. In cranchiid squids, the coelom is enlarged and filled with ammonia to provide neutral buoyancy. In *Vampyroteuthis*, there is no separation between gonocoel and pericardial coelom. The coelom of adult octopods is small, consisting of a restricted genital cavity with its gonoducts and two aquiferous ducts which enclose the pericardial glands, but not the branchial hearts (Fig. 11.12).

Feeding and Digestion

Generally cephalopods are voracious predators on live, often large prey. Their own speed, mobility and acute visual system, together with their arms and tentacles equipped with efficient suckers and hooks, allow them to catch swift prey such as fishes, crustaceans, and other cephalopods, as well as less mobile animals such as gastropods and bivalves. Decapod cephalopods generally have several hundred suckers and/or sharply pointed hooks arranged along the clubs of the two long tentacles and the eight shorter arms. Octopods have only arms which bear suckers. Hooks are obviously very efficient organs for catching and holding prey, and the suckers have enormous adhesive power (Nixon & Dilly 1977).

In *Sepia*, and many other decapods, the tentacles are shot forward to catch the prey. This spectacular attack action occurs in three phases: attention, positioning and seizure (Messenger 1968), and is widespread among sepioids and loliginids, and oegopsids may also catch their prey with the arms. In some oegopsids, such as *Mastigoteuthis*, the tentacles are used like long sucker-covered fishing lines. Benthic octopods may pounce on their prey, the attack being initiated visually. They may also make speculative attacks on rocks likely to have a crab underneath, or they wait until prey comes into contact with an arm, when touch provides the important stimulus to prey capture. Octopods have a web between their arms with which they envelop crabs, one of their favoured prey. Touch is also important in the cirrate octopods and in *Vampyroteuthis*, in which both suckers and cirri detect prey (Aldred *et al.* 1983; Villanueva & Guerra 1991). *Nautilus* hunts by smell and touch, a group of tentacles outspread to form a 'cone of search' (Bidder 1962); the prey, live or dead, are caught by the many adhesive tentacles. The different modes of approach to prey and their capture have been described by Nixon (1987, 1988b).

The arms bring the captured prey to the mouth where it is killed by a bite from the large chitinous jaws, or beak (see Fig. 11.25), powered by strong muscles (Boyle, Mangold & Frösch 1979), or prey are first paralysed. Immobilisation of prey is not a prerequisite for its ingestion, but it is a real advantage when the prey is large or very active. Incirrate octopods and *Sepia* species

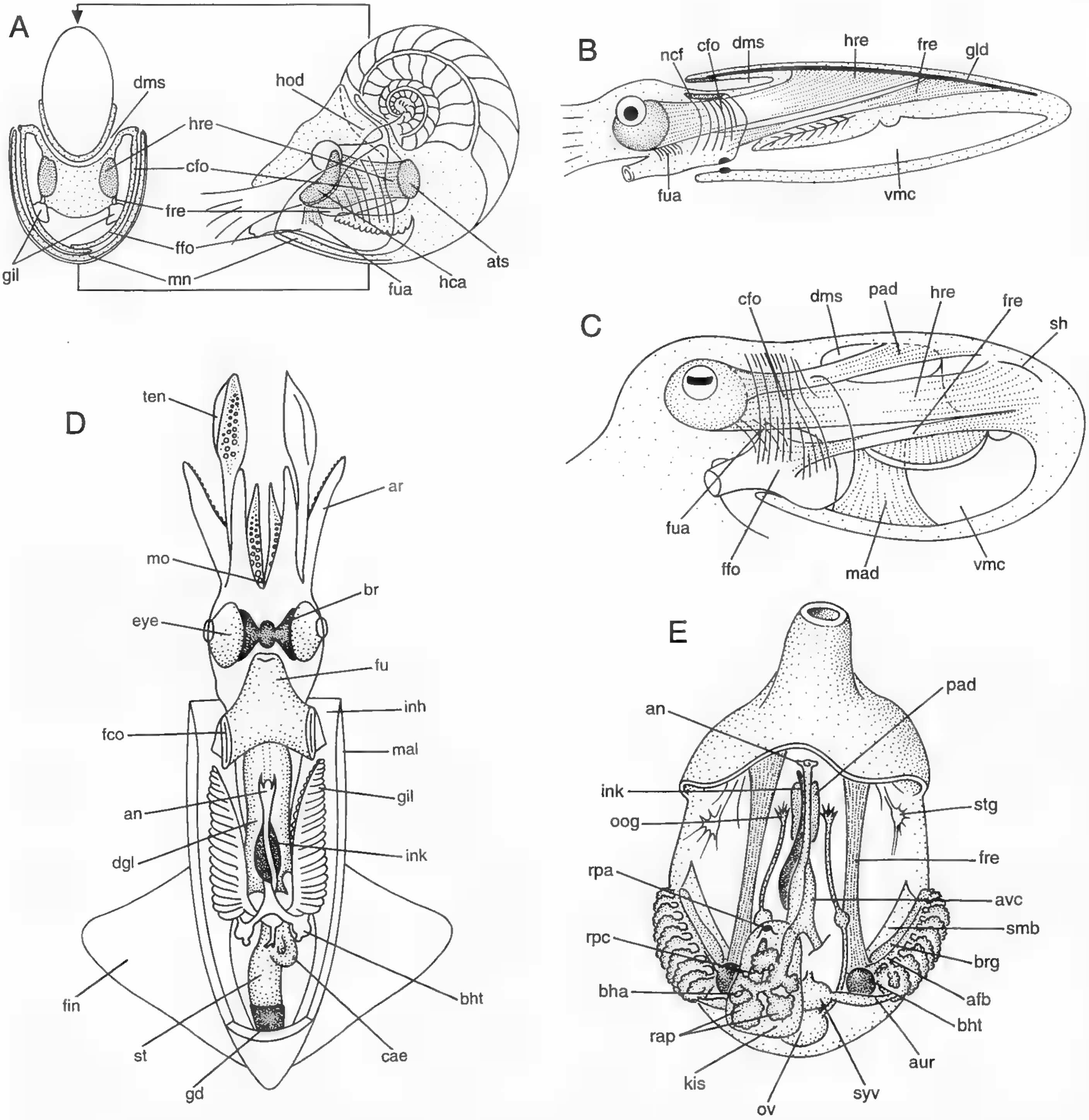

Figure 11.11 A–C, cephalopod mantle cavities, associated muscles and organs: A, *Nautilus* (Nautilidae); **B**, squid; C, octopus. **D**, **E**, organs of the mantle cavity: **D**, squid; **E**, octopus. **afb**, afferent branchial vessel; **an**, anus; **ar**, arm; **ats**, attachment to shell; **aur**, auricle; **avc**, anterior vena cava; **bha**, branchial heart appendage; **bht**, branchial heart; **br**, brain; **brg**, branchial gland; **cae**, caecum; **cfo**, collar fold; **dgl**, digestive gland; **dms**, dorsal mantle space; **eye**, eye; **fco**, funnel connective; **ffo**, funnel fold; **fin**, fin; **fre**, funnel retractor; **fu**, funnel; **fua**, funnel adductors; **gd**, gonad; **gil**, gill; **gld**, gladius; **hca**, head cartilage; **hod**, hood; **hre**, head retractor; **ink**, ink sac; **inh**, inhalant opening; **kis**, kidney sac; **mad**, median pallial adductor; **mal**, cut mantle; **mn**, mantle; **mo**, mouth; **ncf**, nuchal cartilage; **oog**, opening of oviduct; **ov**, ovary; **pad**, pallial adductor; **rap**, renal appendages; **rpa**, renal papilla; **rpc**, renopericardial canal; **sh**, vestiges of shell; **smb**, suspensory membrane; **st**, stomach; **stg**, stellate ganglion; **syv**, systemic ventricle; **ten**, tentacle; **vmc**, ventral mantle cavity. (A–C, E, after Wells 1988; D, after original by M.R. Clarke) [C. Eadie]

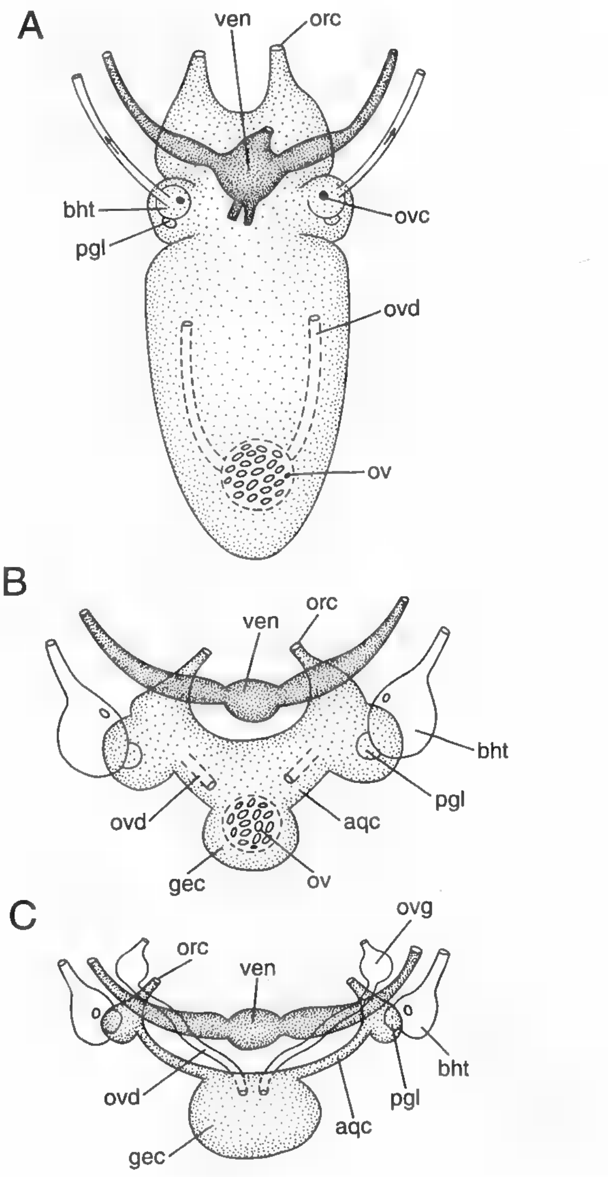

Figure 11.12 Coelomic cavities. **A**, decapod cephalopod. **B**, young octopus. **C**, adult octopus. **aqc**, 'aquiferous' canals; **bht**, branchial heart; **gec**, genital cavity; **orc**, opening of the renopericardial canal; **ov**, ovary; **ovc**, opening of the vena cava into the branchial heart; **ovd**, oviduct; **ovg**, oviducal gland; **pgl**, pericardial gland; **ven**, ventricle. (After Mangold, Bidder & Portmann 1989) [C. Eadie]

poison their prey before cutting them to pieces. The venoms which contain biologically active amines, enzymes and a variety of toxins are delivered by the posterior salivary glands (Koueta & Boucaud-Camou 1986). *Sepia* species bite the prey to inject the poison. Octopuses that feed on crabs pour the poison over the prey often without a detectable wound, but when feeding on molluscs often the venom is introduced through a drilled hole (Nixon & Maconnachie 1988). Squids kill fishes by severing the spinal cord; crustaceans are cut into pieces (Bidder 1950). As far as is known squids do not produce toxic secretions.

Several organs are involved in food intake. They all lie within, or are associated with, the buccal mass (Fig. 11.13). Besides the beak, there is the radula, the tooth-covered, lateral or palatal lobes which push the food toward the oesophagus, the salivary papillae used in drilling holes, and several salivary glands which discharge their secretion into the buccal cavity. These buccal organs are not equally well developed in all cephalopods, and some may even be lacking. Their presence or absence determines the way a species deals with its prey (Young, J.Z. 1977b). Moreover, organs may be used in a different way depending on the kind of prey eaten (Boucher-Rodoni, Boucaud-Camou & Mangold 1987; Nixon 1987, 1988a, 1988b).

The arrangement of the digestive organs in each of the four coleoid orders is shown in Figure 11.14. *Octopus* and all other coastal members of the subfamily Octopodinae have a well-developed crop (Fig. 11.14A) and a long, differentiated intestine, as does *Nautilus*. Sepioids and teuthoids have no crop and have a short, tubular intestine, especially so in squids (Fig. 11.14C, E). These differences primarily reflect different ways of life and feeding. *Octopus* species feed on the bottom, as do *Nautilus*. Species in both genera can eat an enormous amount of food when it is available, and are able to survive prolonged fasting periods. Waste is stored in the intestine and is periodically ejected in strings. Squids feed in open water and usually eat smaller, frequent meals to fuel their high metabolism, and waste is ejected almost constantly. The crop functions as a storage organ. While the first instalment of food passes to the stomach, a freshly ingested meal can remain in the crop for later digestion. In addition to venom, *Octopus* species inject proteolytic enzymes and chitinases produced by the posterior salivary glands into their crustacean prey. The partially digested flesh is removed cleanly and completely from the exoskeleton (Nixon 1984; Grisley & Boyle 1990). This loosening of muscle tissues is not strictly external digestion. *Sepia* species also have proteolytic enzymes in the posterior salivary glands (Koueta & Boucaud-Camou 1986) and no external digestion occurs.

Food from the buccal cavity passes by peristalsis down a straight oesophagus to the stomach. The oesophagus is lined with a cuticle, except in *Nautilus*. In the muscular stomach, also lined with cuticle, food is broken down mechanically and also by enzymes delivered by the digestive gland and, probably, by the posterior salivary glands. Then it passes into the spiral-shaped caecum, a thin-walled, delicate structure with close-set leaflets filling most of the lumen, where digestion *sensu stricto* occurs and where absorption of the nutrients begins. Large indigestible particles are evacuated into the intestine via the vestibule by the action of the ciliated epithelium lining the caecum and intestine. In the loliginids and some oegopsid families, the spiral part of the

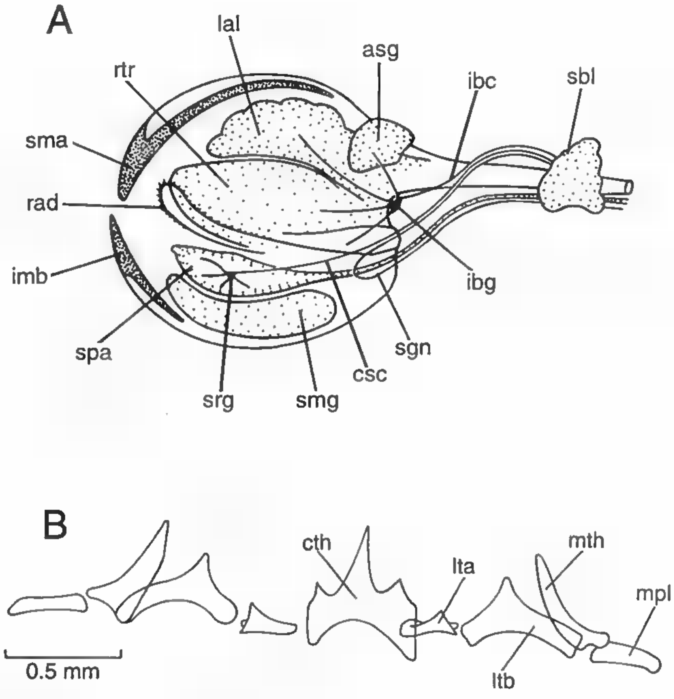

Figure 11.13 The buccal mass of *Octopus vulgaris* (Octopodidae). A, component organs. B, radular teeth. **asg**, anterior salivary gland; **csc**, cerebro-subradular connective; **cth**, central tooth; **ibc**, interbuccal connective; **ibg**, inferior buccal ganglion; **imb**, lower mandible; **lal**, lateral lobe; **lta**, first lateral tooth; **ltb**, second lateral tooth; **mpl**, marginal plate; **mth**, marginal tooth; **rad**, radula; **rtr**, retractor of the radula; **sbl**, superior buccal lobe; **sgn**, nerve of the posterior salivary gland; **sma**, upper mandible; **smg**, submandibular gland; **spa**, salivary papilla; **srg**, subradular ganglion. (A, after Boyle *et al.* 1979; B, after Nixon 1988a) [C. Eadie]

caecum is relatively small, but a simple, large caecal sac is present as well (Fig. 11.14C). Sphincters enable isolation of the stomach and the caecum from the digestive tract. A duct runs into the caecum from the digestive gland, and a digestive groove from its opening runs into the stomach so that material from both the stomach and the caecum can be passed independently to and from the digestive gland (Bidder 1950, 1957, 1966).

The midgut gland generally consists of two parts, the digestive gland or liver, and the appendages of the digestive gland ducts or pancreas (Bidder 1976). The digestive gland is paired in origin and its two ducts pass on each side of the proximal intestine before they merge to enter the caecum (Fig. 11.14); in *Nautilus*, however, the digestive gland comprises three to five lobes. The digestive gland delivers enzymes, and probably is a site of absorption in all cephalopods, including *Loligo* (Boucher-Rodoni & Boucaud-Camou 1987) in which absorption was previously thought to occur in the caecum and intestine only (Bidder 1966). It is also a storage organ. The main digestive cells, or 'boules' cells, contain large proteinaceous inclusions that release proteolytic enzymes by their fragmentation and exocytosis. Carbohydrate-digesting enzymes are probably also produced by the digestive gland and by the caecum. Food particles conducted from the caecum to the digestive glands are absorbed into the digestive cells by endocytosis and digested in large, heterogenous 'boules', the heterolysosomes (Boucaud-Camou & Yim 1980). The residues of intracellular digestion collect in crystalline masses or 'brown bodies' (Bidder 1957) of the digestive cells. These cells expel their contents into the tubules of the gland, the largest of which open into conspicuous lumina that open into the digestive ducts. The digestive duct appendages are enclosed in the digestive gland and covered by the gland's sheath in the octopods, or they lie along the digestive ducts as in sepioids and teuthoids (Fig. 11.14). These organs are absent in *Nautilus*.

The complex digestive processes appear to be under nervous control and/or are regulated by the presence of freshly caught food in the crop or fluid from partly digested food in the lumina of the digestive gland. There is no evidence of hormonal control of digestive processes (Wells & Wells 1990).

The appendages of the digestive ducts are associated with absorption of food, excretion and perhaps most importantly, with water uptake and ion balance (Wells & Wells 1989). Cephalopods swallow water, which enters the intestine. For a review and a summary on feeding and digestion, see Boucaud-Camou & Boucher-Rodoni (1983), and Mangold & Bidder (1989b), respectively.

Digestion is rapid and efficient. Though cephalopods can deal with more than one meal or with a very large meal at one time, the system has its limits. For example, the fluid containing proteolytic enzymes that comes from the digestive gland and the nutrient suspension that goes up to the gland obviously cannot pass simultaneously. Since the ducts merge before entering the caecum, a new enzyme discharge has to wait until the liquid from the caecum has passed to the digestive gland (Boucaud-Camau, Boucher-Rodoni & Mangold 1976).

The metabolism of cephalopods is essentially proteinic. Their bodies are composed primarily of protein and water, and they eat protein. They are not well equipped to cope with carbohydrates and deal very poorly with lipids. A lipid-rich diet passes almost unaffected through the gut (O'Dor, Mangold, Boucher-Rodoni, Wells & Wells 1984). Food conversion is highly efficient. In some cephalopods (*Octopus* species) up to 50% of the food eaten can be converted to body tissue. An octopus is a very energy efficient animal, which eats only two and a half times its own final body weight during its life. However, actively swimming squids need several times this amount, and they eat about 3–15% of their body weight each day (O'Dor & Wells 1987).

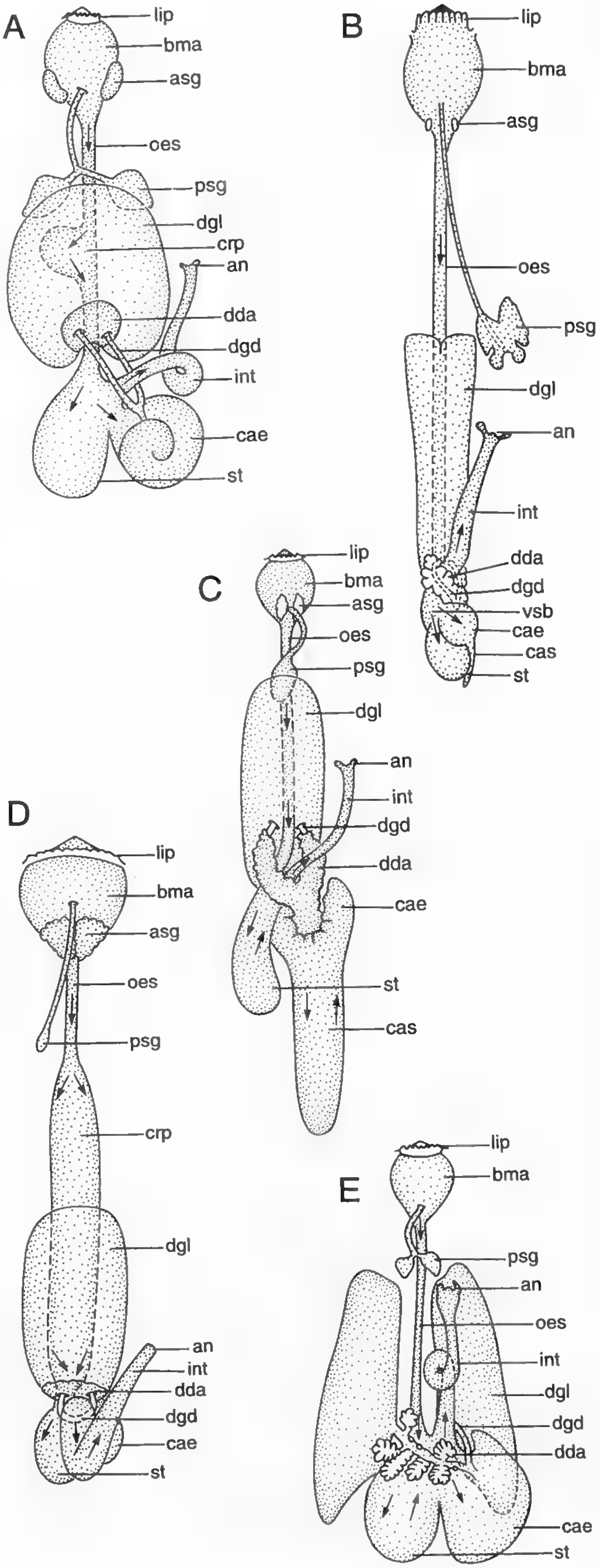

Figure 11.14 Coleoid digestive tracts, ventral views. **A**, *Octopus vulgaris* (Octopoda). **B**, the oegopsid *Abralia trigonura* (Teuthoidea). **C**, the myopsid *Loligo vulgaris* (Teuthoidea). **D**, *Vampyroteuthis infernalis* (Vampyromorpha). **E**, *Sepia officinalis* (Sepioidea). **an**, anus; **asg**, anterior salivary gland; **bma**, buccal mass; **cae**, caecum; **cas**, caecal sac; **crp**, crop; **dda**, digestive duct appendages; **dgd**, digestive gland duct; **dgl**, digestive gland; **int**, intestine; **lip**, lip; **oes**, oesophagus; **psg**, posterior salivary gland; **st**, stomach; **vsb**, vestibule. (A, C, E, after Bidder 1966; B, D, after Mangold & Young in press) [C. Eadie]

Circulation

In the primitive open blood system of lower molluscs, the blood returns gently from the arterial system to the heart through large haemocoelic spaces. In cephalopods, the blood system is closed with capillaries and veins producing the more efficient circulation demanded by such an active locomotive system (Wells 1983). The circulatory system, especially that of coleoids, is in many respects similar to that of vertebrates (Schipp 1987a).

The layout of the arterial system is basically similar in all groups (Fig. 11.15). Oxygenated blood from the gills (two pairs in *Nautilus*, one pair in coleoids), passes through the efferent branchial vessel and enters the systemic heart which consists of a single, large, thick-walled ventricle and two auricles, except in *Nautilus* species, which have four auricles. The blood is expelled from the ventricle through three aortas. The dorsal or cephalic aorta carries blood to the head and has branches to the anterior part of the gut. The posterior, minor or abdominal aorta supplies the mantle and fins, the posterior part of the gut and the funnel, and is the largest of the three in the actively swimming squids. The gonadal aorta is small until the onset of maturity, when it enlarges markedly to supply the developing gonads. Semilunar valves occur between the auricles and the ventricle and at the exit of the cephalic and abdominal aortas, but are absent at the exit of the branchial hearts. The cephalic aorta leaves the ventricle on the right or left side of coleoids and *Nautilus*, respectively.

The venous system, on the other hand, is variable in arrangement, having maximum restriction in the more active squids (Fig. 11.16). In *Nautilus*, there are more and larger haemocoelic spaces. These include the single buccal and paired ophthalmic

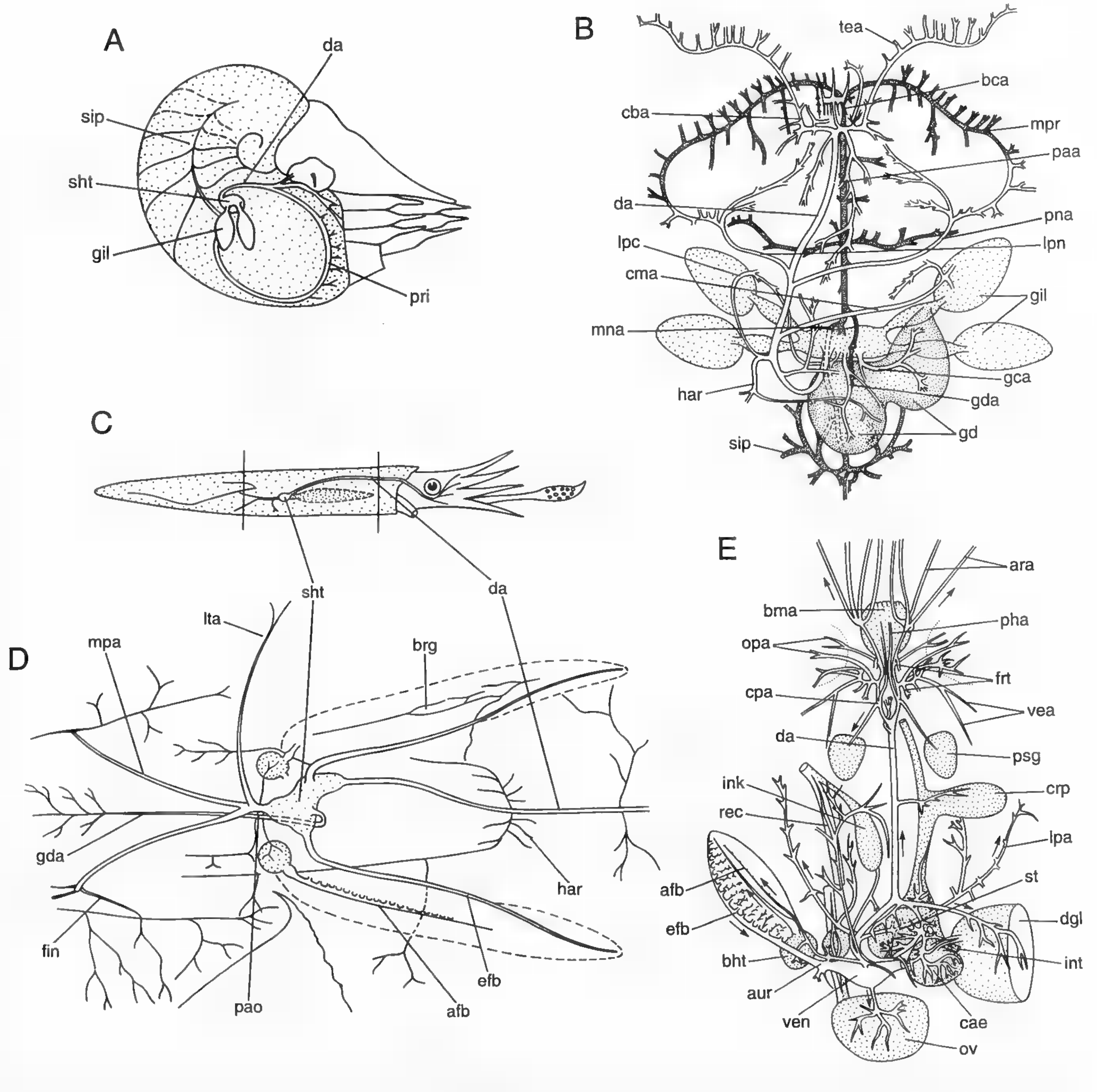

Figure 11.15 Cephalopod arterial systems. **A**, **B**, *Nautilus* species (Nautilidae). **C**, **D**, *Loligo* species (Loliginidae). **E**, *Eledone* species (Octopodidae). **afb**, afferent branchial vessel; **ara**, arm arteries; **aur**, auricle; **bca**, buccal artery; **bht**, branchial heart; **bma**, buccal mass; **brg**, branchial gland; **cae**, caecum; **cba**, cerebral artery; **cma**, right posterior columellar artery; **cpa**, cephalic artery; **crp**, crop; **da**, dorsal aorta; **dgl**, digestive gland; **efb**, efferent branchial vessel; **fin**, fin artery; **frt**, funnel arteries; **gca**, gonoductal artery; **gd**, gonad and ducts; **gda**, gonadal artery; **gil**, gill; **har**, hepatic artery; **ink**, ink sac; **int**, intestine; **lpa**, left pallial artery; **lpc**, left posterior columellar artery; **lpn**, left pallio-nuchal artery; **lta**, lateral pallial artery; **mna**, minor aorta; **mpa**, median pallial artery; **mpr**, marginal pallial artery; **opa**, optic artery; **ov**, ovary; **paa**, pallial artery; **pao**, posterior aorta; **pha**, pharyngeal artery; **pna**, right pallio-nuchal artery; **pri**, pallial ring; **psg**, posterior salivary gland; **rec**, rectum; **sht**, systemic heart; **sip**, siphuncular artery; **st**, stomach; **tea**, tentacular artery; **vea**, visceral envelope artery; **ven**, ventricle. (After Wells 1983) [C. Eadie]

sinuses, a cerebral sinus, a sinus related to the male's spadix, sinuses around the base of the tentacles and a peri-oesophageal-mesenteric sinus surrounding the crop. Incirrate octopods also have a series of sinuses through which the blood is collected. The primary vessel in all cephalopods is the cephalic vein or anterior vena cava which collects blood from the arms and tentacles, the head and the anterior viscera, and splits into two venae cavae (four in *Nautilus*). These pass through the kidney sacs and enter the branchial hearts (absent in *Nautilus*). The branchial hearts are muscular structures that pump the deoxygenated blood through the afferent branchial vessels and the capillaries of the gills where the blood is oxygenated. In *Nautilus*, blood is driven through the gills by contraction of the renal sacs and the pericardial glands (Bourne, Redmond & Johansen 1977, 1978).

As cephalopods are generally active animals with an almost entirely aerobic metabolism, the major task of the circulatory system is to deliver oxygen. The blood sinuses, which in molluscan ancestors also functioned as a static hydroskeleton, are much reduced and are replaced functionally by muscles working against other muscles. The circulatory system thus has to work against the considerable peripheral, muscle-induced pressure, which increases with increasing activity and attains its maximum during jet swimming. It also has to overcome the resistance of the small diameter of the exchange vessels that close the circuit of the system. An additional inherent problem is the very low oxygen carrying capacity of the blood. Despite all these limitations, cephalopods are able to deliver oxygen at a rate comparable with that of active fishes. The problem in achieving this is given by the very title of a review paper by Wells & Smith (1987): 'The performance of the *Octopus* circulatory system: a triumph of engineering over design'. It is achieved by modifications, such as the increased size of the hearts, the strikingly large myocardial diameter of the ventricle, accessory pumps, pulsatile veins, and controlled distribution of the blood to which large parts of the central and peripheral nervous system are dedicated. Furthermore, extensive neurosecretory systems, especially in the cephalic vein and in the pharyngo-ophthalmic veins, also control circulation (Martin & Voigt 1987).

The arterial system is highly differentiated in *Nautilus* and coleoids. The semilunar valves regulate blood flow into the cephalic and posterior aortas. These large resistance vessels, together with the adjoining peripheral vessels, arteries and arterioles, act as a 'Windkessel' or pressure regulator, as their walls are thick and elastic. They transfer the pulsating blood, with relatively high pressure values close to the heart, in a continuous laminar flow with lower pressure towards the periphery. Blood pressure, heart beat rate and cardiac output are lowest in *Nautilus* and highest in muscular squids, with various intermediate values in *Octopus* and *Sepia*. The exchange vessel system in the peripheral organs is an extensive blood sinus in *Nautilus*. Coleoids have true capillaries, with a few sinuses lacking an endothelium, especially in the head region (Schipp 1987b). Venous return is effected through the large propulsive veins and supported by autonomous contractility within the sinuses of peripheral organs, such as the gills, the renal and pericardial appendages and, in coleoids, the branchial hearts.

Unlike the vertebrate heart, the systemic heart of cephalopods responds to greater demand for oxygen during exercise by an increase in the stroke volume and increased pressure, rather than an increase in heart rate. This increase in volume of blood expelled by the ventricle at each beat may be three- or fourfold in *Octopus* species.

Haemocyanin is present in the transparent, viscous blood in a 9% solution. This copper-based respiratory pigment is synthesised in the branchial glands which lie below the gills. The only cells in the blood, the haemocytes (also called amoebocytes) may be phagocytic and comprise 1–2% by volume of the blood. These cells originate in the white bodies that lie in the orbit dorsal to the optic lobe. The oxygen carrying capacity of the blood is less than 4.5% by volume, which, although higher than in other molluscs, is

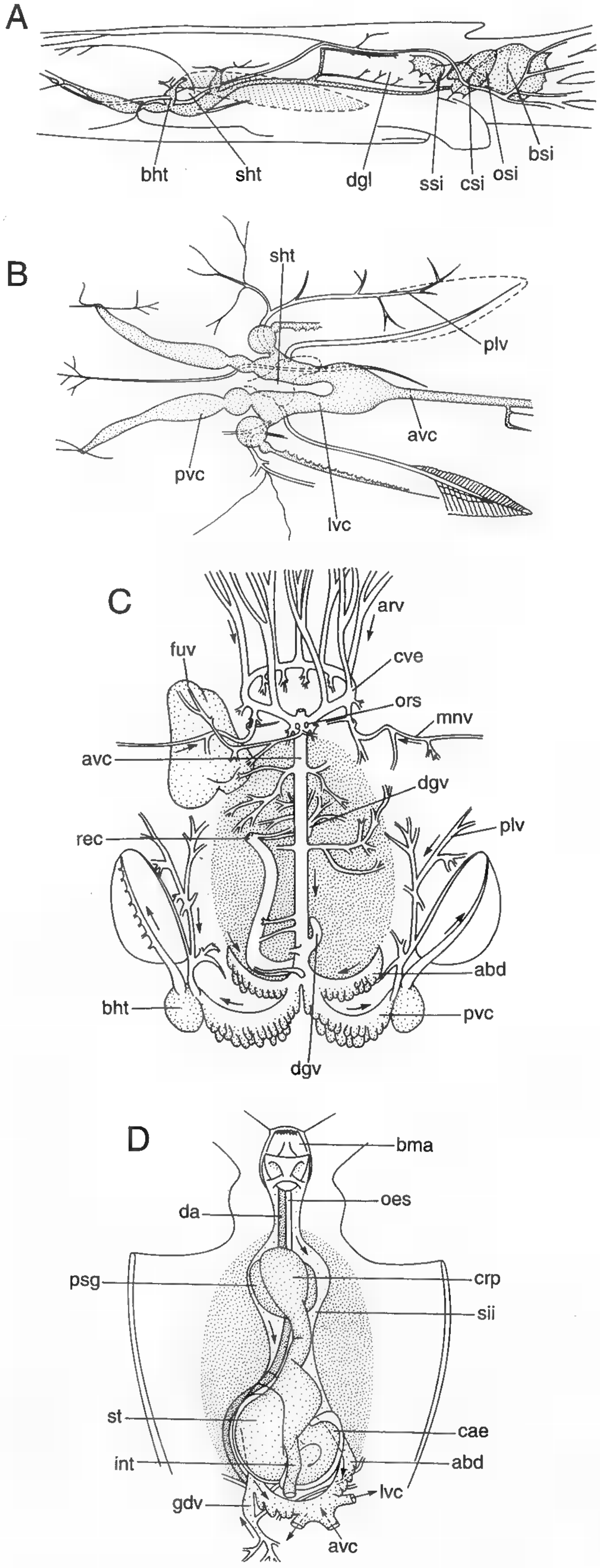

Figure 11.16 Cephalopod venous systems. A, B, *Loligo* species (Loliginidae). C, D, *Eledone* species (Octopodidae). **abd**, abdominal vein; **arv**, arm veins; **avc**, anterior vena cava; **bht**, branchial heart; **bma**, buccal mass; **bsi**, buccal sinus; **cae**, caecum; **crp**, crop; **csi**, cephalic sinus; **cve**, cephalic vein; **da**, dorsal aorta; **dgl**, digestive gland; **dgv**, digestive gland vein; **fuv**, funnel vein; **gdv**, gonadal vein; **int**, intestine; **lvc**, lateral vena cava; **mnv**, mantle vein; **oes**, oesophagus; **ors**, orbital sinus; **osi**, optic sinus; **plv**, pallial vein; **psg**, posterior salivary glands; **pvc**, posterior vena cava; **rec**, rectum; **sht**, systemic heart; **sii**, sinus around gut; **ssi**, salivary sinus; **st**, stomach. (After Wells 1983) [C. Eadie]

low when compared with vertebrates (10–15% in fishes). In coleoids, a very high proportion of the oxygen available at each circuit of the blood through the body is removed by the tissues. This fraction is as much as 93% in *Loligo* and 80% in *Octopus*, whereas in *Nautilus* it is only about 40%. The total blood volume circulates about once every two minutes in *Octopus*.

Excretion

The cephalopod excretory system differs radically from that of other molluscs, primarily by the enlargement of the renal, pericardial and gonadal part of the coelom, and the consequent obliteration of the haemocoel. Together with the closed circulatory system and an efficient branchial circulation, a new relationship between blood, urine and excretory epithelium has evolved. There are also important differences between *Nautilus* and coleoids and between the different coleoid taxa. Cephalopods are ammonotelic and their body fluids are virtually isosmotic with seawater.

In *Nautilus*, blood from the cephalic vein runs via four smaller veins to the four gills (Fig. 11.17A). Each of these veins contains a renal appendage, a sacculate organ into which blood flows and is expelled by each wave of contraction along the vessels. Each renal appendage is enclosed in a renal coelom which usually contains granules of calcium phosphate and opens to the mantle cavity via a nephridiopore. Possibly this acts as a store which is emptied periodically to form the calcified septa of the shell (Schipp & Martin 1981; Martin 1983).

The next structures along the veins are the pericardial glands which also contract regularly and are the equivalent of the branchial hearts of coleoids. The pericardial coelom, which encloses the pericardial glands and the heart, opens into the mantle cavity via pores at the base of the two outer gills. Filtrate from the blood is probably produced by the pericardial glands and is discharged into the pericardial coelom.

In coleoids an appendage, also called a pericardial gland (Fig. 11.17B), occurs on each branchial heart. The walls of this gland contain special cells called podocytes which are involved in the ultrafiltration of fluid from the blood (Schipp, Höhn & Schäfer 1971; Witmer & Martin 1973; Schipp & Hevert 1981). In decapod cephalopods, the filtrate spreads throughout the coelom and most of the organs then take part in resorption of glucose and amino acids. Most of the fluid is carried from the pericardial coelom to the renal sac through the renopericardial canals, which are fine, membranous, funnel-like structures. The fluid then bathes the renal appendages and the digestive gland ducts. The external surface of the latter is covered by the lobular appendages of the digestive ducts, which have a very vascular wall and complete the resorption of metabolites from the filtrate (Schipp & Boletzky 1975).

In octopods the coelom is reduced to a renal sac that encloses only the branchial heart appendages and the renal appendages (Fig. 11.17C). The digestive duct appendages do not filter blood, as this process is carried out entirely by the branchial heart appendages. The filtrate passes from the branchial heart appendage to the renopericardial canal where metabolites are resorbed into the vascular wall. The renal appendages are finely lobulated with thin walls that separate the blood from the filtrate in the renal sac. One of the functions of the renal appendages in coleoids is to acidify the urine in the renal sac which contains high concentrations of ammonium ions, thus ensuring their retention in solution and preventing their passage back into the blood.

The amount of ammonia produced in the renal appendages is only a small part of the total ammonia released into the surrounding seawater (Potts 1965). Ammonia is continuously released by the inner epithelial layer of the gills (Schipp, Mollenhauer & Boletzky 1979), which are in fact the main organs of ammonia excretion. Neutrally buoyant squids replace denser metallic ions by ammonium ions in the coelom and/or in the body tissues (Clarke *et al.* 1979). The cranchiids accumulate up to 40% of the excreted ammonia in the coelom over their life span (Denton, Gilpin-Brown & Shaw 1969). The cuttlefishes and species of *Nautilus*, all of which are buoyant, excrete considerably less ammonia than octopuses and non-buoyant squids (Boucher-Rodoni & Mangold 1994).

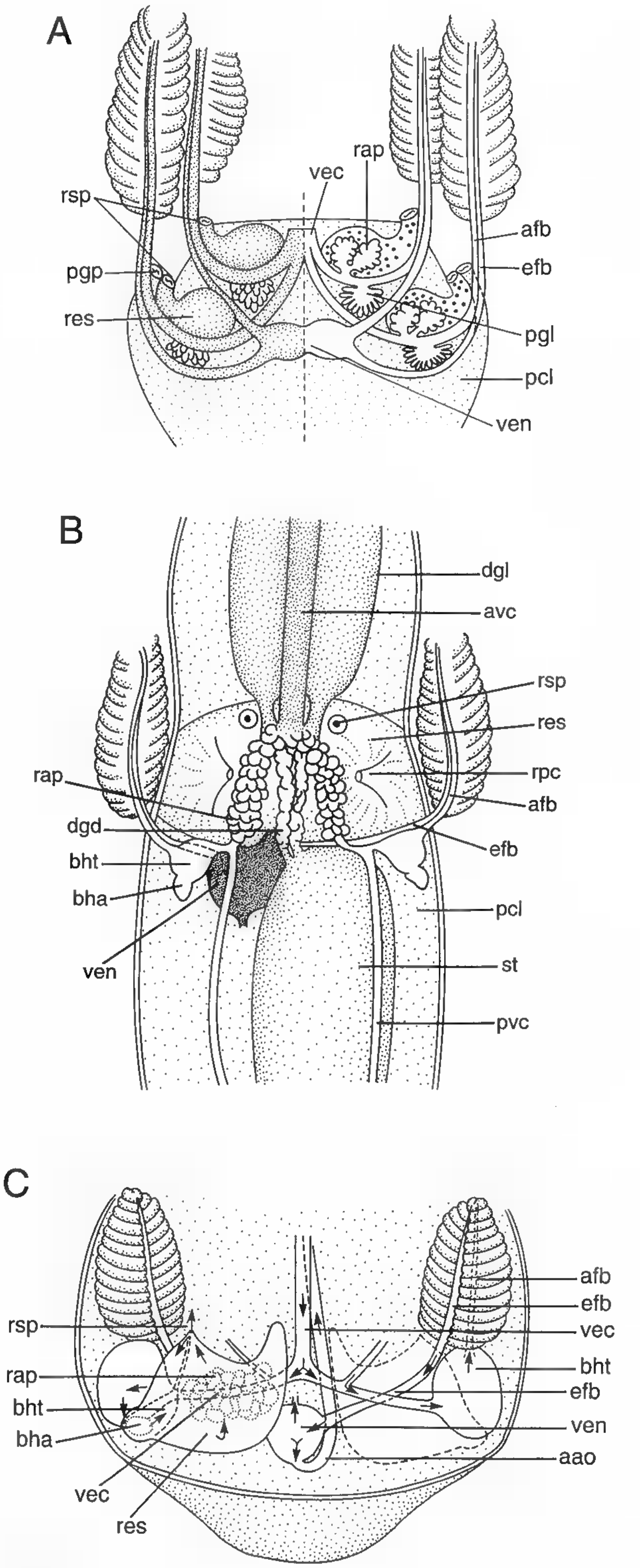

Figure 11.17 Cephalopod excretory systems. **A**, *Nautilus* (Nautilidae). **B**, squid. **C**, octopus. **aao**, anterior aorta; **afb**, afferent branchial vessels; **avc**, anterior vena cava; **bha**, branchial heart appendage; **bht**, branchial heart; **dgd**, digestive gland ducts; **dgl**, digestive gland; **efb**, efferent branchial vessels; **pcl**, pericardial coelom; **pgl**, pericardial gland; **pgp**, pericardial gland pore; **pvc**, posterior vena cava; **rap**, renal appendages; **res**, renal sac; **rpc**, renopericardial canal; **rsp**, renal sac pore; **st**, stomach; **vec**, vena cava; **ven**, ventricle. (After Martin 1983) [C. Eadie]

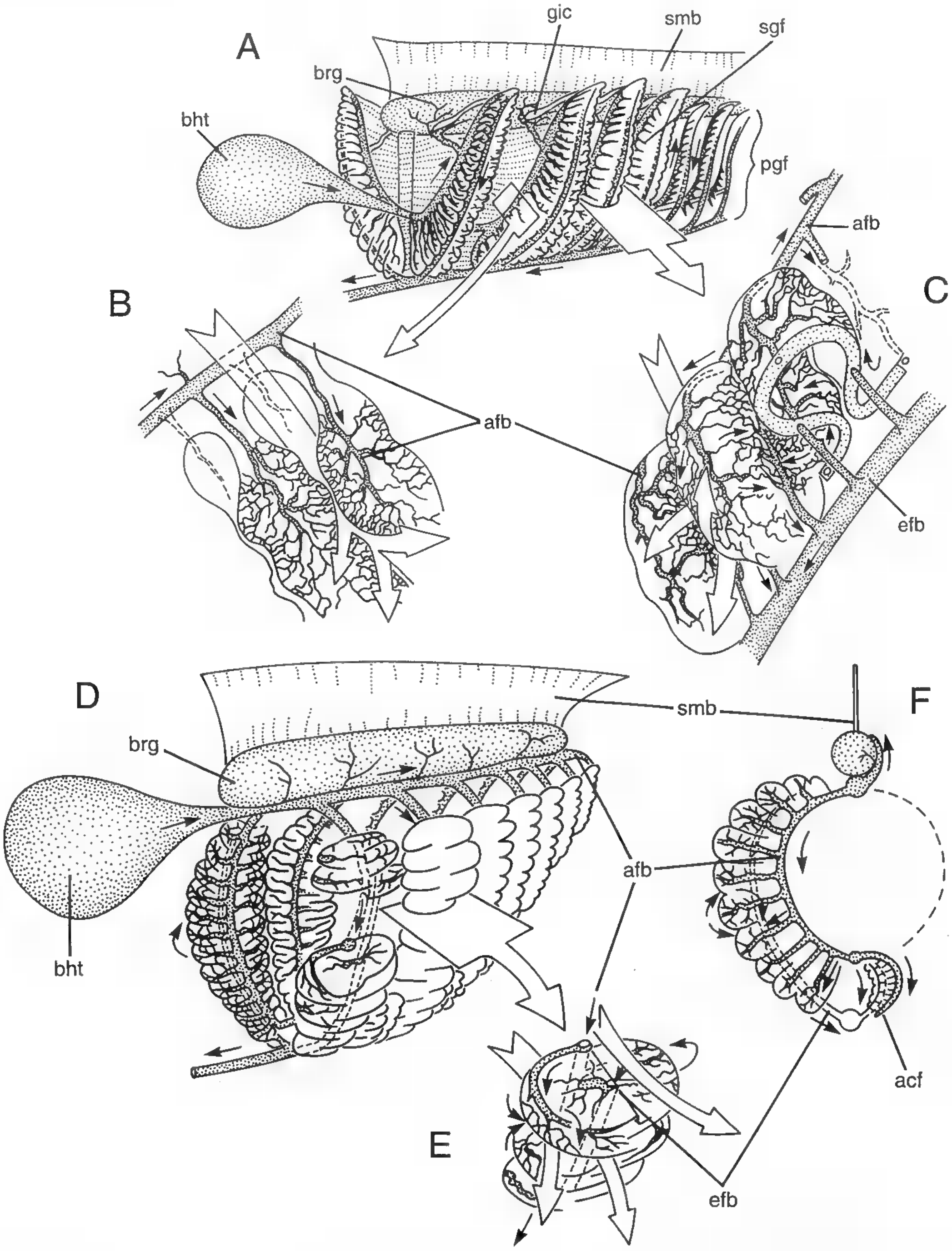

Figure 11.18 Cephalopod gill structure and ventilation. **A–C**, *Sepia* (Sepiidae). **D–F**, *Octopus* (Octopodidae). Black arrows indicate blood flow and white arrows the direction of the respiratory stream. **A**, **D**, blood flow through the gill. **B**, **E**, blood flow through the secondary folds of the respiratory filaments. **C**, **F**, water flow across the secondary folds of the respiratory filaments. **acf**, accessory filament; **afb**, afferent branchial vessels; **bht**, branchial heart; **brg**, branchial gland; **efb**, efferent branchial vessels; **gic**, gill cartilage; **pgf**, primary gill filament; sgf, secondary gill filament; **smb**, suspensory membrane. (After Wells 1983) [C. Eadie]

Respiration

In *Nautilus* with its external shell, the mantle lines the living chamber. The mantle cavity is restricted to the anterior part of the chamber and the viscera occupy the posterior part.

Nautilus has four gills, an outer and an inner pair, whereas coleoids have two gills which extract oxygen from the water drawn into the mantle cavity. The gills are orientated horizontally and divide the mantle cavity into two dorso-lateral prebranchial chambers and a ventral postbranchial chamber (Wells & Wells 1985; Wells 1987, 1988). Water is propelled by the two lobes that together form the equivalent of the coleoid funnel tube and collar. Rhythmic movements produce a continuous flow of water across the gills. The afferent blood vessels are on the dorsal or prebranchial side and the efferent ones are on the ventral or postbranchial side of the gills. The first impression of this arrangement suggests that the water and the blood run in the same direction, which would be inefficient for transport of oxygen between the two. However, by an arrangement of the second order pleats on the main gill lamellae, the blood runs obliquely against the direction of the ventilatory stream, so that uptake of oxygen is facilitated. During inactivity at 15°C the ventilation rate is about 34 ventilation cycles per minute, but when *Nautilus* is active, this can rise to 60 or more per minute at the same temperature. The increase in activity however is accompanied by a fall in the uptake of oxygen from 20% to less than 7%. *Nautilus* relies on anaerobic respiration during periods of high activity, in contrast to coleoids, and can survive for long periods in water of very low oxygen content (Wells, Wells & O'Dor 1992).

The muscular mantle in coleoids encloses the mantle cavity, which extends ventrally along the whole visceral complex. Water is drawn into the mantle cavity by relaxation of the circular muscles and contraction of the radial muscles of the mantle wall. This causes an increase in the area of the mantle surface and a consequent increase in the volume of the mantle cavity. The paired gills are asymmetrical in octopods and often reduced in size

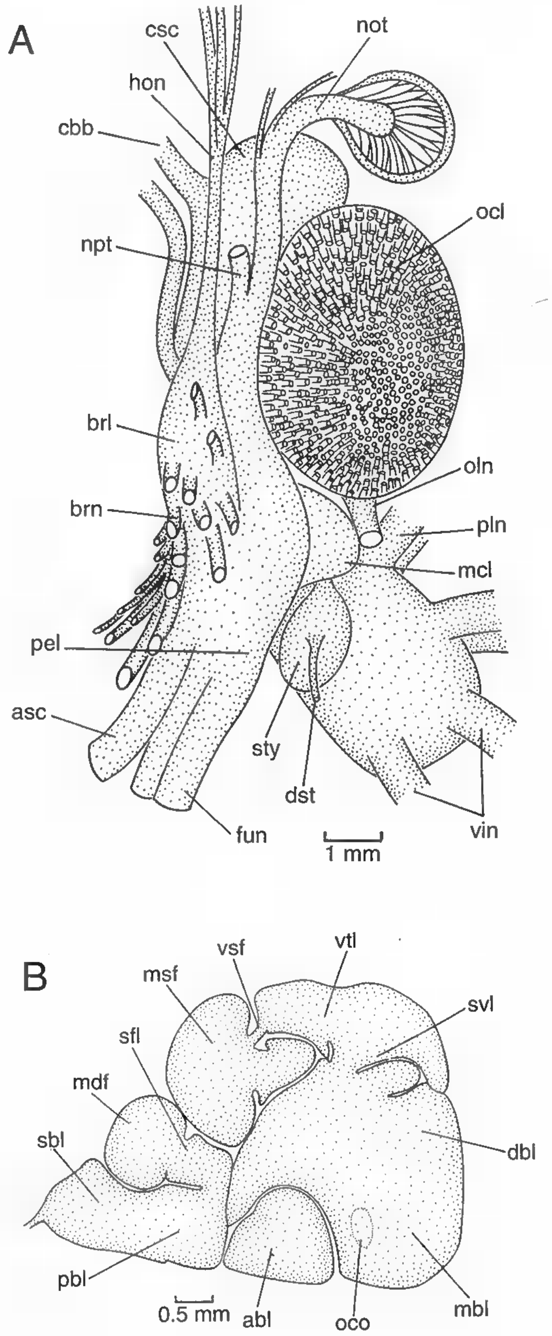

Figure 11.19 Cephalopod nervous structures. **A**, central nervous system of *Nautilus* (Nautilidae). **B**, supra-oesophageal part of the central nervous system of *Octopus vulgaris* (Octopodidae). **abl**, anterior basal lobe; **asc**, anterior suboesophageal commissure; **brl**, brachial lobe of anterior suboesophageal mass; **brn**, branchial nerve; **cbb**, cerebrobuccal connective; **csc**, cerebral (suboesophageal) cord; **dbl**, dorsal basal lobe; **dst**, duct of statocyst, or Köllikers lobe; **fun**, funnel nerve; **hon**, hood nerve; **mbl**, median basal lobe; **mcl**, magnocellular lobe; **mdf**, median inferior frontal lobe; **msf**, median superior frontal lobe; **not**, nerve of posterior ocular tentacle; **npt**, nerve of preocular tentacle; **ocl**, optic lobe; **oco**, optic commissure; **oln**, olfactory nerve; **pbl**, posterior buccal lobe; **pel**, pedal lobe; **pln**, pallial nerves; **sbl**, superior buccal lobe; **sfl**, subfrontal lobe; **sty**, statocyst; **svl**, subvertical lobe; **vin**, visceral nerves; **vsf**, vertical to superior frontal lobe tract; **vtl**, vertical lobe. (After Young, J.Z. 1988a) [C. Eadie]

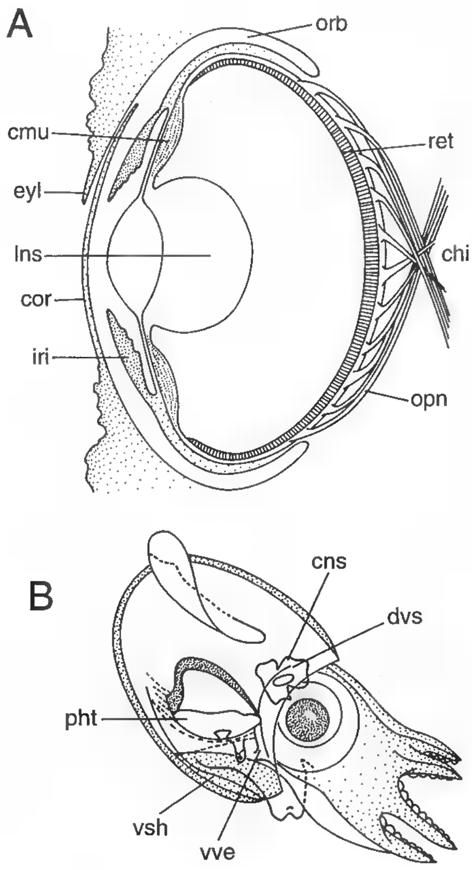

Figure 11.20 Cephalopod light receptors. **A**, eye of *Octopus* (Octopodidae) in longitudinal vertical section. **B**, photosensitive vesicles or extraocular photoreceptors in *Heteroteuthis hawaiiensis* (Sepiolidae). **chi**, chiasma; **cmu**, ciliary muscle; **cns**, central nervous system; **cor**, cornea; **dvs**, dorsal vesicles; **eyl**, eyelid; **iri**, iris; **lns**, lens; **opn**, optic nerves; **orb**, orbit; **pht**, photophore; **ret**, retina; **vsh**, ventral shield; **vve**, ventral vesicles. (A, after Wells 1966; B, after Young, R.E. 1977) [C. Eadie]

in deep sea species, and are symmetrical in decapod cephalopods. They lie between the mantle wall to which they are attached on one side, and the funnel retractor muscle on the medial side (Fig. 11.11B–E). The mantle cavity is thus divided into two parts, a dorso-lateral prebranchial chamber and a single postbranchial space. Because of this arrangement, the incoming water stream is passed between the primary and the secondary gill filaments. The arrangements of the capillaries in the secondary filaments ensures that the blood flows in a direction counter to the water flow and promotes a maximum exchange between the two liquids (Fig. 11.18). Flow across the gills is continuous in spite of the rhythmic ventilation cycle. Oxygen extraction at rest is about 60% in *Octopus* and *Sepia*. As the partial pressure of the water falls, the ventilation stroke volume and frequency both rise. The gill surfaces are not the only sites of oxygen uptake; cutaneous respiration also occurs (Madan personal communication). The morphology, morphometrics and some aspects of the physiology of the gills of some coleoid species are described in detail by Eno (1987, 1994).

Nervous System and Sense Organs

Cephalopods have a well-developed nervous system. It probably evolved from one resembling the polyplacophoran condition, in which the three main nerve cords are concentrated to form a brain organised into discrete lobes with specialised functions. However, peripheral nerve cells have also been retained which permit peripheral reflexes, especially in the brachial nerve cords of the arms. Indeed, the essence of the nervous organisation of cephalopods has been to maintain peripheral reflex systems but to superimpose a central nervous system which makes the decisions (Young, J.Z. 1988a).

There are fewer lobes (13) in the brain of *Nautilus* than in the coleoid brain. The ventral region of the cerebral cord (Fig. 11.19A) is concerned with feeding and connects with the buccal ganglion, and a dorsal region connects with the lateral visual and tactile systems. Laterally placed brachiopedal cords consist of an anterior brachial part with nerves to the digital, buccal and ocular tentacles and to the hood, and a posterior, pedal part innervating the funnel. The suboesophageal cord sends nerves to the pallial and visceral organs. The magnocellular lobes, to each side of the point of confluence of the three cords, contain the largest cells of the brain and are probably important motor lobes. The olfactory lobe and the olfactory organs are larger than in any

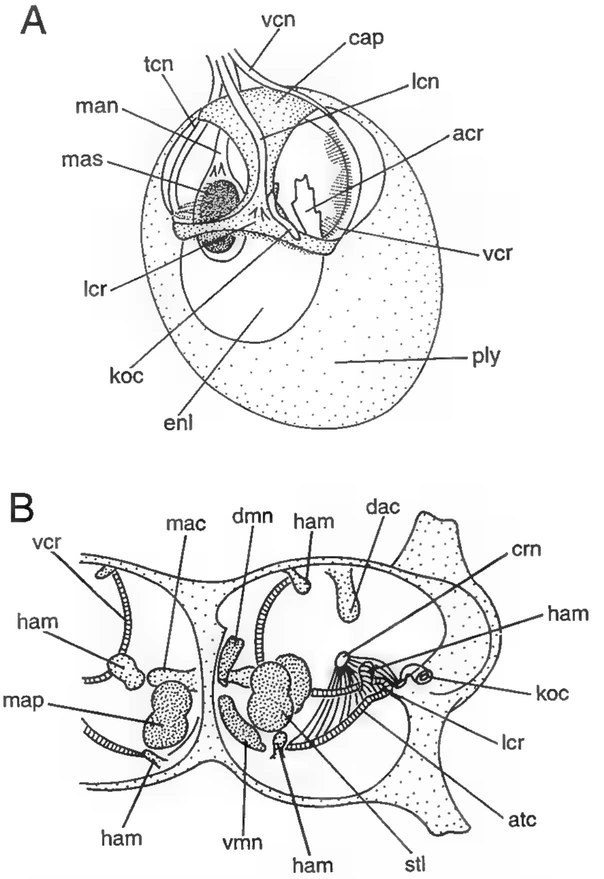

Figure 11.21 Cephalopod statocysts. A, *Octopus* (Octopodidae). B, *Sepiola* (Sepiolidae). **acr**, anticrista; **atc**, anterior transverse crista; **cap**, cartilaginous capsule; **crn**, crista nerve; **dac**, dorsal anticristae; **dmn**, dorsal macula neglecta; **enl**, endolymph; **ham**, hamuli; **koc**, Kölliker's canal; **lcn**, nerves to longitudinal cristae; **lcr**, longitudinal cristae; **mac**, median anticristae; **man**, macular nerve; **map**, macula principes; **mas**, macula with statolith; **ply**, perilymph; **stl**, statolith; **tcn**, nerves to transverse cristae; **vcn**, nerves to vertical cristae; **vcr**, vertical cristae; **vmn**, ventral macula neglecta. (After Nesis 1987) [C. Eadie]

other cephalopods, reflecting the animal's scavenging habits. The large optic lobes are simple in structure and presumably cannot perform detailed visual discrimination, and this is correlated with the simplicity of the eyes (Young, J.Z. 1965a, 1987, 1988a). The brain of *Nautilus* lacks the system of basal and peduncle lobes with the fine parallel fibres that are so well developed in coleoids. *Nautilus* also has no stellate ganglia or giant fibres.

The number of lobes is variable in coleoids, but there may be as many as 38 lobes with separate functions (Fig. 11.19B). The magnocellular lobes are much more highly developed than in *Nautilus*, with connections to the cerebral, optic, pedal and palliovisceral lobes, as well as commissures connecting them together. They control the actions of mantle and arms. The suboesophageal parts of the two sides are fused to form a compact mass containing brachial, pedal and palliovisceral parts which contain identifiable lobes controlling the arms, chromatophores, eye movements, the funnel, respiratory, locomotor and visceral activities as well as a region which is probably involved in initiating attack. Lobes controlling fins are also present in decapod cephalopods and finned octopods. Although each lobe has a primary function, overlap in the functions of lobes probably accounts for the highly integrated behaviour of coleoids.

As a development of the dorsal part of the cerebral cord of *Nautilus*, coleoids have a frontal/vertical lobe system which may vary from 5% to 20% of the brain volume. This system is entirely concerned with the regulation of the tendency to attack prey by storing memories and by control of the various motor centres in other regions of the brain. Some of the variation in its relative volume among coleoids can be correlated with their depth distribution and habits or with the extent of taxonomic relationships (Wirz 1955, 1959; Young, J.Z. 1977b; Maddock & Young 1987). Compared with sepioids and teuthoids with similar distribution, octopods tend to have smaller vertical lobes, but the surface is folded more which may allow a more complicated organisation as in the mammalian cortex. The frontal/vertical lobe system is particularly large in sepioids and loliginids, though smaller in oegopsids from deeper water, and large in *Vampyroteuthis infernalis*. It is also large in the epibenthic incirrates, but smaller in those from deeper water and very small in cirrates. Octopods, especially the epibenthic incirrates and the cirrates, have a well-developed inferior frontal system with several lobes that are associated with memorising and identifying tactile stimuli (Young, J.Z. 1965b). In the epipelagic and bathypelagic forms, the frontal/vertical lobe system is distinctly smaller, though all lobes are present. It is not only smaller but also simpler in sepioids and teuthoids.

Although most groups of the Sepioidea are benthic, apparently they rely more on visual information. Indeed, the optic lobes, which vary greatly in relative volume from 14–72% of the rest of the brain, are larger in decapod cephalopods than in octopods living at comparable depths and are especially large in deep-sea decapods. They are larger in epipelagic octopods than in the typical benthic species. The basal parts of the supra-oesophageal lobes consist of motor centres which represent about 20% of the brain's volume, excluding the optic lobes, and receive sensory input from the eyes and statocysts, and control movements. The anterior basal and peduncle lobes, considered to be analogous to the vertebrate cerebellum (Hobbs & Young 1973), cover the same relative size range in all orders and differences are difficult to explain (Maddock & Young 1987). Octopods have larger suboesophageal lobes, especially the brachial ones, than sepioids and teuthoids.

The arms of octopods each have a special peripheral nervous system that has the structure of an elongated ganglion (Graziadei 1971). The system comprises nerve ganglia, subserving motor and interconnection functions, and peripheral nerve cells that represent the sensory system. The nerve cords of the eight arms of *Octopus* together contain more than twice the number of cells in the central nervous system (Young, J.Z. 1963). The arms perform both motor and sensory functions. They are involved in walking movements, prey seizure and rejection of unwanted objects. They also receive a great deal of mechanical and chemical information about the immediate environment. Not surprisingly, the brachial nervous system of decapod cephalopods is simpler in structure.

Coleoids have two stellate ganglia, located in the mantle wall, lateral to the cephalic retractor muscles. These ganglia are connected to the palliovisceral lobe of the central nervous system by the pallial nerves and facilitate control of the mantle. The stellar nerves carry terminal motor fibres which originate in the cells of the ganglion to the mantle muscles. They also carry motor fibres to the chromatophores and the skin. The cell bodies of these latter fibres originate in the central nervous system and pass through the stellate ganglion without synapses. The general structure of the stellate ganglia is essentially the same in *Octopus*, *Sepia* and *Loligo* (Young, J.Z. 1972). The ganglion is divided into two parts that presumably reflect the respiratory and locomotive functions of the mantle. In sepioids and teuthoids, the ganglion controls respiration and gentle cruising, whereas the rapid escape jetting is under the control of the giant fibre system.

The giant fibre system which connects the central nervous system with the mantle muscles consists of three orders of cells and fibres (I, II, III). The two first order cells lie on each side in the magnocellular lobes, their axons forming a chiasma which differs among sepioids, loliginids and oegopsids (Martin 1977), and making contact with the axons of the giant cells II located in the palliovisceral lobe. The neurons of the giant cells II go to the cephalic and funnel retractor muscles and to the funnel while the axons establish contact with the giant fibres III which run in the stellar nerves to the mantle. This system ensures the immediate and simultaneous action of mantle, fins and retractor muscles of both sides needed by the fast-swimming jet propelled teuthoids. However, this system is present in almost all teuthoids, including the cranchiids, in all sepioids (even in *Spirula*) and in the finned octopods. Only the incirrate octopods and *Vampyroteuthis* have no giant fibre system (Young, J.Z. 1977b). As these fibres are very much larger than mammalian fibres and have very large cells, they have provided an extremely valuable tool for the study of basic cell and neural physiology (Gilpin-Brown 1977).

The central nervous systems of *Octopus vulgaris* and three *Loligo* species have been described thoroughly by J.Z. Young (1971, 1974, 1976, 1977a, 1979) and Messenger (1979). There is also a 77-page summary on the nervous system in the *Traité de Zoologie* (Mangold 1989a).

The eyes are large in almost all coleoids and have a general design similar to that of fish and vertebrates in general (Fig. 11.20A) except that the retina is not inverted (Naef 1928; Packard 1972). All morphological, behavioural and physiological evidence suggests that the performance of the cephalopod eye is comparable to that of a vertebrate, and that vision plays a major role in the life of most coleoids (Messenger 1981). Nevertheless, the sight of *Nautilus* is not good. There is no lens and acuity relies on the small size of the pupil, as in a pinhole camera (but see Muntz 1987, 1994a, 1994b). Information on the morphology and function of the *Nautilus* eye is given by Barber (1987) and Muntz (1987, 1994a).

The coleoid eye can resolve brightness differences, discriminate form, and distinguish sizes and different orientation. General theories of shape recognition are due largely to Sutherland (1959 and following papers; see Messenger 1981 for literature). Octopuses can easily distinguish horizontally and vertically orientated rectangles but they cannot discriminate obliquely orientated rectangles. However, at least some cephalopods can distinguish the plane of polarisation of light. The ability to perform complex shape discriminations was demonstrated by Muntz (1970). Cephalopods, or more precisely, *Octopus* species, are colour blind. They can distinguish brightness but cannot resolve hues (Messenger, Wilson & Hedge 1973; Messenger 1977b). It is likely that mesopelagic species, especially those with light organs, can distinguish between wavelengths since they are able to adjust the light they emit to that registered by their extraocular photoreceptors. Messenger (1981, 1991) provided detailed information on structure and function of the cephalopod eye, and the extensive literature on the subject.

Many coleoids have extra-ocular photoreceptors, termed photosensitive vesicles (Fig. 11.20B; Mauro 1977; Young, R.E. 1977, 1978). In octopods, these are known as epistellar bodies and lie in the mantle at the posterior end of the stellate ganglia. In decapod cephalopods, they lie close to the olfactory lobe on each side of the brain. These organs have no dioptric, or refractive, apparatus and little is known about their function. In many mesopelagic squids they appear to monitor the quality of down-welling light to regulate light production by the photophores for counter-illumination (Young, R.E. & Roper 1976, 1977; Young, R.E. 1977; Young, R.E. & Mencher 1980). It is possible that in some species the vesicles are concerned with control of diurnal vertical migration. The largest vesicles are found in those cranchiids known to breed at great depth (Maddock & Young 1987).

The statocysts provide a cephalopod with information about its position and direction of movement. Cephalopods have developed remarkable systems for moving their eyes as the body turns so that they can keep an image stationary on the retina, a requisite for carnivores that hunt by sight (Wells 1960). The morphological and physiological characteristics of their statocyst-eye muscle system show similarities to the vestibulo-optic system of their competitors, the fish (Packard 1972; Budelmann & Young 1984; Young, J.Z. 1988b).

The statocysts occupy separate cavities in the skull below the brain. In *Nautilus*, each is a simple sac open to the exterior, lined with hair cells and containing numerous small statoliths. It is probably only a gravity receptor. In all coleoids (Fig. 11.21), there are nerve cells in the statocyst and the receptors are differentiated into maculae with associated calcareous stones or statoliths for detection of linear acceleration, and into cristae or ridges of hair cells that detect angular acceleration (Young, J.Z. 1960, 1989; Budelmann 1970, 1975, 1976, 1977, 1990). These ridges are arranged in the wall of the statocyst to provide a differential

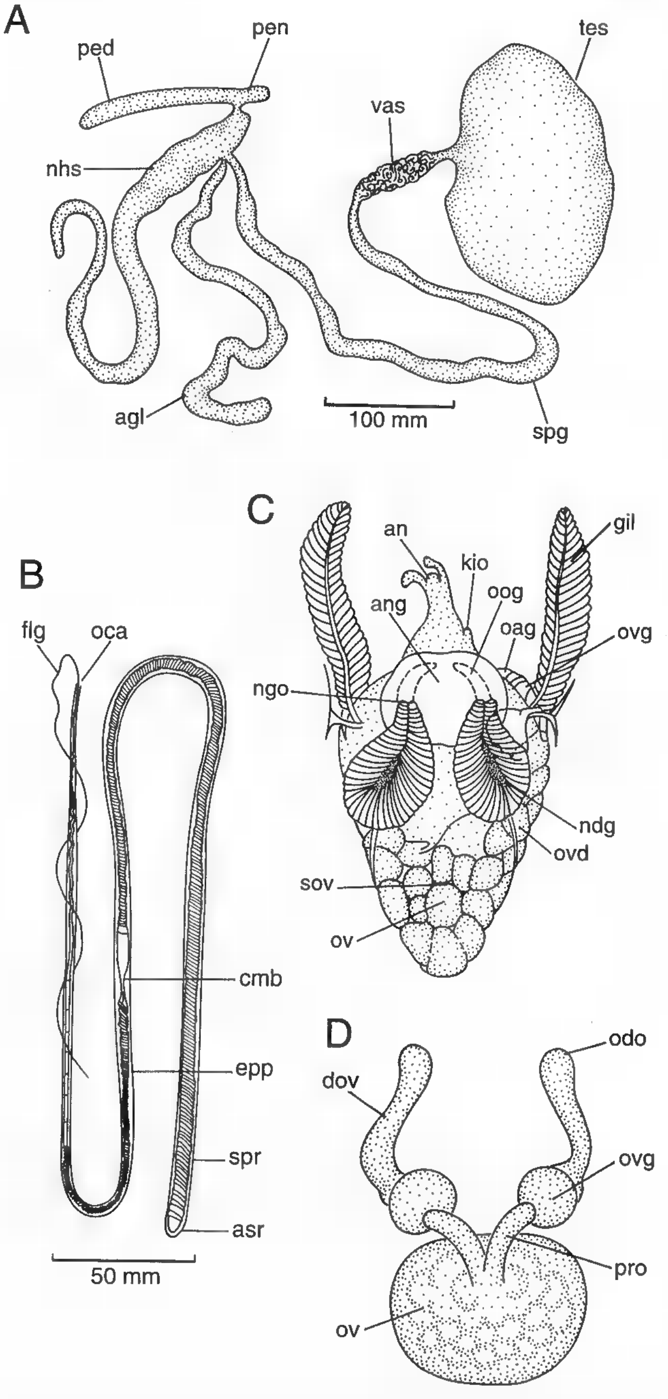

Figure 11.22 Cephalopod reproductive structures. **A**, male organs of *Octopus magnificus* (Octopodidae). **B**, spermatophore of *Octopus magnificus*. **C**, female reproductive organs of a sepioid. **D**, female reproductive organs of an octopus. **agl**, accessory gland; **an**, anus; **ang**, accessory nidamental gland; **asr**, aboral end of sperm reservoir; **cmb**, cement body of sperm reservoir; **dov**, distal oviduct; **epp**, ejaculatory apparatus; **flg**, flagellum; **gil**, gill; **kio**, kidney opening; **ndg**, nidamental gland; **ngo**, nidamental gland opening; **nhs**, Needham's sac; **oag**, opening of accessory nidamental gland; **oca**, oral cap; **odo**, opening of the distal oviduct; **oog**, opening of oviducal gland; **ov**, ovary; **ovd**, oviduct; **ovg**, oviducal gland; **ped**, penis diverticulum; **pen**, penis; **pro**, proximal oviduct; **sov**, beginning of oviduct; **spg**, spermatophoric gland; **spr**, sperm reservoir; **tes**, testis; **vas**, vas deferens. (A, B, after Villanueva, Sanchez & Compagno Roeleveld 1991; C, D, after Nesis 1987) [C. Eadie]

detection of acceleration in different planes. The hairs are linked together to form cupulae and the system integrates the information to record both direction and velocity of turning. In all octopods and in *Vampyroteuthis*, the statocyst forms an inner sac filled with endolymph. This sac is suspended within an outer sac filled with perilymph (Fig. 11.21A). There is no outer sac in decapod cephalopods. In many decapod species the walls have finger-like intrusions called anticristae and hamuli which guide the flow of the endolymph (Stephen & Young 1978). In the fastest jet-swimmers the intrusions become large and join together so that channels analogous to the semicircular canals of vertebrates are produced (Young, J.Z. 1988b).

Touch is extremely important in cephalopods that live in benthic habitats, such as *Nautilus* and octopodid species. Mechanoreceptors and chemoreceptors are probably distributed all over the skin, as a reaction to touch is immediate, but they are particularly abundant in special organs. Behavioural evidence suggests that all tentacles of *Nautilus* bear mechanoreceptors. Sensory cells have been identified in the ocular tentacles and some digital tentacles (Bidder 1962; Fukuda, Mikami & Kawamoto 1977). The sensory cells of the rhinophore, an organ that consists of a sac of cells located just below the eye, are very likely to be chemoreceptors (Barber 1987); their structure closely resembles that of the cells of the so-called olfactory organ in coleoids, a papilla or depression located between the eyes and the mantle aperture (Woodhams & Messenger 1974).

In coleoids, the mechanoreceptors and chemoreceptors are mainly located in the rims of the suckers and in the lips. The sucker receptor cells and their connections with the nervous system have been investigated by Graziadei (1965) and by Graziadei & Gagne (1976). There are several types of receptors located in three different zones of the sucker epithelium. Their fine structure and localisation allow one to distinguish the different types of cells that react to mechanical stimuli from those that perceive chemical stimuli. The number of receptor cells is distinctly larger in *Octopus* than in decapod cephalopods.

Touch discrimination and learning have been studied extensively by Wells (1978 and earlier papers; for a summary see also Mangold 1989b).

Although it was known decades ago (Baglioni 1910) that *Octopus* responds to disturbances of the water and to sound waves, a lateral line system able to sense local water movements, analogous to that of fishes, was discovered only recently. Sundermann (1978) and Sundermann-Meister (1983) described ciliated cells that form antero-posteriorly directed lines in the head and arm skin in *Loligo vulgaris* and *Sepia officinalis*. It has been suggested that these cells are mechanoreceptors. Hanlon & Budelmann (1987) and Budelmann & Bleckmann (1988) have recently presented convincing evidence that this system is indeed analogous to the lateral lines of fishes and serves for detection of prey and avoidance of predators by means other than visual perception.

Reproduction

Cephalopods are dioecious. Males and females grow to different sizes or different proportions in some species, and this phenomenon reaches its extreme with male dwarfs in some pelagic incirrate octopods, for example, *Argonauta*. Colour and photophore patterns can also be sexually dimorphic.

The gonads, originally paired, form a single mass at the posterior end of the mantle cavity. Males of *Nautilus* and almost all coleoids have a single gonoduct which is a highly complex structure comprising ducts, glands and storage organs. Female oegopsids and incirrate octopods have two gonoducts, whereas *Vampyroteuthis*, cirrate octopods, sepioids and loliginids have only one gonoduct. Octopods and *Vampyroteuthis* have only oviducal glands. Generally decapod females have nidamental and accessory nidamental glands (Fig. 11.22).

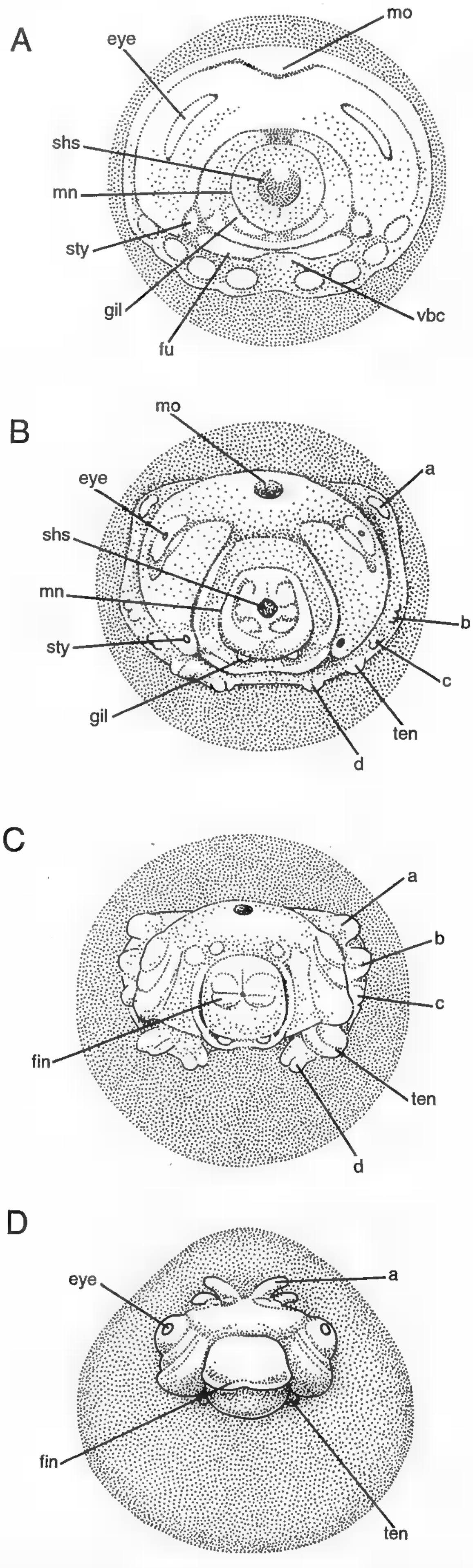

Figure 11.23 Four stages (after Naef 1923) in the organogenesis of *Sepia officinalis* (Sepiidae), a coleoid species with large eggs (7 mm in diameter). **A**, stage VII. **B**, stage IX. **C**, stage X. **D**, stage XII–XIII. **a–d**, dorsal to ventral arms, respectively; **eye**, eye; **fin**, fin; **fu**, funnel; **gil**, gill; **mn**, mantle; **mo**, mouth; **shs**, shell sac; **sty**, statocyst; **ten**, tentacle; **vbc**, ventral area of brachial crown where funnel arises. (After Grassé & Mangold 1989, after Naef 1923) [D. Wahl]

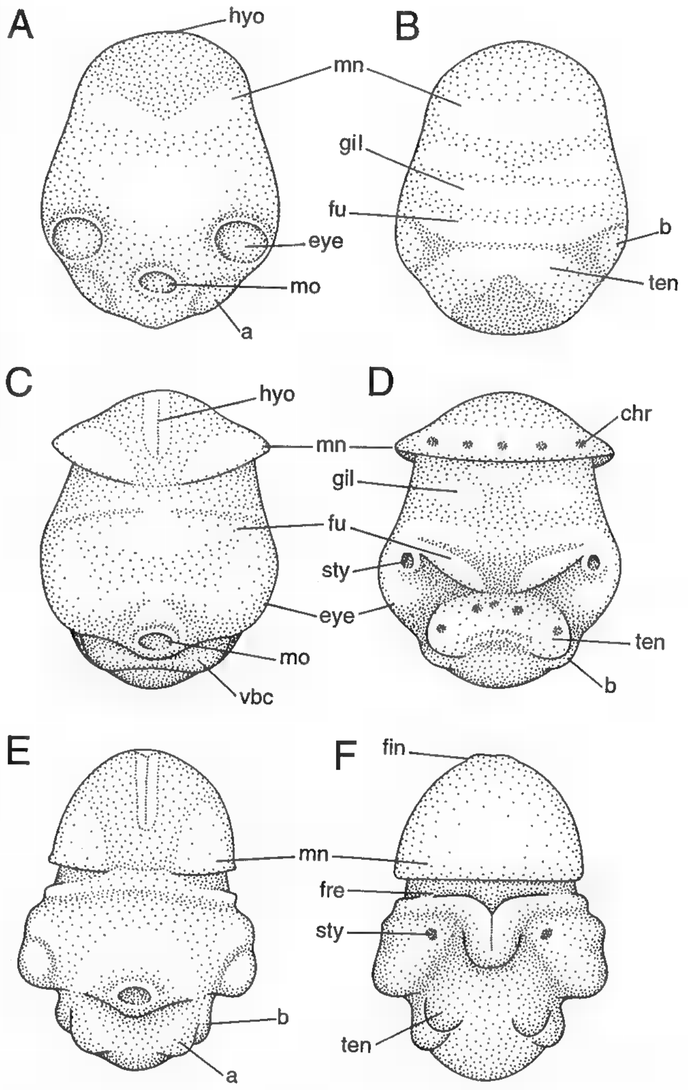

Figure 11.24 Stages (after Naef 1923) in the organogenesis of an ommastrephid species, a coleoid with very small eggs (1 mm in diameter). **A**, stage VIII, dorsal view. **B**, stage VIII, ventral view. **C**, **D**, stage X. **E**, **F**, stage XII. **a**, **b**, arms; **chr**, chromatophore; **eye**, eye; **fin**, fin; **fre**, funnel retractor; **fu**, funnel; **gil**, gill; **hyo**, Hoyle's organ; **mn**, mantle; **mo**, mouth; **sty**, statocyst; **ten**, tentacle; **vbc**, ventral area of brachial crown where funnel arises. (After Grassé & Mangold 1989, after Naef 1923) [C. Eadie]

In male *Nautilus*, four modified buccal tentacles form a spadix which is used to pass the sperm rope to the female. Coleoid males frequently have one or two modified arms, the hectocotylus, specialised for the transfer of spermatophores. Spermatophores which contain the spermatozoa (Fig. 11.22B; Franzen 1967), are produced in the spermatophoric glands of the gonoduct and stored in the spermatophoric or Needham's sac. They leave the duct via the terminal organ (also termed a penis; see discussion in Hochberg & Mangold in press). The structure and function of the spermatophores were reviewed by Mann, Martin & Thiersch (1966, 1970). Males generally become mature earlier and at a smaller size than females. Once mature, they continue to produce spermatophores almost to the end of their life cycle. The number and size of spermatophores vary greatly between species. The largest spermatophores are produced by octopods, which generally produce fewer than sepioids and teuthoids.

During mating, spermatophores are inserted into the mantle cavity (Pl. 18.5) or into the oviduct itself, or attached either to the head or near the oviducal opening in clusters. Alternatively, sperm may be transferred to special spermathecal sacs on the buccal membrane or in the mantle cavity. In *Octopus*, sperm may survive as long as 10 months (Mangold 1987). *Octopus* species store the sperm in the oviducal glands (Frösch & Marthy 1975), whereas the spermatophores of *Eledone* penetrate the ovary. The hectocotylus of the dwarf male of some incirrate pelagic octopods, for example, in the genera *Tremoctopus* and *Ocythoe*, becomes detached and is left in the mantle cavity of the female. In *Argonauta*, it is deposited in the shell, or brood chamber, of the female. Cephalopod mating often is accompanied by a courtship display that involves display of vivid chromatophore patterns and terminates in copulation. Mating behaviour and copulation vary among species and depend primarily, but not exclusively, on where the spermatophores or sperm are stored, for example, head to head, or head to mantle (Mangold-Wirz 1963). Copulation may be very brief, as in teuthoids, take several hours as in *Octopus* species, or last up to 30 hours in *Nautilus*.

Depending on the taxon, fertilisation of the mature ova may take place in the ovary, the oviducal glands, the mantle cavity or in the cone formed by the outstretched arms (*Sepia*, *Loligo*). In sepioids, loliginids and most oegopsids, oviducal glands and nidamental glands produce inner and outer gelatinous protective envelopes, respectively, for the eggs. The outer layer is generally wrapped spirally around the single egg or a strand of eggs. Most sepioids have large eggs that are laid singly and are attached to a solid substratum, such as shells, coral or sponges. Typically, teuthoid eggs are released in strands or strings, although there are some exceptions. The inshore loliginids spawn elongate gelatinous egg capsules. These may contain from a few to over 100 eggs depending on the species, and are attached in masses to hard substrata on the sea bottom (Pls 18.6–18.8). The spawn in oegopsids is known only for a few nectonic and oceanic species. They may produce large, gelatinous masses over 2 m long and 0.3 m in diameter or large flat ribbons. The jelly forms a globular, amorphous mass in *Illex illecebrosus* (O'Dor, Balch & Amaratunga 1982). Some mesopelagic squids lay eggs singly (Young, R.E. & Harman 1985).

Teuthoid eggs generally are very small, around 1 mm in diameter whereas those of loliginids are somewhat larger (1–3 mm; 6 mm in *Sepioteuthis*). Individual incirrate octopod eggs are surrounded by the chorion only, because the oviducal glands do not provide a gelatinous envelope. The chorion is stretched out into a stalk at one end and the eggs of benthic species are attached to a substratum, either singly or interwoven in festoons, in a protected little cave, crevice, molluscan shell or even human artefacts. The oviducal glands produce the cement to attach the eggs (Frösch & Marthy 1975). Incirrate octopod females brood their eggs until the young hatch (Pl. 20.4). Eggs of the family Octopodidae vary greatly in size, from about 2 mm to over 35 mm in length (Hochberg, Nixon & Toll 1992). Some benthic incirrate octopods, such as *Octopus burryi* and *Hapalochlaena maculosa* carry their eggs in the arms (Pl. 19.2). The eggs of *Ocythoe* develop in the oviducts (Naef 1923; Roper & Sweeney 1976). The eggs of cirrate octopods are very large and enclosed in a hard coat produced by the oviducal gland. They are laid singly and are not protected by the females (Boletzky 1982).

The number of eggs laid by a female varies greatly among coleoid species. There is a relationship between egg size, egg number and size of the female. Small species with relatively large eggs may spawn fewer than 30 eggs, for example in the genus *Sepiola*, whereas females of large, oceanic species, such as *Thysanoteuthis rhombus*, may spawn a few million very small eggs.

Embryology

The embryonic development of cephalopods differs from that of all other molluscs; unique features are the bilaterally symmetrical, superficial cleavage leading to a discoblastula, epibolic gastrulation and integration of the large, uncleaved yolk mass into a central yolk organ which is distinct from the definitive digestive system (Boletzky 1987b, 1987c, 1988, 1989). The phase of cleavage or blastulation comprises the developmental stages 0 to I as defined by Naef (1928) or stages 1 to 9 as defined by Arnold (1965). Cleavage furrows cut across the blastodisc but do not penetrate the yolk mass. In small eggs, the outer ends of the furrows, approach but do not actually reach, the equator of the egg. In larger eggs, the area of cleavage forms only a flat disc rather than a hollow cap at the animal pole. Gastrulation, the formation of germ layers and their proliferation over the surface of the egg, starts at stage II–III of Naef (Marthy 1976; Singley 1977).

Early organogenesis is characterised by a two-dimensional layout of organ areas that are gradually subdivided into distinct organ rudiments (Naef 1928). Organ areas are differentiated close to the animal pole before the edge of the gastrular cap has reached the equator of the yolk mass. As soon as the outer yolk sac envelope is closed at the vegetative pole, the cap forming the embryo proper undergoes a progressive radial contraction. Several folding events then occur (Figs 11.23, 11.24), including formation of primary eye folds, invagination of the statocysts, stomodeal invagination and shell sac formation by the closure of a circular fold on the mantle surface (Boletzky 1987b). The midgut rudiment closes around the yolk mass and finally clips off the constricted end of the syncytium to form the inner yolk sac. A further constriction of the yolk mass occurs as the massive developing central nervous system closes around the yolk, and makes the neck between the inner and outer yolk even narrower.

In sepioid and teuthoid embryos, the surfaces of the embryo proper and the outer yolk sac are covered by dense sets of active cilia, whereas in octopod embryos, ciliation is restricted to the outer yolk sac. Here a gradual reversal of the direction of the ciliary beat at early organogenetic stages leads to the peculiar first inversion, first noted by Portmann (1933) and fully described by Boletzky (1976; see also Boletzky & Fioroni 1990).

The outer yolk sac acts as a heart, and moves blood from spaces within the outer sac into the sinuses lying inside the embryo by waves of contraction in the envelope. These sinuses become differentiated as part of the definitive venous system. Arteries, heart and branchial system differentiate later. The outer yolk sac in *Nautilus* has an elaborate system of blood vessels (Arnold & Carlson 1986) instead of a continuous haemal space. The arm rudiments of coleoids become distinct within the arm crown anlage by the time of separation from the rudiments of the funnel tube. Decapod embryos of medium to large size show five pairs of rudiments from the beginning of arm differentiation, of which the fourth pair are the tentacles (Figs 11.23, 11.24). In some small embryos such as those of ommastrephid squids, some arm pairs are differentiated only in post-hatching stages (O'Dor, Balch, Foy, Hirtle & Johnston 1982). Octopod embryos always have four pairs of arm rudiments. Sucker arrangements always originate in a single series on each arm.

In later embryonic stages, the contents of the inner yolk sac are partly extruded to the outer yolk sac, though not in ommastrephids. Generally at stage XI the inner yolk sac reaches its minimal size. At this stage, all organ complexes lie in their definite positions relative to each other. The subsequent stages are characterised by linear body growth and further histological differentiation. This late phase, in nearly all cephalopods, starts with an increase in size of the inner yolk sac, which provides a nutrient reservoir after hatching.

Important modifications to the integumental surface during the later embryonic stages play a crucial role in the hatching process. Hatching in squids depends on the coordinated action of the enzyme of the hatching gland, or Hoyle's organ, and of the ciliary apparatus which allows the hatchlings to move through the channels opened by the enzyme. In *Sepia*, the ciliary bands typical of squids are differentiated only in close proximity to the hatching gland. The mantle apex of sepiolid hatchlings is equipped with a tough spine-like organ associated with the hatching gland (Boletzky 1991). The Kölliker organs of incirrate octopods provide a one way guiding structure during hatching.

Development in cephalopods is direct, so that the hatchlings of species with large eggs look like miniatures of the adults (Pls 18.1, 18.2), whereas species with small eggs only show gradual changes in proportions. In a few species, more rapid changes occur at a certain stage of growth and this can be regarded as separating the paralarval stage from the subadult stage (Young, R.E. & Harman 1988; Sweeney *et al.* 1992).

One of the most spectacular events in recent cephalopod embryological research is the successful rearing of *Nautilus* embryos at the Waikiki Aquarium (Arnold & Carlson 1986; Arnold 1987, 1988; Arnold, Awai & Carlson 1990). The work in progress provides direct evidence of homologous patterns in the embryogenesis of very distant taxa (Boletzky 1987d).

NATURAL HISTORY

Life History

Life histories of the overwhelming majority of cephalopods are still unknown, and our knowledge on life cycles within the class is very fragmentary (Boyle 1983, 1987). Information comes from biological studies in the field and from laboratory observations. One of the major problems in field studies is the scarcity of hatchlings, even in regions where spawn is collected, and they have been identified in relatively few species (Sweeney *et al.* 1992). It has been possible to rear a few species from eggs to spawning in the laboratory (Boletzky & Hanlon 1983; Hanlon, Turk & Lee 1991). This is relatively easy in species that have benthic young, such as sepioids and some octopodids, but is much more difficult in species that have planktonic hatchlings. Despite this, a few loliginids have been cultured successfully but, so far, it has not yet been possible to rear oegopsids (Sakurai *et al.* 1995). The latter only survive for a few days and die when their yolk reserves are used up. *Octopus vulgaris* has been reared through the planktonic stage to settlement (Itami, Izawa, Maeda & Nakai 1963; Villavueva 1994, 1995; Sakurai *et al.* 1995; Nixon & Mangold 1996).

Our knowledge of growth in cephalopods is derived primarily from a combination of laboratory rearing studies and fisheries related field surveys of commercially important species. Very little is known about species that cannot be reared and are not fished regularly (Clarke 1993).

Ageing of coleoids is difficult, because they have only a limited number of hard structures where one can look for daily growth rings or layers. The best candidate appears to be the statolith, at least in teuthoids. Progress has been made in recent years, but more research is needed (CIAC workshop in Japan, 1991; Jereb, Ragonese & Boletzky 1991; Okutani, O'Dor & Kubodera 1993).

Species of *Nautilus* have a life span of about 20 years and are iteroparous, laying very large eggs, a few at a time, over several years. On the other hand, coleoids grow very fast, at rates comparable to those of the fastest growing fishes. They are generally thought to be short-lived animals with life spans of six to eight months up to two or three years, and some large or cold-water species may live for four or more years (Jarre, Clarke & Pauly 1991; Clarke 1993; see also Mangold 1987 and Mangold, Young & Nixon 1993).

For the last 30 years, there has been general consensus that spawning in coleoid cephalopods is a terminal event followed by death, that is, coleoids are semelparous (Kirkendall & Stenseth 1985). This life history pattern is consistent with, or can be explained by, the action of the hormone of the optic glands. These glands are located on the optic stalks and their activity is under neural control by the subpedunculate lobes (Wells & Wells 1959). The optic gland hormone probably delivers messages in the following order: feed and grow, reproduce, die. Environmental factors such as light and temperature, and food availability may determine the speed at which this programme runs (Van Heukelem 1979). Many coleoids, especially oegopsids and incirrate octopods, do indeed conform to this pattern. One of the best known semelparous species is *Octopus vulgaris*. Tait (1986) demonstrated that a drastic, irreversible breakdown of mantle and arm musculature in females and males causes death. He had no evidence for the existence of more than one hormone responsible for sexual maturation and breakdown of body proteins leading to senescence and death, thus confirming the hypothesis that coleoid cephalopods are exclusively semelparous because of endocrinological constraints.

However, evidence now suggests that some members of all coleoid orders are multiple spawners (Harman, Young, Reid, Mangold, Suzuki & Hixon 1989). This is less surprising in species that lay large eggs such as the cirrate octopods, some deep-sea Octopodidae and *Sepia*, or in small species with relatively large eggs such as the Sepiolidae. But multiple spawners occur also among oceanic species with tiny eggs. Species may spawn several times and feed and grow between two spawning events or there may be a protracted spawning period that extends over the last third or half of a female's life-span (Boletzky 1986, 1987a; Mangold 1987; Mangold *et al.* 1993). In the cirrate genus *Opisthoteuthis*, spawning is continuous and lasts probably over several years (Villanueva 1992). Terminal reproduction requires only one hormone (Tait 1986), but the multiple spawning mode of reproduction, seemingly, would require some type of feedback system. Indeed, studies in progress on *Sepia officinalis* have shown that the control system is not as simple as hitherto believed (Henry & Boucaud-Camou 1993, 1994; Henry, Koueta, Boucaud & Lubet 1994). A spawning hormone, or neurohormone, does indeed exist, and the factor that stimulates mitosis in gonadal as well as in follicle cells (Koueta & Boucaud-Camou 1991; Henry & Boucaud-Camou 1993, 1994; Henry, Koueta, Boucaud & Lubet 1994) is not the same as the one that is responsible for vitellogenesis.

Estimates of fecundity can be made only for terminal spawners. In multiple spawners, counting of the number of mature oocytes in the ovary at any given time cannot yield an accurate estimate of fecundity.

In spite of their short life spans, in comparison with *Nautilus*, coleoid cephalopods exhibit the whole range of reproductive strategies from truly semelparous to iteroparous, or uniseasonal-iteroparous, according to the terminology of Kirkendall & Stenseth (1985).

Ecology

Cephalopods are marine and live in all oceans and seas, except in the Black Sea. However, a few species, such as *Lolliguncula brevis* in the Gulf of Mexico, are found in low salinity water in estuaries or mangrove swamps. *Loliolus noctiluca* has been reported to occur in salinities of 23‰ in Australian estuaries. Cephalopods range from the seashore to the deepest ocean and are adapted for life in mid-water to a bottom life amongst coral, rock, mud or buried in sand (Pls 20.5, 20.6). Their life styles range from strictly benthic (sessile) to nectonic and oceanic. They occupy virtually all marine niches and this great variety has led to the structural, physiological and behavioural diversity described above.

Nautilus species forage mainly close to the bottom and may scavenge, but all coleoid species are opportunistic, voracious carnivores and select from a very broad spectrum of fish, crustaceans, molluscs including cephalopods and, to a lesser extent, echinoderms and polychaetes (Nixon 1987). Diet may change in the course of the lifetime. Many coleoids eat small crustaceans when young and then change to fish, molluscs and larger species of crustaceans as they grow, as described for sepiolids and loliginids in Chapter 13. Bottom living octopods are often territorial and live in dens from which they make feeding sorties. Sepiids and sepiolids can, by movements of the fins and funnel, quickly bury themselves in sand so that only their eyes protrude. Tentacles can then be shot forwards to take unsuspecting prawns. During dawn and dusk, however, they hunt in open waters. Some oceanic octopods shelter within or on other organisms: *Ocythoe* males live in salps and *Argonauta* rides the backs of jellyfish.

Complicated cryptic body patterns are most highly developed in inshore species. Most of them also have protective skins over their eyes and move into mid-water at night; some have a pelagic, paralarval phase. Some teuthoids live on the continental shelf, have lenses protected by a cornea, and live on or close to the bottom during daylight. Most species live mainly in mid-water (oegopsids) and lack a cornea, and pelagic octopods occupy the open oceans from the surface to great depths, for which they have developed many cryptic devices (see External Characteristics, Behaviour, this Chapter). Egg masses of few teuthoids have been collected but some spawn on the bottom in very deep water and others in the epipelagic, warmer and well-illuminated layers of the sea.

Some species stay in the same, often upper, layers during their whole life, others gradually migrate downwards as they grow. Many species adopt a pattern of diel vertical migration over distances of several hundred metres (Clarke & Lu 1974, 1975; Lu & Clarke 1975a, 1975b; Roper & Young 1975). For small animals this can represent an enormous physical achievement; *Spirula* may travel vertically as much as 200 thousand times its body length twice a day (Clarke 1969). During daytime these mesopelagic coleoids are probably rather inactive but they become active and feed at the shallower end of their habitat range during the night.

Benthic species such as the Octopodidae and many sepioids stay in the same area during their whole life. Eventually they may go into slightly deeper waters under bad weather conditions (Mangold-Wirz 1963), but they do not undertake large horizontal migrations. Home ranges of *Octopus* species may not cover more than a few hundred square metres. Dispersion in benthic species with planktonic hatchlings, such as in many octopodids, may be easier than in those with benthic young. Many teuthoids, especially the ommastrephids and, to a lesser extent, some loliginids, make extensive migrations, mostly between feeding grounds and spawning grounds. For example, the ommastrephid *Illex illecebrosus* feeds in the northern part of its distribution and the females, still immature, migrate southwards over a distance of 2000 km to spawn in warmer waters (O'Dor 1983). The juveniles return again to the feeding grounds.

Juveniles and small cephalopod species, especially oceanic ones, are very vulnerable to predation by larger fish or crustaceans. The main predators of subadult and adult cephalopods are cetaceans and seals, and large fishes such as sharks and tunas (Clarke 1980, 1985, 1986a, 1987, 1996). Near the sea surface, seabirds are also important predators of squids. The chitinous beaks of cephalopods found in the stomach contents of predators are very useful for such studies. Differences in features of the rostrum, lateral wall, wings and jaw angle of the lower mandible generally enable identifications to be made to family or genus, and often to species level (Fig. 11.25; Clarke 1986b). Further, the beaks are resistant to digestion and tend to accumulate in the stomach of some predators, so providing large numbers for diet analysis; over 18 000 beaks have been collected from one sperm whale.

In addition to viruses, bacteria and fungi (Hanlon & Forsythe 1990), three phyla of Protista and six phyla of Metazoa are symbionts or parasites of cephalopods (Hochberg 1983). These include several monogenetic and almost 20 digenetic trematodes, many larval cestodes and nematodes and adults of two species of acanthocephalans, leeches on *Octopus*, polychaetes in egg masses of *Loligo*, and a few crustaceans in the mantle cavity. Several groups such as the dicyemids are unique to cephalopods. Many viruses and fungi are pathogenic to cephalopods.

Very little is known about intraspecific groups but populations which spawn in separate locations and/or at different seasons are recognised in some species (Carvalho, Thompson & Stoner 1992; Nesis 1993; see also Boyle & Pierce 1994).

Behaviour

Although many experiments on behaviour, especially learning processes, have been conducted on a few species of inshore *Octopus* and *Sepia*, less is known about the loliginids and very little for the oegopsids and oceanic octopods which do not survive capture or live for long in aquaria.

Inshore octopods may live in rock holes, tin cans, old car tyres and other man-made objects and may improve the home site with sand, stones and shells gathered from nearby or from eaten prey. Intraspecific aggression between octopuses is well known (Pls 20.1, 20.2) and larger ones are dominant and have the first

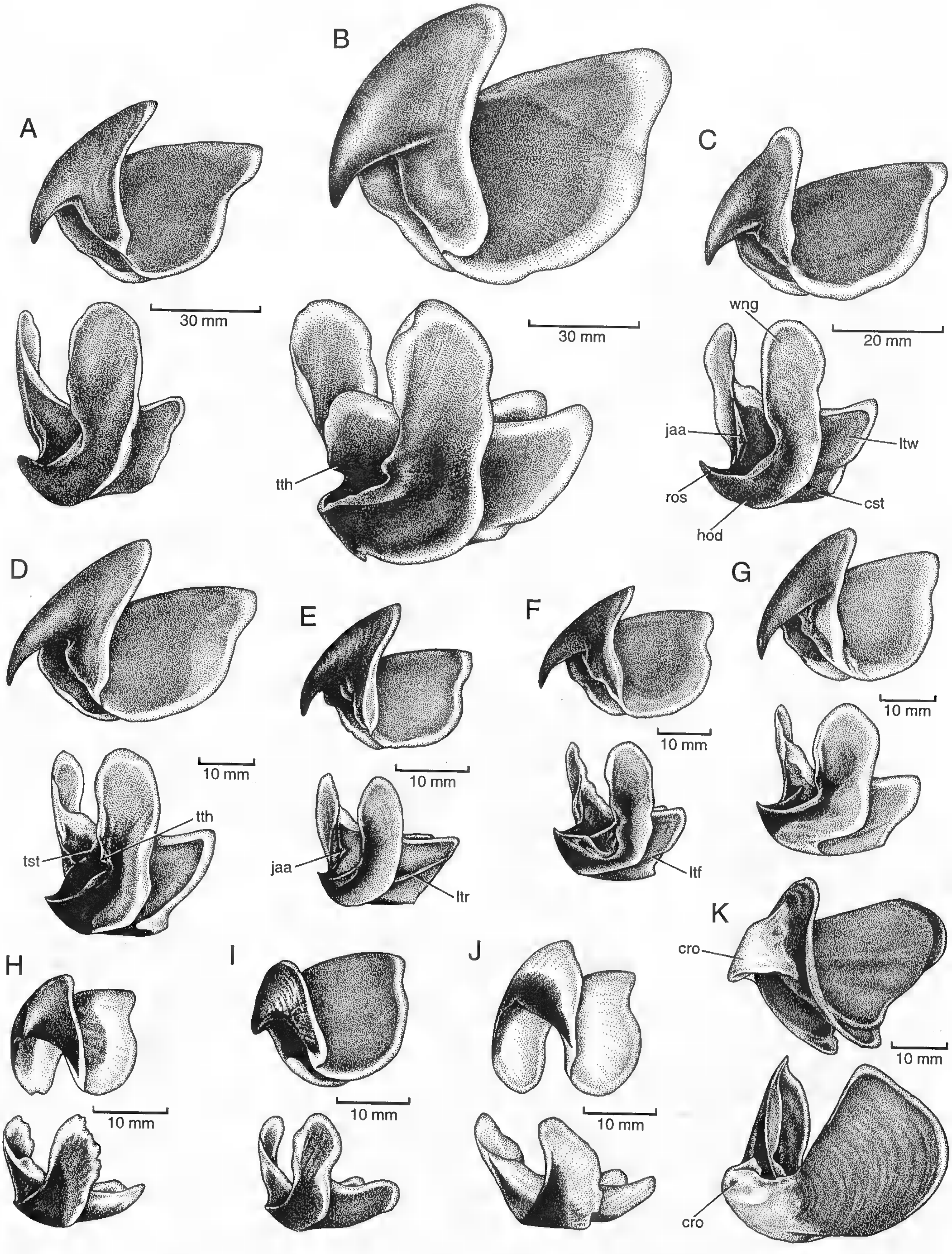

Figure 11.25 Cephalopod beaks. The upper and lower mandibles have been separated. In life the upper mandible lies between the widespread wings of the lower mandible. The beaks are identifiable to family, usually to genus, and often to species, using morphological features or ratios of measurements. The technique is particularly useful in the study of beaks found in stomachs of cephalopod predators (Clarke, M.R. 1986b). **A**, *Sepia apama* (Sepiidae). **B**, *Architeuthis* species (Architeuthidae). **C**, *Pholidoteuthis boschmai* (Pholidoteuthidae). **D**, *Todarodes filippovae* (Ommastrephidae). **E**, *Histioteuthis miranda* (Histioteuthidae). **F**, *Moroteuthis ingens* male (Onychoteuthidae). **G**, *Moroteuthis ingens* female. **H**, *Argonauta nodosa* (Argonautidae). **I**, *Octopus maorum* (Octopodidae). **J**, *Tremoctopus violaceus* (Tremoctopodidae). **K**, *Nautilus repertus* (Nautilidae). Chitinised areas are darker than the clear or pale cartilage. **cro**, calcified rostrum; **cst**, crest; **hod**, hood; **jaa**, jaw angle; **ltf**, lateral wall fold; **ltr**, lateral wall ridge; **ltw**, lateral wall; **ros**, rostrum; **tst**, transparent strip; **tth**, tooth; **wng**, wing. [K. Hollis}

choice of a home site. Although *Octopus* species are generally solitary and territorial, other members of the family, such as *Eledone* species, are gregarious.

Shoaling by juvenile decapod cephalopods has rarely been seen, but subadults and adults in most species shoal by maintaining closely similar orientation and spacing in size groups. In a few non-cannibalistic species, shoals include a larger size range.

Communication between cephalopods by means of colour patterns, and probably also by means of photophores in meso- and bathypelagic teuthoids, is complicated and elaborate in some species (Hanlon 1982).

Interaction between males may be accompanied by special and obvious chromatophore patterns. In some *Sepia* species, the male shows a zebra pattern on the arms while circling and pushing in front of a female. The most persistent male, often after several hours, will mate with the female and stay with her for several days. Three components of this sequence in *S. apama* are shown in Figure 11.26. In some teuthoids, males also fight each other for females and show distinctive patterns. Others mate in spawning aggregations and do not show any obvious pairing behaviour. Male octopuses often have a few enlarged suckers which they display to females, presumably for species recognition. In some octopus species, there is only a short courtship, but in others, striking patterns are displayed by the male, for example, in *Octopus horridus*. Photophores sometimes differ in arrangement between closely related species and between sexes. Photophore patterns probably aid species and sex identification as well as facilitating shoaling and, perhaps, being involved in sexual displays (Robison & Young 1981; Young, R.E. 1983).

Much of the life of many cephalopods is divided into inactive and active phases. Change from one state to the other often takes place at dusk and dawn, the greatest activity is displayed during dim light or darkness, and this activity mainly comprises searching for prey.

Figure 11.26 Confrontation, courtship and mating in *Sepia apama* (Sepiidae). **A**, a challenging male (foreground) in a ritual confrontation with a resident male at a good laying site; the resident responds with agonistic colour rippling over the body. **B**, during confrontation a male may spread his arms, displaying a zebra pattern and emphasising his overall size. **C**, while his competitor looks on, the successful male (left) mates with the female, wrapping his arms and buccal web around the female's head before depositing spermatophores within her mantle cavity with his left lower arm. (After Bavendam 1995) [C. Eadie]

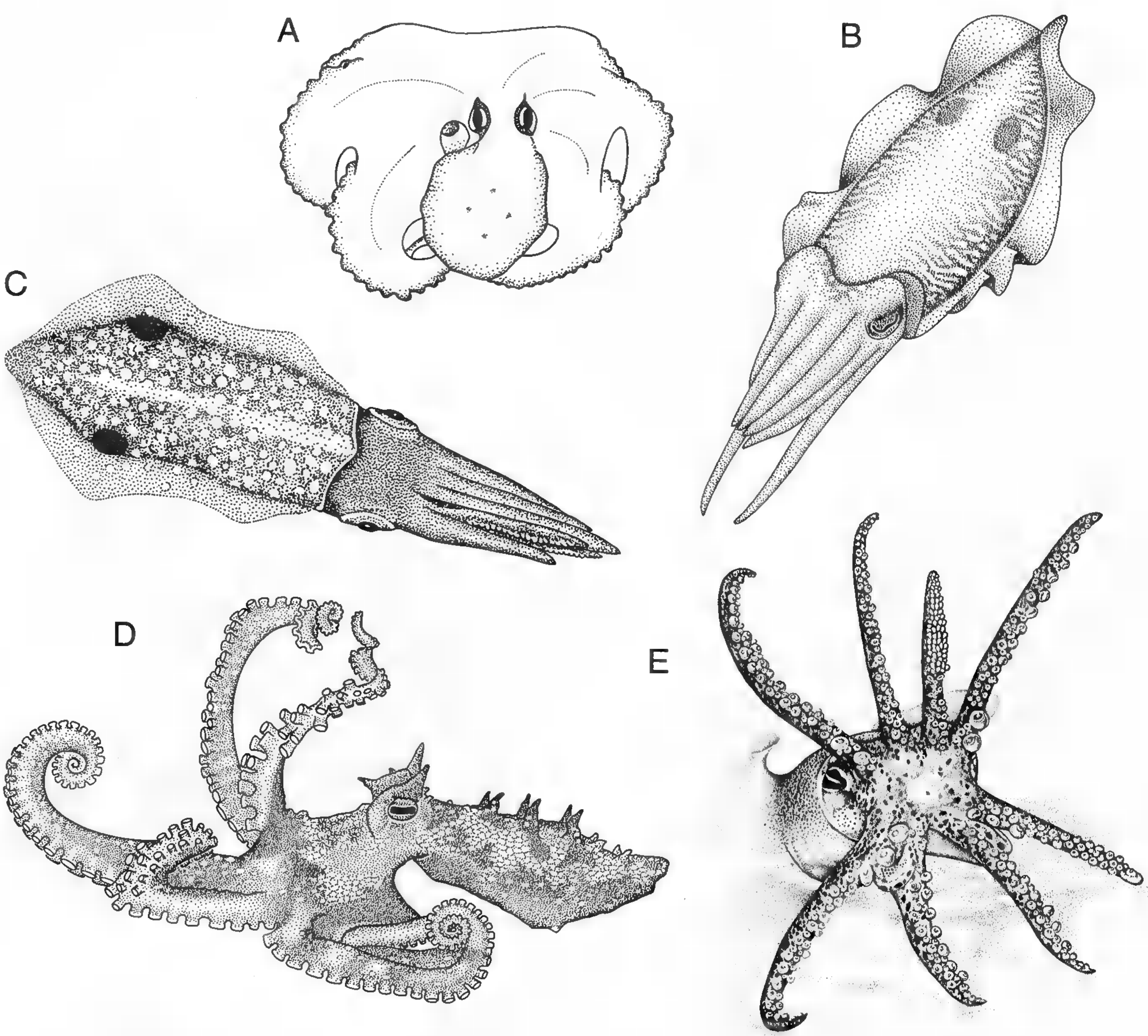

Figure 11.27 Body patterns formed by colour, texture and posture. **A–C**, dymantic, or frightening, patterns in *Octopus* (Octopodidae), *Sepia* (Sepiidae) and *Sepioteuthis* (Loliginidae), respectively. **D**, flamboyant display in a young *Octopus vulgaris* (Octopodidae), interpreted as a response to disturbance. **E**, adult *Euprymna tasmanica* (Sepiolidae)in a defence pose. (A, after Packard & Sanders 1971; B, modified after Chichery 1980; C, modified after Moynihan & Rodaniche 1982; D, after Packard & Hochberg 1977; E, after photograph by R.H. Kuiter)
[B, D, C. Eadie; A, C, D. Wahl; E, K. Hollis & C. Eadie]

Many species attack any moving objects noticeably smaller than themselves, but will attack immobile animals and even rocks. Tactile and chemosensory investigation then ensues. Chemosensory information is also probably used before contact in some octopods. *Sepia* ambushes its prey by careful positioning and then seizes it by the rapid extension of its tentacles. Hatchlings of many species attack their prey in the same manner as adults. Oceanic ommastrephid squids have been observed to jet rapidly past myctophid fishes near the surface, then dart forwards and to the side, at the same time opening their arms like a flower to envelop the prey. Smooth suckers and 'studs' along the stalks of the long tentacles allow many oceanic teuthoids to 'press-stud' the clubs together like tongs (Clarke 1966). Some pelagic octopods hold the stinging tentacles of siphonophores along their arms either for offence or defence. In teuthoids, some photophores on the tips of the two long tentacles or on the tips of the eight shorter arms, can be hidden by a covering of black skin. These are probably used to attract prey organisms, which can be lured closer to the mouth by contraction of the tentacle stalks. The latter may be as much as ten times the body length and can act effectively as a fishing line.

The ink from the ink sac is used by many cephalopods as a deterrent. In addition to melanin, the black ink contains mucus and, in some species, a skin irritant. It is squirted from the mantle cavity through the funnel below the mantle. According to its composition, it can become a blinding and irritating visual screen or can retain a less diffuse shape similar to the size and shape of a cephalopod, from which the ink-ejecting animal hastily retires in a changed colour state. A variation of the mechanism in a few loliginids and sepiolids, especially in the oceanic sepiolid, *Heteroteuthis*, involves squirting out luminescent bacteria from ink sac associated photophores. This causes a spectacular display of brilliant sparks which fades only after half an hour or so and can be blinding to a dark-adapted eye and a most effective discouragement to a would-be predator. Some large photophores directed forwards from the eyes and head are probably used to illuminate and possibly dazzle dark-adapted prey.

Chromatophores and iridophores, as well as leucophores when present, skin texture and body postures can all combine to provide a means by which specific moving patterns can be used to baffle prey, frighten attackers or pacify shoal companions. An octopus may deter attackers by opening and turning its arms backwards to present a barrier of suckers, or it may turn white except for dark eye spots and spread the web to present a large circular outline (Fig. 11.27). Packard & Sanders (1969, 1971) described what an octopus can show to other octopuses, to potential prey and to predators, and how the different patterns mature and change during the early juvenile phase (see also Packard & Hochberg 1977). Hanlon & Messenger (1988) described and illustrated

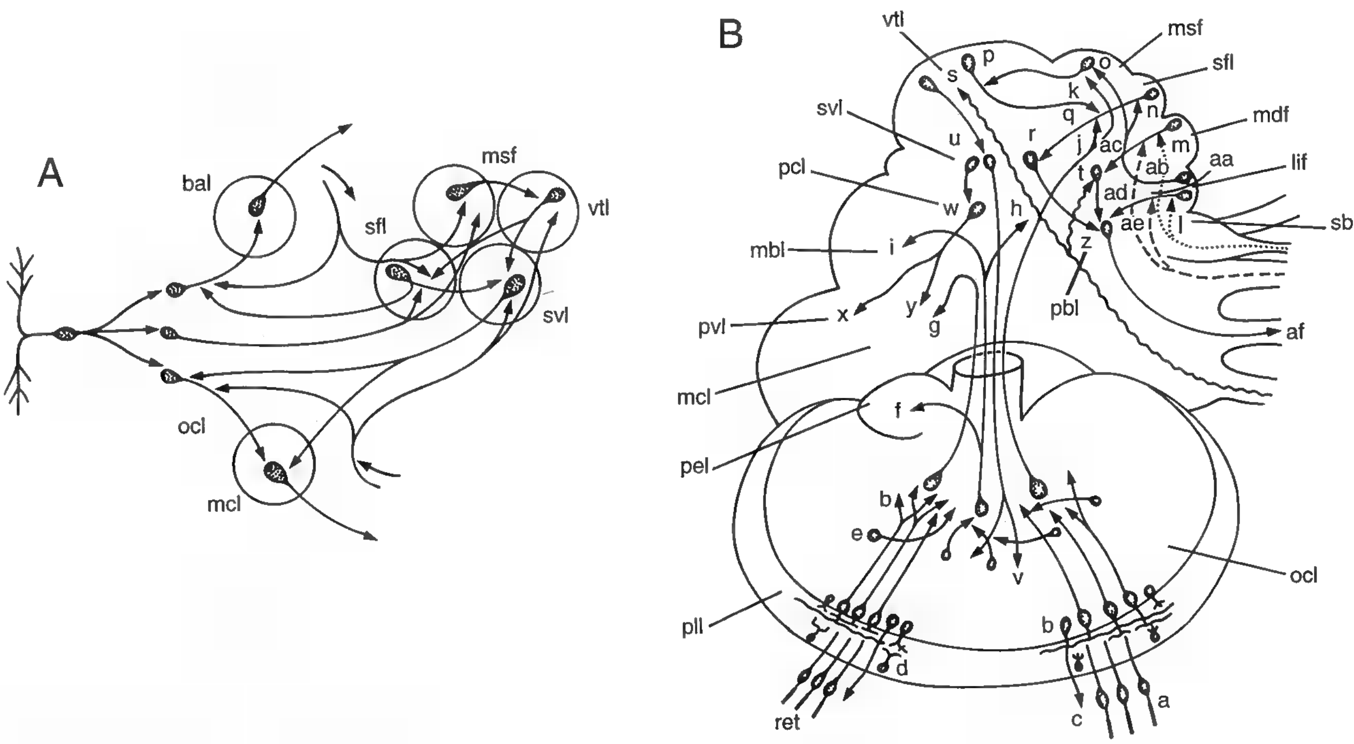

Figure 11.28 Models of learning in *Octopus* (Octopodidae). A, scheme of alternative pathways from the visual feature detectors of an octopus, showing output pathways for attack or retreat. A third pathway leads to the four matrices of the vertical lobe system, where particular patterns of visual signals are combined with those of taste to increase the future tendency to attack, or with signals of pain to reduce it. B, diagram of the connections of the visual and tactile learning system of an octopus. **bal**, basal lobes; **lif**, lateral inferior lobe; **mbl**, median basal lobe; **mcl**, magnocellular lobe; **mdf**, median inferior frontal lobe; **msf**, median superior frontal lobe; **ocl**, optic lobe; **pbl**, posterior buccal lobe; **pcl**, precommissural lobe; **pel**, pedal lobe; **pll**, plexiform layer; **pvl**, palliovisceral lobe; **ret**, retina; **sbl**, superior buccal lobe; **sfl**, lateral superior frontal lobe; **svl**, subvertical lobe; **vtl**, vertical lobe; **a**, retina; **b**, second order visual cells (feature detectors); **c**, centrifugal cells; **d**, amacrine cells; **e**, tangential cells; **f**, optic–peduncle; **g**, optic–magnocellular; **h**, optic–anterior basal; **i**, optic–median basal; **j**, optic–lateral superior frontal; **k**, optic–median superior frontal; **l**, taste fibres–lateral inferior frontal; **m**, taste fibres–median inferior frontal; **n**, lateral inferior frontal–lateral superior frontal; **o**, lateral inferior frontal–median superior frontal; **p**, median superior frontal–vertical; **q**, vertical–lateral superior frontal; **r**, lateral superior frontal–subvertical; **s**, pain fibres–vertical; **t**, pain fibres–subfrontal; **u**, vertical–subvertical; **v**, subvertical–optic; **w**, subvertical–precommissural; **x**, precommissural–palliovisceral; **y**, precommissural–magnocellular; **z**, subvertical–posterior buccal; **aa**, chemotactile fibres–lateral inferior frontal; **ab**, chemotactile fibres–median inferior frontal; **ac**, median inferior frontal–subfrontal; **ad**, subfrontal–posterior buccal; **ae**, lateral inferior frontal–posterior buccal; **af**, motor fibres from posterior buccal to arms. (After Young, J.Z. 1991) [C. Eadie]

adaptive colouration in young cuttlefish. The behaviour of octopodid hatchlings, both planktonic and benthic, has been discussed by Boletzky (1977), and many aspects of behaviour in juvenile cephalopods have been described by the same author (1987c). Our knowledge of cephalopod behaviour has been summarised superbly by Hanlon & Messenger (1996).

Many cephalopods have a dark, dorsal side which minimises the contrast in the sunlight shining from above. One of the most striking examples is seen in a cuttlefish, in which an animal turned upside down expands the chromatophores on its ventral side and contracts those on its back (Ferguson & Messenger 1991). Many mesopelagic oegopsids employ a mechanism called 'ventral bioluminescent countershading' (Young, R.E. 1973, 1977, 1983). This is a highly sophisticated means of obliterating their silhouette against down-welling light so that they cannot be seen by predators living further down in the water column. Squids which can effectively make themselves invisible from below have photophores and occupy depths where light levels are compatible with countershading during day, twilight and night. The photophores shield opaque structures with bioluminescence, by producing blue, highly directed light. The squid detect down-welling light and regulate the intensity and colour (wavelength) of their bioluminescence to match it (Young, R.E. & Roper 1976, 1977; Young, R.E. & Mencher 1980).

Since the 1940s, the study of cephalopod behaviour has been primarily concerned with learning and memory. Ever since Boycott and J.Z. Young began to investigate the functions of particular parts of the cephalopod brain, researchers have been astounded by the incredible learning capacity and memory of *Octopus*. J.Z. Young and his co-workers and students continued to study learning processes extensively over many years, mainly in *Octopus* and *Sepia*; synopses of their work may be found in Wells (1962, 1978), J.Z. Young (1964), Sanders (1975), Messenger (1977a), and Mangold (1989a). The widely accepted models proposed by J.Z. Young are represented in Figure 11.28.

Cephalopod hatchlings begin with a limited set of reaction patterns that allow them to make the right choices (innate responses) and these are gradually modified. Once hatchlings have left the protected environment of the egg, they encounter situations where they begin to learn. The learning capacity is related to the size of the brain, especially to that of the vertical lobe system which is distinctly smaller in hatchlings than in adults (Wirz 1954; Messenger 1973, 1977a). The number of correct answers increases with the increasing size of the learning centres. Among other phenomena, ageing, on the other hand, is characterised by a dramatic drop in successful prey capture (Chichery & Chichery 1992a, 1992b).

Economic Significance

Cephalopods have been fished on an artisanal basis for several thousand years and were well known to the ancient Greeks and Chinese as highly valued food. Worldwide commercial fisheries for cephalopods have developed since about 1960 when the Japanese fishing companies expanded operations well beyond their regional waters in the effort to fulfil increased demands for cephalopod products (Rathjen & Voss 1987).

Estimates of potential cephalopod resources worldwide are 100–500 million tonnes per year (Gulland 1971; Voss 1977a), based on the role cephalopods are known to play in marine ecosystems. Cephalopods appear to be subdominant predators that tend to increase in biomass when their predators and competitors are depleted because of heavy fishing pressure. This has been observed in the fin fisheries of the Sahara Bank, the north-western Atlantic and in the Gulf of Thailand (Roper *et al.* 1984). It also is well established that cephalopods are extremely important ecologically in the food pyramids of all oceans, and they are regular, significant components in the diets of oceanic birds, fishes, pinnipeds and cetaceans (Clarke 1987). Data from analysis of predation suggest that a great variety of species are important throughout the oceans. Calculations of the weight of squid consumed by these predators indicate that squid biomass is in the same order as that of fishes. For example, the largest toothed whale, the sperm whale, consumes at least 100 million tonnes of squid each year (Clarke 1987). This is comparable to the total annual fishery production worldwide, and amounts to about one half of the weight of all people on earth.

The assessment and prediction of population levels and dynamics of cephalopods has been difficult, particularly for teuthoids which are difficult to catch. Furthermore, the brief period prior to spawning (1–3 years) in cephalopods, and their susceptibility to environmental changes, creates fisheries that are very unpredictable. Catches often fluctuate dramatically. These factors make the management of cephalopod fisheries very challenging. In order to sustain catch levels, cephalopod fisheries have expanded across the world's oceans.

Since the early 1960s the world cephalopod catch has increased from around 0.5 million tonnes to over 2.3 million tonnes by 1990. World catches of squids and cuttlefish increased by 57% and 84%, respectively, between 1970 and 1980, while the total increase of all other fishery products was only 8% (Roper *et al.* 1984). The total world landings of cephalopods in 1977 was 1.23 million tonnes, with squid making up about 80% of the catch. By 1987 total catches of cephalopods reached 2.3 million tonnes (FAO unpublished data 1990). The value of cephalopods purchased by the 10 leading importing countries in 1987 was US$1.38 billion for 521 781 tonnes, about a quarter of the world catch (ITC 1989).

Japan catches about 36% of the total world catch, followed by Korea, 12.3%. Interestingly, in recent years developing countries have accounted for an increasing share of the world catch – 46% in 1988. Most of these countries have no tradition of eating cephalopods, so the harvest is sold on the world market, providing a much needed source of hard currency. Leading exporting countries in 1987 were Thailand, Morocco and Mauritania (ITC 1989).

The major cephalopod producing areas in the early 1990s are the north-western Pacific (Murata 1990; Okutani 1990; Takeda 1990), traditionally the most important region, and the south-west Atlantic ocean. Catches of squids in the latter region increased from 31 000 tonnes in 1980 to over 743 000 tonnes in 1987. The ommastrephid, *Illex argentinus*, accounted for 650 000 tonnes of this total (FAO unpublished data 1990).

The north-west Pacific fishery for *Todarodes pacificus* (Ommastrephidae) reached a peak in 1952 when 600 000 tonnes were caught by Japanese fishermen. Current catches have fallen to less than 200 000 tonnes (Suzuki 1990). *Todarodes pacificus* is caught exclusively by jigging, which provides a product of superior quality. *Ommastrephes bartrami* is the basis of a major fishery in the region, accounting for over 200 000 tonnes annually. This pelagic fishery employs drifting gillnets. This gear has spurred much international controversy because of its non-selective capture of fishes, marine mammals and oceanic birds, for example. Use of these nets has been halted by international convention. As drift gill nets produced 10% of the cephalopods caught, other techniques are being investigated to ensure the continued production and utilisation of the resource (H. Hatanaka personal communication to C.F.E. Roper).

The various methods and techniques used for capturing cephalopods have been reviewed by Hamabe, Hamuro, & Ogura (1982), Ogura (1983) and Rathjen (1984, 1989, 1991). The most widely used method is jigging which accounts for 40% of the world catch of cephalopods, all squids. The technique is employed primarily at night when the squids are attracted to the ship by bright lights. Jigs with numerous barbless hooks are lowered and retrieved with a jigging motion by an automated machine. Large, modern vessels up to 70 m in length are equipped with 50 to 70 double-reeled, computer-controlled jigging machines capable of catching 35 tonnes a night. Ommastrephid squids are the primary target for this technique, as are some of the loliginids.

Otter trawls capture about 25% of the world catch of cephalopods, predominantly benthic and epibenthic species of squids, cuttlefishes and octopuses. Trawling is an especially efficient method for catching cephalopods, but because they are soft-bodied, they tend to be damaged in the net and yield a product generally inferior to the jig-caught squids. Trawler/processor vessels of 70 m and larger can process over 80 tonnes of cephalopods a day. Trawling can be highly detrimental to benthic habitats due to physical damage to the seafloor and because trawls are non-selective, both in sizes and species of organisms. In view of the potential for serious adverse affects on cephalopod fisheries through habitat destruction and stock depletion, it has been recommended that traditional cephalopod fisheries be reduced in intensity and spread out over broader areas. Alternative methods also should be developed and pursued (Roper & Rathjen 1992).

The remaining 25% of the cephalopod catch is taken by a variety of methods. Among them are the seine (lampara) net fishery for *Loligo opalescens* off California and trolling with hand jigs off Japan for other loliginid species. Octopuses traditionally have been captured in clay pots, wooden traps and mesh baskets, but PVC pipe may prove to be the pot of the future. Other fishing gear of regional importance include beach seines, lift nets and set nets.

Although estimates of potential resources of cephalopods run to the hundreds of millions of tonnes (Clarke 1996), it is unrealistic to expect a huge increase of fisheries in a short period of time. Even to double the world production to four or five million tonnes will require a commitment of ships and processing/handling facilities that might be uneconomic under current world conditions. Nevertheless, in time the great challenge will be to develop the fisheries on a rational biological basis to ensure sustained yields. It becomes increasingly important that cephalopod fisheries be monitored and managed specifically through the accumulation and analysis of long-term biological and population data (Roper & Rathjen 1992).

Methods of Study

The methods of studying cephalopods were discussed extensively during the workshop on the Biology and Resource Potential of Cephalopods, held in Melbourne in 1981 (Boletzky & Hanlon 1983; Roper 1983; Roper & Sweeney 1983; Roper & Voss 1983). Roper (1984) presented a number of possible future directions of cephalopod research, particularly in biology, systematics and fisheries biology. Several useful chapters on techniques for using squids as experimental animals for physiological and biochemical research appear in Gilbert, Adelman & Arnold (1990).

We wish to emphasise the taxonomic importance of observing the colour patterns, skin textures and body postures of live animals, especially of those that belong to the Sepiidae and Octopodinae (Hanlon 1988; Roper & Hochberg 1988; Toll 1991; Hochberg & Mangold in press). Records of these on colour film or videotape would be especially useful. The chromatophore patterns of hatchlings also should be carefully examined (Packard 1985; Young, R.E. & Harman 1988).

The genetic structure of some cephalopod populations has been approached classically by analysis of the enzymatic polymorphism (Woodruff, Mulvey, Saunders & Carpenter 1983; Thorpe & Havenhand 1986; Levy, Haimovici & Conceicao 1988; Carvalho & Pitcher 1989a, 1989b; Carvalho *et al.* 1992). Immuno- and/or electrophoretic techniques have been used to analyse eye lens proteins (Swanborn 1971; Tranvouez & Boucher-Rodoni 1990). In relation to the development of cellular and molecular biology, a number of techniques, among them sequencing of nucleic acids, open new promising perspectives in the study of the taxonomy and phylogeny of cephalopods at all taxonomic levels (Hudelot 1966; Bonnaud, Boucher-Rodoni & Monnerot 1994, 1996; Boucher-Rodoni & Bonnaud 1996).

REFERENCE MATERIAL

The material illustrated in Figures 11.2 and 11.25 is held in the Museum of Victoria (NMV), under the following registration numbers: Fig. 11.2 – F78297; Fig. 11.25B – F78297; Fig. 11.25F, G – F74462; Fig. 11.25I – F77900.

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SUBCLASS NAUTILOIDEA

CHAPTER 12

GENERAL DESCRIPTION

The subclass Nautiloidea is predominantly a Lower Palaeozoic group, since all members had originated, and more than half were extinct, by the end of the Silurian. The genus *Nautilus* (Fig. 12.1) is the only living representative of this once-abundant group of externally shelled cephalopods.

The classification at an ordinal level has to be based on shell characters, since only *Nautilus* and various coleoid groups remain to give full evidence of soft parts. The secreted shell, or conch, consists of two portions: the posterior phragmocone, which is divided by septa into chambers termed camerae; and the anterior, undivided body chamber, which houses most of the soft tissues of the animal. Shell features of systematic value include the overall form of the conch, the shape of the opening of the body chamber or aperture, the structure of the septa and septal foramina, and the extent and position of cameral deposits of calcium carbonate.

The present overview of some morphological features of fossil nautiloids, and their biogeography in the Australian region, provides perspectives on the morphological development of the extant Nautilidae, and the origin and evolution of the subclass Coleoidea.

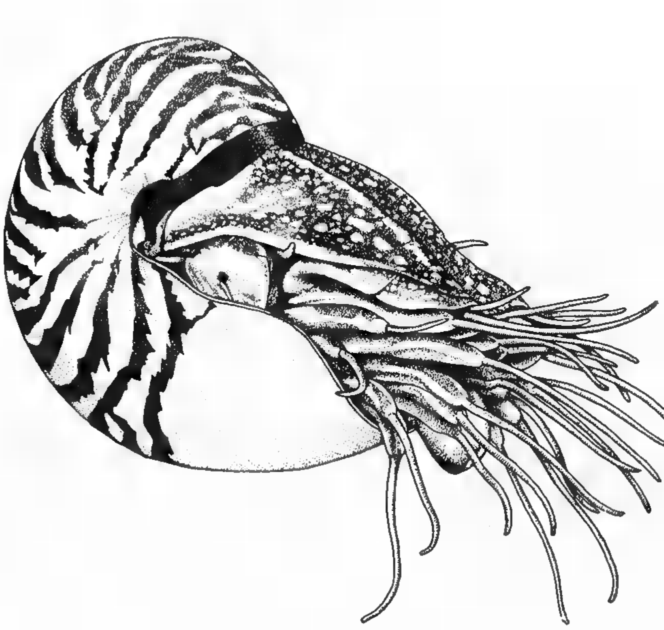

Figure 12.1 *Nautilus pompilius* (Nautilidae), swimming forwards with the siphon recurved posteriorly and the tentacles extended. This search posture is characteristic of an animal approaching a scent source it has detected. (After photograph by W.B. Saunders) [H. Lewis]

CLASSIFICATION

The structures and means by which counter-balancing of the shell has been achieved are of prime importance to modern classification (for example, Teichert 1967, 1988; Wade 1988) and are the major features used to characterise the 15 recognised orders comprising the Nautiloidea as treated here. Opinions on supra-ordinal status vary in the number of accepted subclasses. Teichert (1988) grouped these orders into four subclasses; one of these combined the superorders Plectronoceratoidea and Orthoceratoidea to form the subclass Orthoceratoidea, which Teichert regarded as the 'central stock' of cephalopod evolution. Wade (1988) recognised six superorders in a single subclass Nautiloidea (Fig. 12.9). The phylogeny of the subclass is illustrated in Figure 12.2 (after Wade 1988; Teichert & Moore 1964; Teichert 1967, 1988).

The Ellesmerocerida, in the superorder Plectronoceratoidea, is considered to be ancestral to the other five superorders. The Nautiloidea is, and probably the Discosoroidea, Actinoceratoidea and Endoceratoidea were, independent of the coleoid dibranchiate radiation (Wade 1988). The Orthocerida lineage shares two important soft part features with the Dibranchia (Mehl 1984).

Subsequent use of the terms 'Nautiloidea' and 'nautiloid' in this chapter refer to the subclass, unless specified as the superorder Nautiloidea or the superfamily Nautiloidea.

MORPHOLOGY

From the Cambrian through to the Recent, nautiloideans have laid down their aragonite shells on a basic 'nautiloid' plan of shell conchiolin (Grégoire 1967, 1988). This arrangement differs from the monoplacophoran plan (Grégoire 1967), though modern phylogenies concur in suggesting the Monoplacophora as the ancestral molluscan(?) group, with a brave disregard of this remarkably constant character.

Shell and Siphuncle

All Nautiloidea have chambered shells formed of a series of buoyancy chambers or camerae which are formed sequentially by the secretion of transverse septa by the mantle at the rear of an adoral living chamber, as the animal grows (Fig. 12.3). The periphery of each concave septum is attached firmly to the wall of the shell. The unattached central portion of the septum is perforated and extends posteriorly to form a cylindrical septal neck (Fig. 12.3).

The living chamber, connected to the apical chamber by a siphuncular tube with semipermeable walls, ends blindly as a caecum in the apical chamber. The siphuncular tube, termed the ectosiphuncle, and the flesh and epithelium that lays it down, termed the endosiphuncle, together should be called the siphuncle (Flower 1964b), although either may be called a siphuncle if the context is clear.

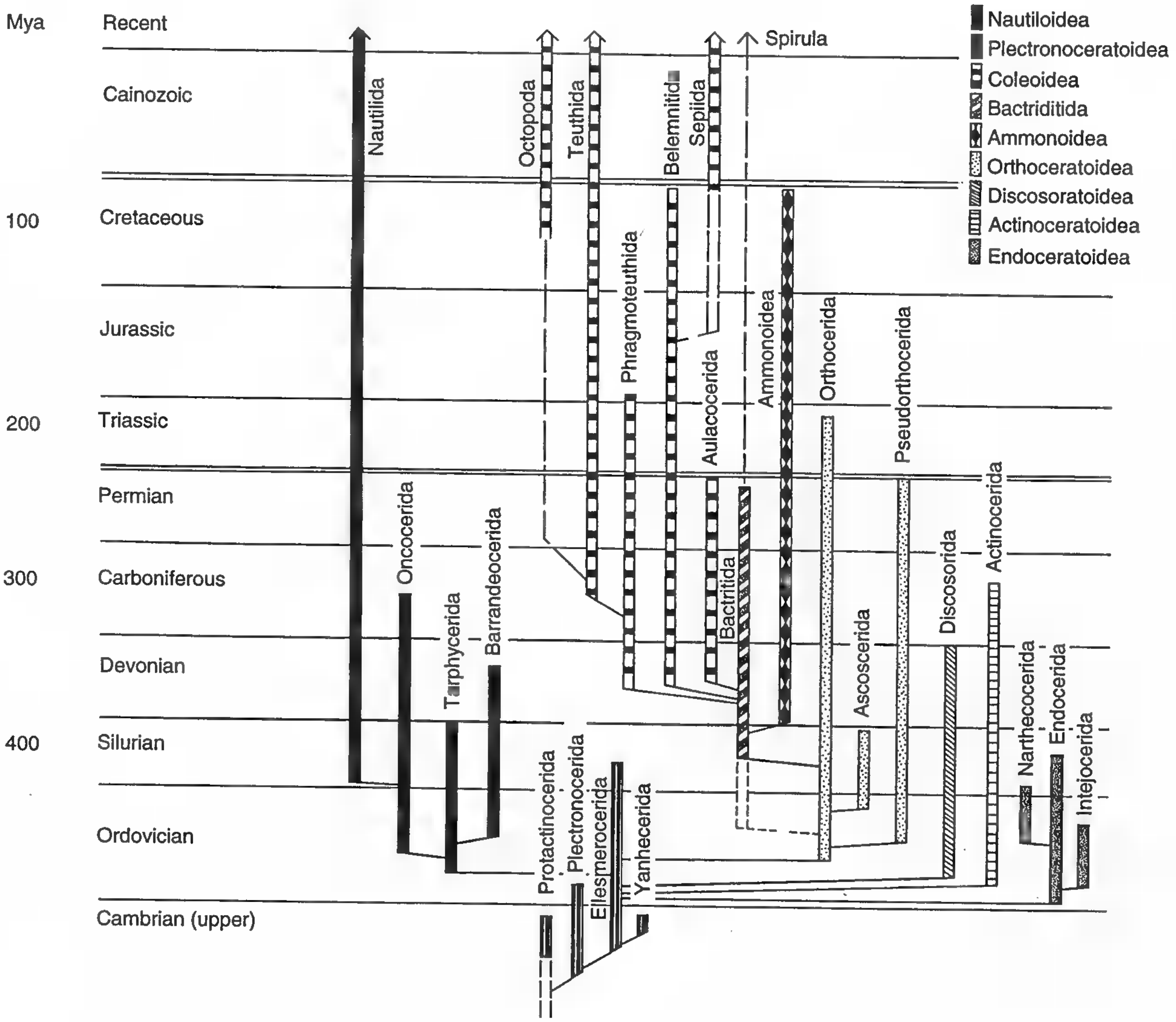

Figure 12.2 A phylogeny of subclass Nautiloidea, showing the relationships and stratigraphic ranges of the six nautiloid superorders and the 16 orders they comprise. The appearance and radiation of the modern dibranchiate groups (Coleoidea, Bactriditida and Ammonoidea) are indicated also. The superorder level best expresses the overall relationships and diverse adaptations of these taxa. **mya**, millions of years before present. (After Teichert 1964, 1967; Wade in press) [M. Wade]

The ectosiphuncle consists of a series of cylindrical connecting rings, that link and attach to successive septal necks. It is present in modern *Nautilus*. In the earliest Nautilida the siphuncular mantle primarily deposited organo-calcareous, radiate ectosiphuncular structure (Kummel 1964) similar to that seen in the Oncocerida (Fig. 12.4B, C), but this feature was lost early on. In later Endocerida and Actinocerida, the posterior tip of the siphuncle was open or was modified, as the whole apex of the shell is filled with endosiphuncular deposit (for example, *Nanno*). This feature evolved more than once, but is characteristic of the lineage from Piloceratidae to Endoceratidae (Endocerida; Flower 1958).

In most of the Nautiloidea, the siphuncular epithelium could be reactivated adapically, unlike the situation in *Nautilus* and its ancestors. This epithelium laid down aragonitic siphuncular deposits of several kinds, and is associated with cameral deposits in many nautiloids, in a way that is poorly understood (Crick 1982; Crick & Ottensman 1983). There is no fixed order for the commencement of endosiphuncular or cameral deposits, even in one species.

Differences in ratios of trace elements in the shell deposits laid down by the mantle (the shell wall and septa) and cameral deposits argue strongly against the existence of a 'cameral mantle' as the active agent in cameral deposition of normal nautiloids such as *Mitorthoceras* (Crick & Ottensman 1983).

Buoyancy and Ballast Mechanisms

Siphuncular and cameral deposits were important as overall ballast, pertinent to neutral buoyancy, orientation and hydrostatic equilibrium. The strength they imparted to the shell was also a factor in determining the depth-range at which these animals could operate without implosion (Teichert 1933). The ability to hold the body chamber in an attitude in which the shell supported the body with minimal recourse to muscle-power was important. Flower (1955a, 1957b) demonstrated the relationship between size-increase, the periodic addition of float chambers, and the addition of calcareous matter towards the apex of the shell which increases the weight posteriorly. Together these features enabled elongate animals to lie level in the water, with the centre of buoyancy above the centre of gravity, or coincident with it. Coiling and septal crowding are two other mechanisms which hold the centre of buoyancy above the centre of gravity (Flower 1957b). Diaphragms across the siphuncle usually accompany septal crowding, indicating the point to which the endosiphuncular flesh has been resorbed, and of apical camerae flooded by seepage, forming liquid ballast (Wade 1988).

Presumably most Plectronocerida were nectobenthic in habit, although their ballasting was appropriate for swimming, and even the earliest plectronoceratids must have had considerable locomotor ability. These early forms lacked diaphragms, but were sufficiently small that ballast would not have been crucial to locomotion.

In the few later nautiloids that did not counterbalance, constriction of the shell aperture reduced the muscular effort required to hold animal and shell together. This is quite characteristic of breviconic shells, either with secondary ballast (Discosorida) or without it (Oncocerida).

The partial replacement of liquid with heavier aragonite as ballast was a critical step in the evolution of larger forms. Cambrian Ellesmerocerida were usually very slim longicones up to 150 mm or so in length, and round to oval in transverse section. By the end of the Cambrian or early Ordovician, the dorso-ventral angle of the apex had increased in recently developed genera, and shell length had reached 200 mm or more in genera such as *Metaellesmeroceras.*

A wave of breviconic Ellesmerocerida burst into the fossil record simultaneously in North America, China, Australia, Siberia and Europe. They identify the most widespread 'Gasconadian' or Lower Canadian fauna. Though endoconic and primitively circular in cross section, the shell had become compressed in many forms, depressed in some others, and most held at least juvenile traces of curvature. The larva of this group appears to have been quite large when shell formation began. The lack of a protoconch in all Ellesmerocerida (Flower 1964a) implies its origin in the Orthoceratoidea, to be perfected in Bactritoidea and subclass Dibranchia in general. Early longiconic Ellesmerocerida may have had a protoconch, but the fragile apex of the shell is unknown.

The Endocerida developed from a wide breviconic form without a protoconch. The three oldest known species, from Gasconadian (Lower Tremadoc) age rocks of north-western Queensland and China, are the first shells showing calcareous matter secreted as a counterbalance, with growth lines delimiting the endocones, and an axial space or endosiphotube, as found in later Endocerida.

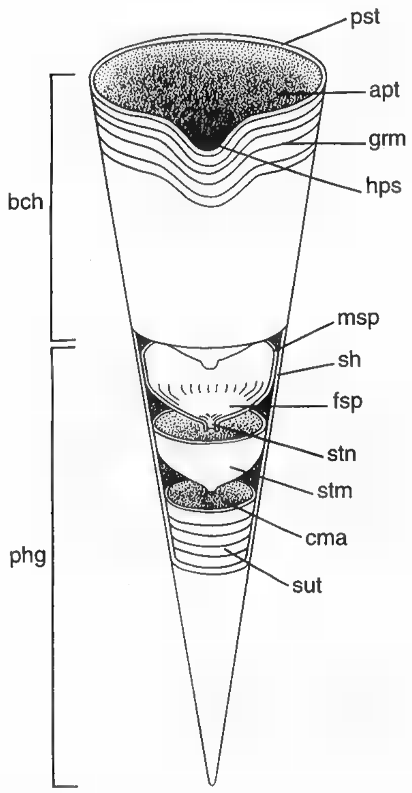

Figure 12.3 A straight, or orthoconic, nautiloid shell, illustrating the basic structure. The anterior septa are shown more widely spaced than they were in life to show their form. **apt**, aperture; **bch**, body chamber; **cma**, camera; **fsp**, free part of septum; **grm**, growth lines; **hps**, hyponomic sinus, which indicates the position of the mid-ventral line; **msp**, mural part of septum; **phg**, phragmocone; **pst**, peristome; **sh**, shell wall; **stm**, septum; **stn**, septal neck; **sut**, suture. (After Teichert 1964a) [D. Wahl]

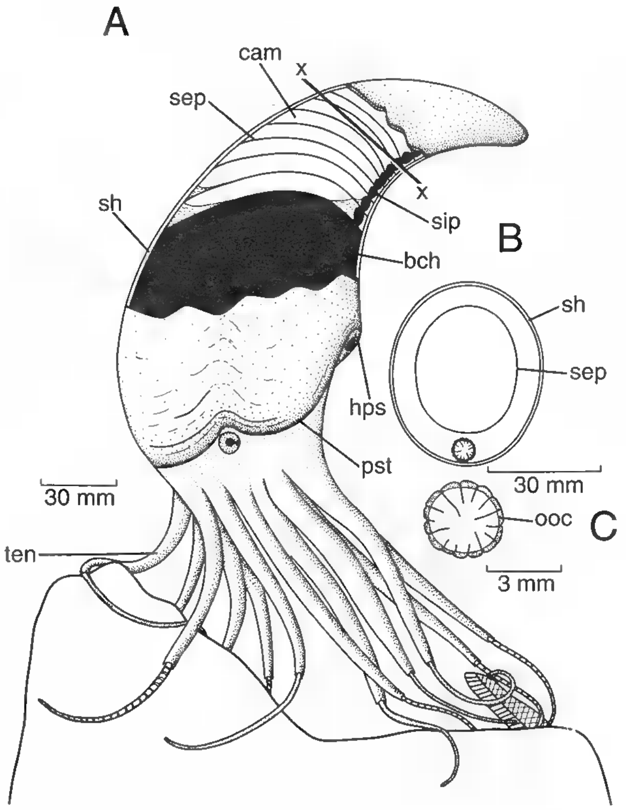

Figure 12.4 Oncocerida, family Polyelasmeroceridae. These thick-walled brevicones were nectobenthic, and had fewer tentacles than modern *Nautilus*. **A**, restoration of the animal in the position assumed in life; part of the shell has been removed to show the septa and siphuncle. **B**, anterior view of transverse section at X – X, intersecting a septum and the siphuncle. **C**, siphuncle showing the dark, organocalcite outer layer and inwardly directed lamellae arising from it; during fossilisation, the inner layer was replaced by clear calcite. **bch**, body of the animal in the body chamber; **cam**, air-filled camera, or chamber; **hps**, hyponomic sinus; **ooc**, organocalcite; **pst**, peristome; **sep**, edge of sectioned septum; **sh**, shell; **sip**, siphuncle; **ten**, tentacle, modelled on the distal cirrus and proximal tentacular sheath of a *Nautilus* tentacle. [S.P. Collin]

The Actinocerida were next to change from the form of ballast found in the Ellesmerocerida. As with the Discosorida, the ancestral stock of Actinocerida is unknown. Members of both groups have inflated connecting rings and are first found in decidedly older rocks in Australia than elsewhere (Wade 1977a, 1977b; Chen, T.E. 1983). In large species of the longiconic Actinocerida and breviconic Discosorida the initial portion of the shell, or apical camera, is large and cap-shaped. Longiconic early Discosorida can taper extremely or increase rapidly in size in the early shell; the latter may have led to brevicony.

Shortly after the Endocerida arose, ectoconically curved Ellesmerocerida (Bassleroceratidae) also appeared, and later gave rise to fully coiled forms, the early Tarphycerida. The wide variation in the time of appearance for the superorder Nautiloidea in various phylogenetic charts is due chiefly to the inclusion of Bassleroceratidae either in Ellesmerocerida (as here) or of its removal to Tarphycerida to place it with its probable descendants. Teichert (1988) maintained that Tarphycerida and Oncocerida originated separately from Bassleroceratidae (see Fig. 12.2).

The Orthoceratoidea was the last group in which a different ballast mechanism developed. Most forms utilised cameral deposits or cameral and siphuncular deposits. Some animals had empty shells, and probably used permanent adapic liquid ballast, like large *Sepia*. Conversely, the degree of calcareous deposition in the siphuncles, or siphuncles and camerae, of this and the other substantially straight-shelled superorders (Endoceratoidea, Actinoceratoidea and Discosoroidea), suggests that liquid formed part of their ballast at least in the deposition areas.

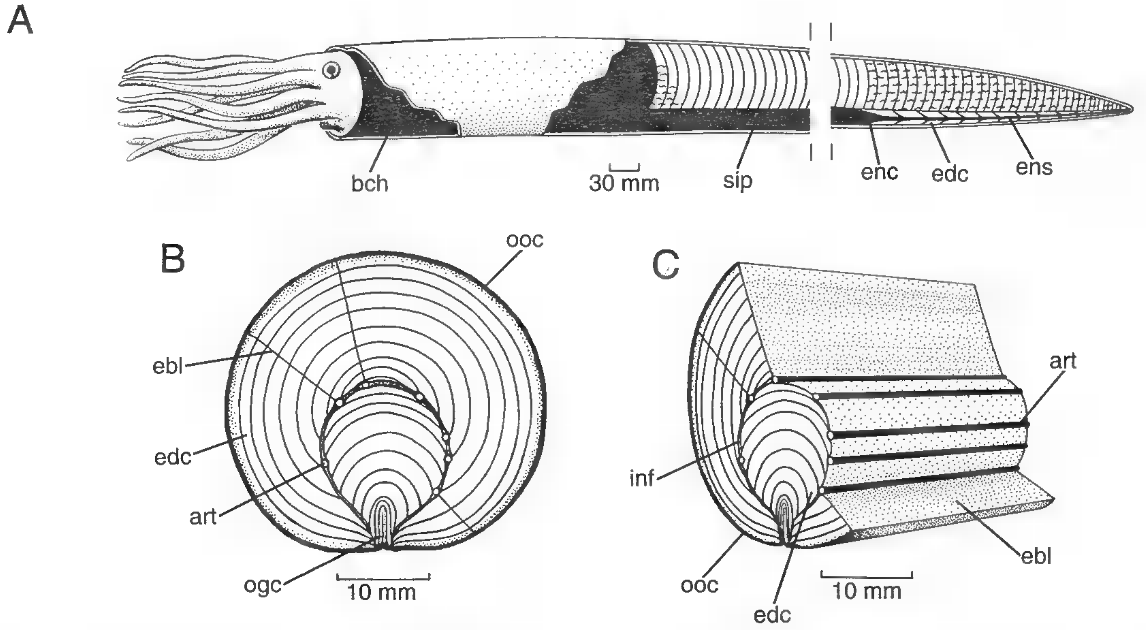

Figure 12.5 Endocerida. A, restoration of an animal in its shell. The gap represents 20–30 chambers in an animal of this size (shell length about 1.2 m). The epithelium of the mantle and siphuncle is shown in black; endocones are indicated diagrammatically in the calcareous deposit. B, endocone deposits and arterial system in an undescribed species of *Williamsoceras* from the upper Lower Ordovician, showing arterial system; approximately every fifth endocone is indicated. C, the same specimen split along the sites of endosiphuncular blades, and infula. **art**, tubular artery, shown restored in C; **bch**, body of animal within body chamber; **ebl**, endosiphuncular blade; **edc**, endocone; **enc**, endosiphocone; **ens**, endosiphotube; **inf**, infula; **ogc**, organocalcite, indicating infolding of siphuncular epithelium before deposition of endocones began; **ooc**, outer organocalcite; **sip**, siphuncle. [M.A. Saul]

An endoceridan is illustrated in Figure 12.5A–C. Groups of eight tentacular impressions and impressions of straight shells surrounding scuffled detritus have been attributed to Endocerida, the first nautiloids to carry calcareous and water ballast. The length of the largest ever found is estimated to be 9 m, with the proportions of a slender telegraph pole, and remnants in the Coolibah Formation indicate a shell 2–3 m in length and 80–120 mm in cross-section.

Blood Vascular Systems

In Australian material, impressions of the blood vascular system are found only in the siphuncle of taxa with calcareous deposits in the endosiphuncles. Each of these siphuncles is much larger, relative to cameral size, than that in *Nautilus*, so the systems revealed in the fossils are correspondingly more complex. Arterial systems are characterised by multiple longitudinal arteries that had fairly thick, organic walls. Venous systems have been preserved organically only in Actinocerida, but their general shape can be inferred in *Gouldoceras* (Discosorida).

Endoceridan arterial systems of adapically diminishing, rather straight, organic-walled tubes are preserved widely in representatives of the Allotrioceratidae and Najaceratidae (Flower 1955b, 1964b, 1968). In both families, the endosiphocone apex is compressed and attenuated adapically into a sheet draped around one or more infoldings of the endocone deposits into the endosiphocone (Wade unpublished data). The resulting infula has a double organic wall and often encloses longitudinal organic tubes or arteries (Flower 1964b). The largest number known (seven) occurs in Nora Formation fossils of the taxon *Cacheoceras* (Hill, Playford & Woods 1969), in which longitudinal arteries are present in many of the intersects between infulae.

In an unnamed species of the allotrioceratid genus *Williamsoceras*, the infula encloses several arterial tubes, and separates between the general endocone growth and the deposit laid down by a mid-ventral infolding of the siphuncular epithelium (Fig. 12.5B, C). In the Australian material, endocones are preserved well only in *Rossoceras*. The return venous system is assumed to have been a series of sinuses, like those in *Nautilus*.

The beaded siphuncles of Actinocerida contain the best known and the most peculiar circulatory systems (Teichert 1933, 1935; Flower 1939, 1957a, 1964b; Wade 1977a, 1977b). The blood-vascular system of an undescribed species of *Polydesmia* (Upper Lower Ordovician, Hanson River Beds, Northern Territory) is typical of Actinocerida (Fig. 12.6A–C). The annular actinoceridan siphuncular deposits may be very asymmetric, protruding adaxially, and changing the narrow interannular space between any two complete annulae from a disc; this is the plesiomorphic actinoceridan shape. The axial arteries delivered into 'radial' segmental arteries in the interannulae which could be very oblique (Fig. 12.6A–C). These arteries entered the perispatium, a blood sinus between the siphuncular filling and the connecting ring (Teichert 1933, 1935; Teichert 1964b), which allowed gas/liquid exchanges with the camerae through the epithelium and adjacent semipermeable connecting ring (Fig. 12.6B, C).

The discosoridan circulatory system is most easily interpreted (Fig. 12.7A–C). Two systems of 'canals' with different orientations became enclosed in the calcareous endosiphuncular deposit during growth. Peripheral to the axial space, a system of narrow, rather straight-walled canals extended backward and slightly outwards for about two segments before dividing and spreading laterally in the next segment. A system of inwardly broadening canals led through the radially crystallised endosiphuncular deposits, straight into the axial space ventrally, and dorsally into the mid-segmental spaces which are placed eccentrically about the axial space (Fig. 12.7B). The system of 'canals' which strongly displaced the developing calcareous deposit is interpreted as arterial.

The second or venous system displaced the calcareous deposits only slightly. However, it displaced the multiple arterial system to a peripheral position in or adjacent to the axial space, probably because this venous circulation is in a single large venous sinus, as in *Nautilus*. Logically, a capillary system would have linked the arteries and the venous system.

We may assume that the different siphuncular circulatory systems in each order developed from an original ellesmeroceridan system almost as simple as that preserved in the small *Nautilus* siphuncles, and the more elaborate systems developed independently in taxa that developed eurysiphonate, or large, siphuncles. The single artery in *Nautilus* is likely to represent a simplification of a more complex system.

Connecting Rings

The ectosiphuncle of fossils has been under scrutiny for many years, particularly by Flower (1955b, 1964a, 1964b). Broadly, connecting rings have been classified as three-layered like those of *Protactinoceras* (Fig. 12.8E) or modern *Nautilus*, or 'thin'. As *Nautilus* itself was designated as 'thin' until 25 years ago, thinness should be equated with 'unknown' rather than with 'single-walled' because of difficulty in preserving and detecting layering in siphuncle walls. The amount and arrangement of calcareous matter may be uniform or locally varied in different taxa. On a small scale, there were specialisations. In many endoceridans, an 'eyelet' of a different textured material found in the adapic edge of the connecting rings (Flower 1955a, 1955b, 1964b) may have been a barrier to reduce flooding of the adjacent chamber. The characteristic bullettes enabled recognition of generally simple, longiconic forms in Australia and China (Flower & Teichert 1957). Bullettes are thickenings developed within the connecting rings where they extend adapically through the neck immediately preceding each siphuncle segment.

Bifid connecting rings have been figured by Chen, J.-Y. & Teichert (1983) in several Protactinocerida, and occur in Australian *Protactinoceras* (compare Fig. 12.8E with Fig. 12.8C, D).

The richly phosphatic connecting rings of *Bactroceras latisiphonatum* (Hewitt & Stait 1985) are a rarity. Originally placed in the Ellesmerocerida, this species has unusually long chambers and some cameral deposits, features with a strong resemblance to those of Orthocerida. It was thus well on the way towards Orthocerida.

THE AUSTRALIAN FOSSIL RECORD

Taxonomic work on Australian Nautiloidea is proceeding rapidly at present. Cambrian and Ordovician faunas are moderately well known (Fig. 12.9). The Silurian and Upper Palaeozoic nautiloids are less numerous than those of the Ordovician faunas, but still much richer than have been described. Much less stratigraphic detail is available for the Middle and Late Palaeozoic faunas than for Early Palaeozoic faunas. The absence of nautiloids in the Carboniferous reflects the predominance of non-marine sediments in the region, although Australian marine Carboniferous beds indicate glacial to subglacial conditions at that time. Fossils are lacking for the Triassic and Jurassic, as marine deposits of this time are almost unknown in Australia, and the record of Cretaceous to Tertiary rocks is abbreviated.

The superorder Plectronocerida is represented by the rare *Paraplectronoceras* in the upper Cambrian, above the Protactinocerida.

The Protactinocerida is known at present only from China, and from the genus *Protactinoceras* of the Upper Cambrian of north-western Queensland (Fig. 12.8A–E).

The Ellesmerocerida is represented in the Australian Cambrian by 21 genera (Fig. 12.9). The cosmopolitan Lower Ordovician (Gasconadian) fauna which developed subsequently, included the oldest known Endocerida, from North China and north-western Queensland. Description of this fauna requires adequate studies of variability, both in the abundant, partly fragmented material and in several equally damaged representatives of genera and species elsewhere. Numerous slightly younger Ellesmerocerida occur in the Lower Ordovician of Western Australia (Canning Basin) (Fig. 12.9). *Cyrtocerina* is an unusual genus with extremely thick connecting rings; other similar forms are found in the Canning Basin (*Eothinoceras*), Amadeus Basin (*Bathmoceras*) and Tasmania (*Centrocyrtocerina*). Ellesmerocerida tended to be minor components of the nautiloid faunas after the Lower Ordovician.

The oldest endoceridans in Australia are an undescribed genus and *Proterocamerocerina*, first described from northern China (Chen, J.-Y. & Zou 1984). An undescribed species of the latter occurs in the Mort Member of the Ninmaroo Formation. These early Endocerida are derived from moderately large Ellesmerocerida with endoconically curved, breviconic shells that widened rapidly, at least when young, and were part of a mid Lower Canadian or Late Gasconadian fauna.

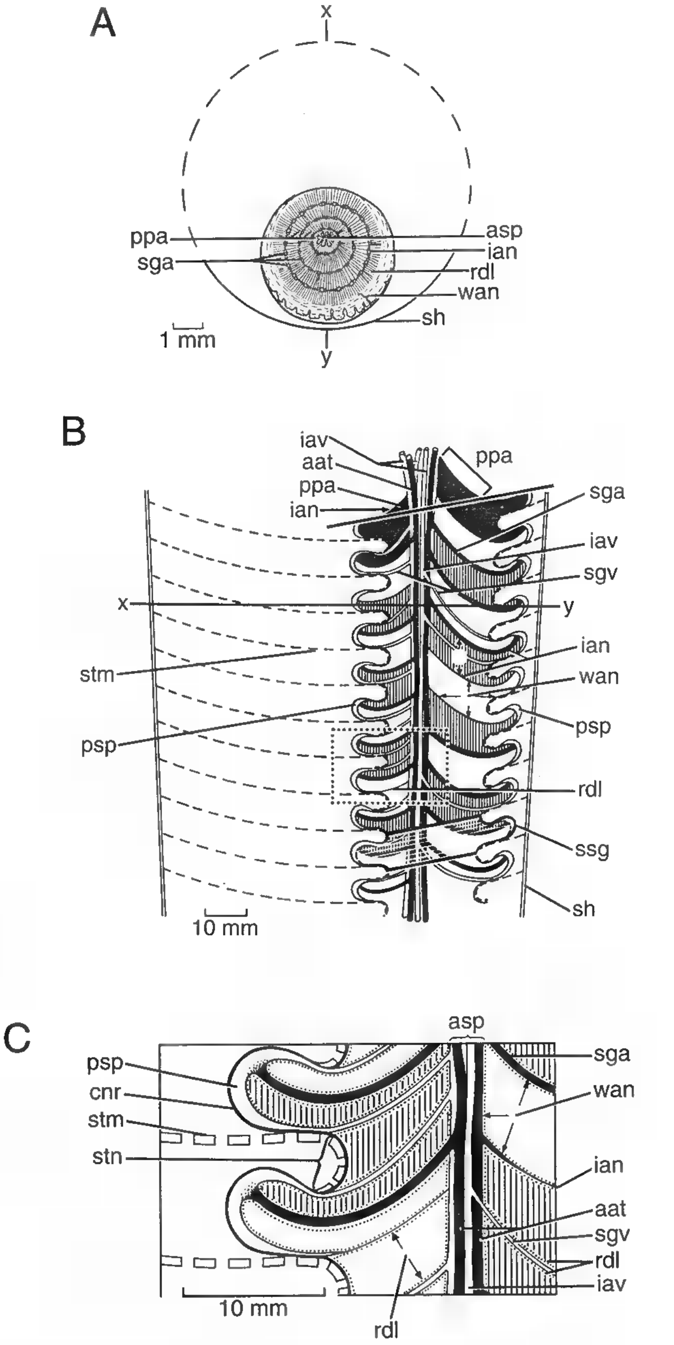

Figure 12.6 The actinoceridan blood-vascular system, illustrated in *Polydesmia* sp. A, venter, partial septa and siphuncle of adult, showing transverse section at X–Y in B. B, sagittal section through a young specimen. C, an enlargement of the box marked in B. **aat**, axial arteries; **asp**, axial space or canal; **cnr**, connecting ring; **ian**, interannulus; **iav**, axial veins – inferred; **ppa**, protruded part of annulus; **psp**, perispatium; **rdl**, radial lamellae; **sga**, segmental arteries or radial canals; **sgv**, segmental veins; **sh**, shell; **ssg**, siphuncular segment; **stm**, septum; **stn**, septal neck; **wan**, walls of annulus. [M.A. Saul]

The genera *Coreanoceras* (basal upper Lower Ordovician), from north-western Queensland and adjacent Northern Territory, and *Manchuroceras*, from the lower Coolibah Formation, are the earliest advanced Endocerida. Endocerida were common in the upper Lower and lower Middle Ordovician faunas, *Anthoceras* being particularly widespread. This genus occurs in the Canning Basin, Amadeus Basin, Georgina Basin and at Mt Arrowsmith (north-western New South Wales). A diverse endoceridan fauna from the upper Canadian of Tasmania includes *Manchuroceras*, *Piloceras* and *Yehlioceras* (Teichert 1947). Endocerida were also important in the Whiterockian faunas of Tasmania and Georgina Basin, and declined in importance thereafter.

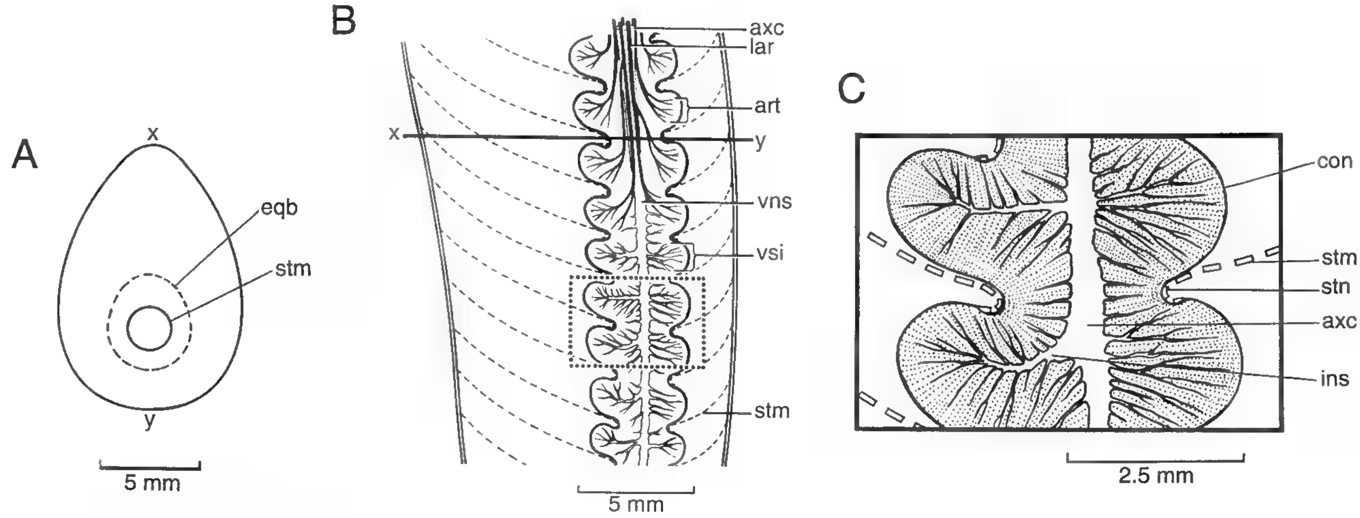

Figure 12.7 The discosoridan circulatory system, illustrated in *Gouldoceras synchonena*. **A**, diagrammatic transverse section of shell, showing appearance at X–Y in B. **B**, sagittal section of beaded siphuncle, showing the eccentric position of the axial cavity, and the arrangement of crystals forming a siphuncular deposit radial to the connecting ring surfaces. **C**, enlarged view of section outlined in B. **art**, small arteries; **axc**, eccentric position of axial cavity; **con**, connecting ring; **eqb**, equatorial bulge of segment; **ins**, lenticular intrasegmental space; **lar**, multiple longitudinal arteries; **stm**, septum; **stn**, septal neck; **vns**, axial venous system; **vsi**, venous sinuses. [M.A. Saul]

The oldest Actinocerida (including *Armenoceras* and an undescribed genus) are among the earliest Coolibah Formation nautiloids (Fig. 12.9). A possible actinoceridan occurs earlier still, in the top level of the Kelly Creek Formation (late Demingian, very late Tremadoc). Actinocerids of early Middle Ordovician age approximating those in North America are known for the Whiterockian Stairway Sandstone, Amadeus Basin (Stait & Laurie 1985), the Whiterockian of Tasmania (*Wutinoceras* and *Adamsoceras*; Stait 1984), and for the Chazyan (*Armenoceras*).

Few actinoceridans are known from sequences younger than the Ordovician. *Ormoceras* and *Actinoceras* have been reported from the Silurian of Yass (Teichert & Glenister 1952); the oldest stratigraphic record of the latter genus is from the Whiterockian in the Georgina Basin, where it occurs earlier than *Wutinoceras*. *Armenoceras* is the oldest described genus of Actinocerida in Australia, though it occurs later elsewhere. *Fibroceras* and *Polydesmia* occur together in the Hanson River Beds, Northern Territory, as they do in China (Lai 1985).

Early Australian Discosorida appear to be members of the family Pseudowutinoceratidae. They may have diverged during the same period of ellesmeroceridan diversification as the Actinocerida, since the shells of early members of both groups are similar. The oldest occurs in the Georgina Basin in the early Lower Arenig or Middle Canadian part of the Coolibah Formation. *Madiganella* is common in the Upper Canadian to Whiterockian of the Amadeus Basin (Teichert & Glenister 1952; Stait & Laurie 1985). This group increased greatly in importance in the Middle Ordovician, a little after the actinoceridan acme, and dominated the Middle and Upper Ordovician of Tasmania, although they were represented only by the family Gouldoceratidae (Stait 1984b). The Discosorida were also important in the Devonian.

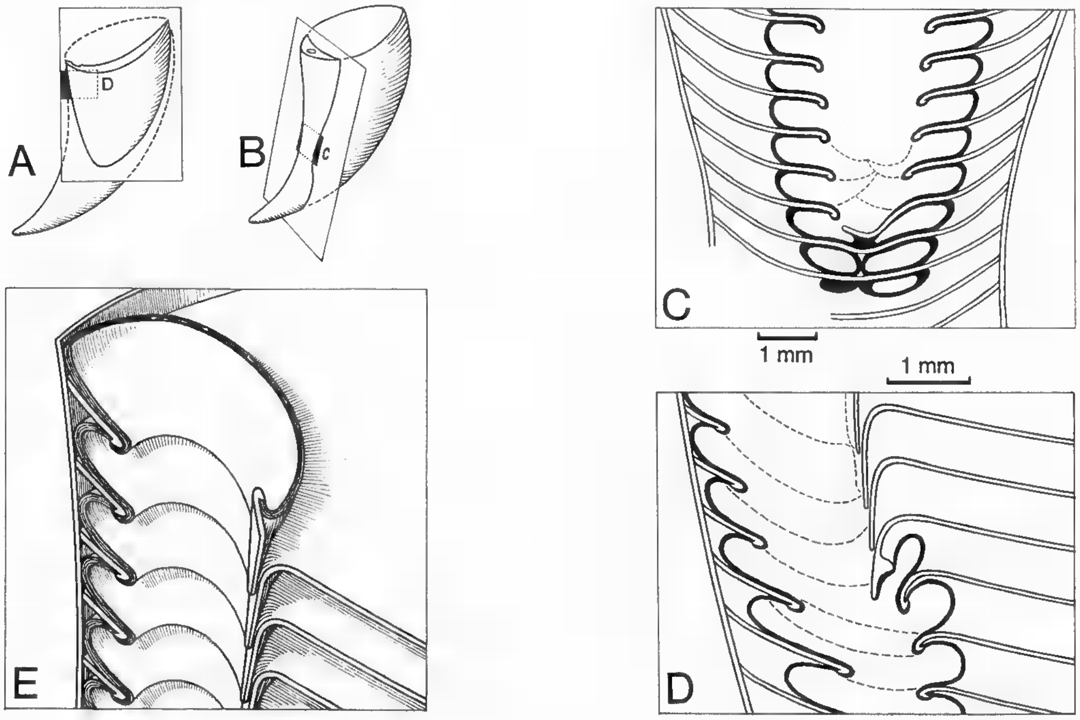

Figure 12.8 *Protactinoceras* from North China and Australia. A, B, showing position and orientation of sections through sub-adult (C) and young (D) phragmocones. C, D, illustrating the dorsally bifid 'bulge' of the bilateral connecting rings; dashed lines indicate incomplete diaphragms in C. E, sagittal section of adult, from etched, polished sections of Australian material, to show the triple layering observable in well-preserved, organocalcite connecting rings. Thick black lines indicate this organocalcite in C and D. Clear shell material is shown as white in sections C–E. (C, D, after Chen, J.-Y. & Teichert 1983; E, after Wade unpublished data, courtesy Queensland Museum) [M.A. Saul]

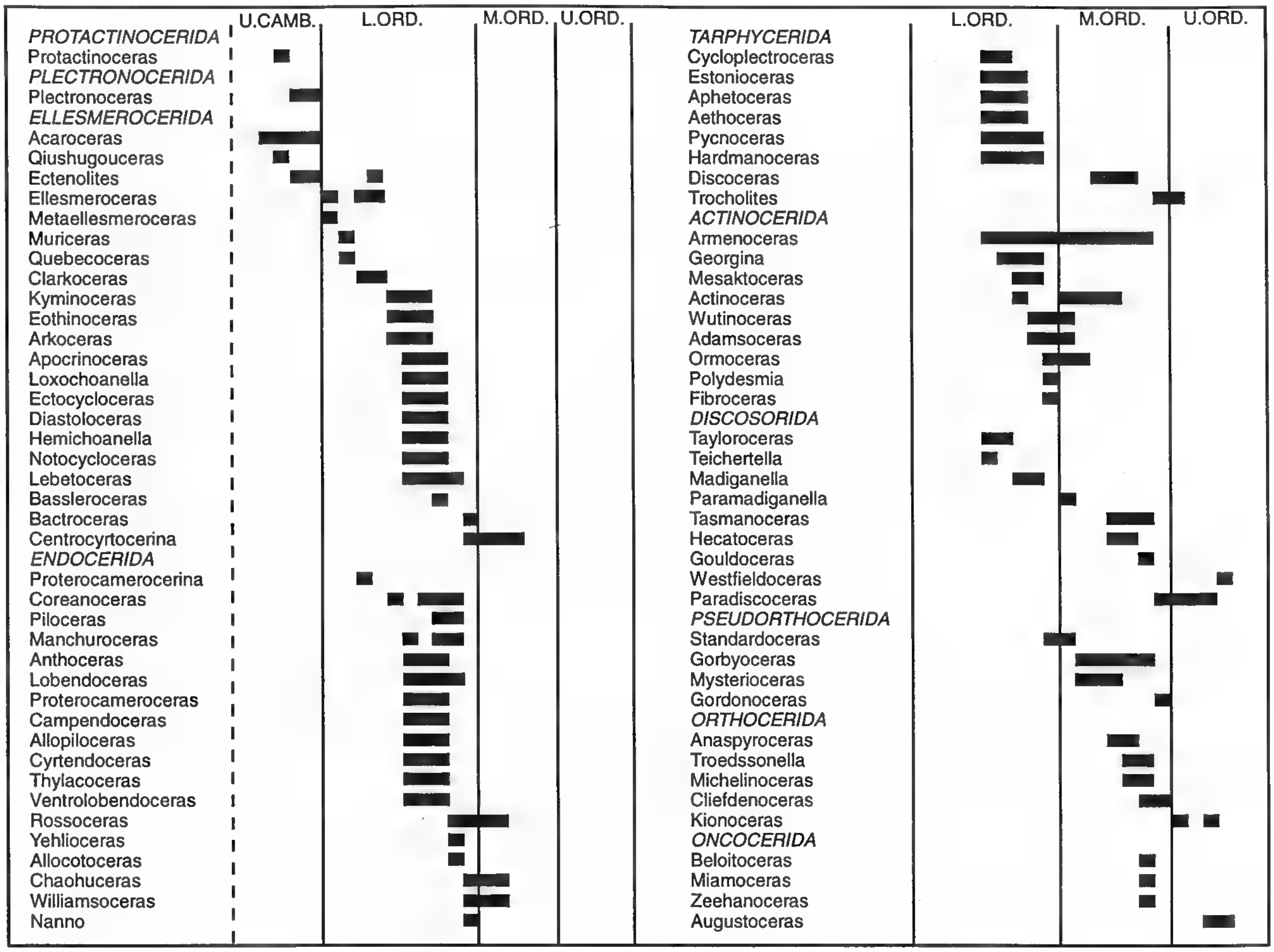

Figure 12.9 Stratigraphic ranges and ordinal positions of nautiloid genera described or identified from the Upper Cambrian and Ordovician rocks of Australia before 1989. The identification of the internationally agreed Cambrian-Ordovician boundary marker – the base of the *Cordylodus intermedius* conodont zone – is based on microfossils that are not yet correlated with certainty in Australian rocks. **M.ORD.**, Middle Ordovician; **L.ORD.**, Lower Ordovician; **U.CAMB.**, Upper Cambrian; **U.ORD.**, Upper Ordovician. [I. Hallam]

Last to diversify, the Orthocerida, were never a major part of the (predominantly Lower) Ordovician fauna of Australia, but became more important during the remainder of the Palaeozoic. The Ordovician forms tended to be widespread, though some endemic or rather restricted genera, such as *Standardoceras*, *Gordonoceras*, *Mysterioceras* and *Stromatoceras* are known from Tasmania, especially in the late Middle and Late Ordovician (Stait & Flower 1985). *Graftonoceras*, *Dawsonoceras*, *Kionoceras*, *Geisonocerina* and *Protokionoceras* are all known from the Silurian of New South Wales and Victoria.

The Devonian orthoceridan faunas are widespread; *Dolorthoceras*, *Buchanoceras* and *Plagiostromoceras* are known from the Lower Devonian, and *Sceptrites*, *Buchanoceras* and *Michelinoceras* are recorded from the Middle Devonian of Victoria. Teichert (1939, 1940) described *Michelinoceras*, *Galtoceras*, *Wadeoceras*, *Conostrichoceras* and *Cayutoceras* from the Upper Devonian of Western Australia. Teichert & Glenister (1952) recorded the orthoceridan genera *Mooreoceras* *Pseudorthoceras*, and *Brachycycloceras* from the Permian of Western Australia.

The earliest Australian tarphyceridan is a long-ranging species of *Cycloplectroceras* which occurs from 6 m above the base to the top of the Coolibah Formation, upper Middle and Upper Canadian. Elsewhere, the genera *Pycnoceras* and *Discoceras* are known from the Tasmanian Ordovician, and *Paradiscoceras*, *Cleifdenoceras* and *Trocholites* are recorded from central New South Wales.

Only four oncoceridan genera are known from the Ordovician of Australia, all from Tasmania (Stait 1982). They are much more common in the Devonian (Teichert & Glenister 1952) especially *Macrodomoceras, Polyelasmoceras*, *Brachydomoceras* and *Plectinoceras* from the Middle Devonian of Victoria. They are not known from any other time period.

The earliest records of the Upper Palaeozoic to Recent order Nautilida are from Devonian rocks in north-eastern Queensland; the nautiloid component of that fauna is largely undescribed. A large form, probably a new genus allied to *Subvestinautilus*, occurs at Big Bend on the Burdekin River north of Charters Towers. A very rare *Diademoceras* from Storm Dam, Wando Vale Station has so thick a shell (4 mm) that it must have been benthic. A possible member of the superfamily Trigonoceratoidea was found nearby. *Litogyroceras* is recorded from the Middle Devonian of Victoria (Teichert & Glenister 1952), and a fauna including *Domatoceras*, *Stearoceras*, *Titanoceras* and *Phacoceras* is known from the Permian of Western Australia (Teichert 1951).

Both marine and terrestrial faunas changed dramatically at the close of the Triassic. The only known survivor of eight Upper Triassic families after the Jurassic was the genus *Cenoceras*, from which the Recent superfamily Nautiloidea radiated. The Australian representatives and their local ranges are illustrated in Figure 12.10. The oldest Australian members of the superfamily Nautiloidea in Australia are two genera of Albian age (upper Lower Cretaceous) that occur together in parts of the Great Artesian Basin. They have been confounded as one species, perhaps since two of the four

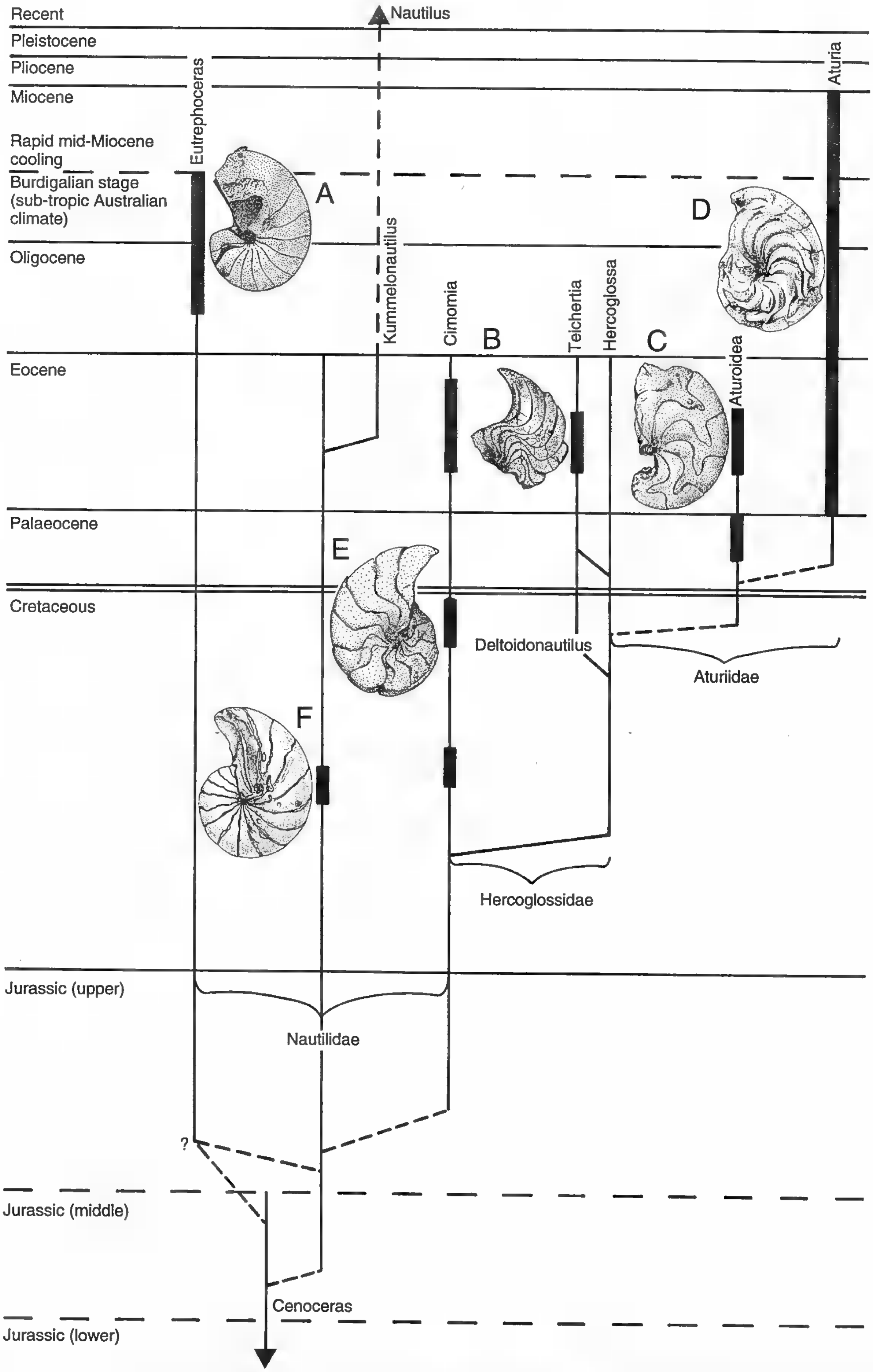

Figure 12.10 Phylogeny of the superfamily Nautiloidea. Thin lines indicate total ranges and dashed lines show uncertain links in the phylogeny; thick lines show the ranges of Australian representatives. Lineages divide where a new morphology has eventuated, not at the earliest possible ancestor or the last possible derivative. A, *Eutrephoceras geelongensis*, Upper Eocene, Murray River, South Australia. B, *Teichertia prora*, Middle Eocene, Giralia Range, Western Australia. C, *Aturia stansburiensis*, Late Oligocene, Yorke Peninsula, South Australia. D, *Aturoidea brunnschweileri*, Middle Eocene, Giralia Range, Western Australia. E, *Kummelonautilus hendersoni*, Albian, Great Artesian Basin. F, *Cimomia tenuicostata*, Upper Cretaceous, Giralia-Cardabia Range, Western Australia. (*E. geelongensis*, after McGowran 1959; *K. hendersoni*, after Etheridge 1901; *C. tenuicostata*, *T. prora*, *A. brunnschweileri*, after Glenister *et al.* 1956; *A. clarkei*, after Glaessner 1955)
[I. Hallam]

specimens on which Etheridge (1901) based *Nautilus hendersoni* probably belong to *Kummelonautilus*. As the suture of the type species of *Kummelonautilus* has not been described, all assignments to *Kummelonautilus* retain an element of doubt. Etheridge remarked on the variability of the suture, from quite strongly curved to rather straight. The latter is typical of the second genus, the rarer, more rotund *Cimomia*. This *Cimomia* species is probably the only undescribed Cretaceous-Tertiary form at present. *Kummelonautilus* is central in the phylogeny which Teichert & Matsumoto (1987) proposed for *Nautilus*. The creation of this genus, and assignment to it of species formerly placed in either *Cimomia* or *Eutrephoceras* has effectively isolated the latter, the only member of the superfamily Nautiloidea with relatively straight sutures (Fig. 12.10).

A beak or rhyncholite reminiscent of *Leptocheilus* (range Upper Jurassic to Lower Cretaceous) is present in a specimen with a heavy umbilical callus, originally over 160 mm diameter, and tentatively identified as *Kummelonautilus hendersoni*.

Kummelonautilus hendersoni (Toolebuc Formation to Macunda Formation) appears to be the oldest Australian member of the Nautilidae. The shell of *Kummelonautilus* is notably more compressed than many upper Triassic to Upper Jurassic *Cenoceras*, but is accepted as a descendant of the latter (Teichert & Matsumoto 1987). The shell ornament of *Cenoceras* is typical of that found in juvenile *Nautilus*; the shell of *Cimomia* appears to be smooth, except in *C. tenuicostata* (Fig. 12.10).

The phylogeny of early nautilids is far from understood, and the depauperate Australian fauna is uninformative. *Cimomia* is the more common of the two nautiloid genera in the Carpentaria sub-basin, a little more recent than many *K. hendersoni*, and specimens occur closer to oceanic water. *Kummelonautilus* and *Cenoceras* are believed to coexist in Uppermost Middle Jurassic and *Eutrephoceras* and *Cimomia* had appeared in Upper Jurassic. The last two are similar in shell shape, but so different in sutures as to suggest a relatively disjunct ancestry (Fig. 12.10).

Cimomia appears to be the progenitor of *Hercoglossa*, from which arose *Deltoidonautilus* and *Teichertia* (Fig. 12.10). These derivatives, with angular margins and 'hercoglossan' sutures, are accepted as genera of the family Hercoglossidae. *Aturoidea* appears to have evolved in Upper Cretaceous from certain *Hercoglossa* (Fig. 12.10), from which it differs significantly in several features shared with *Aturia*.

Deltoidonautilus had evolved by the Upper Cretaceous, although the Australian material originally assigned to this genus formed part of a new genus *Teichertia* (Glenister, Miller & Furnish 1956). Though the latter genus is morphologically somewhat intermediate between *Hercoglossa* and *Deltoidonautilus*, it occurs too recently to be intermediate in the lineage. Whether its progenitor was *Deltoidonautilus* or *Hercoglossa* is unknown. These three genera make up the Hercoglossidae.

The superfamily Nautiloidea is represented therefore by three or four families (Nautilidae, Eutrephoceratidae, Hercoglossidae and Aturiidae) depending on whether *Eutrephoceras* is included in the Nautilidae or placed in a monotypic family.

Overall, the Australian record of the superfamily Nautiloidea is rather poor. Marine Jurassic and lower Lower Cretaceous (pre-Aptian) marine deposits are rare, but the Hercoglossidae and one of the older *Cimomia* species were confined to Western Australia and apparently preferred warmer conditions, as indicated by some of the associated Foraminifera. The South Pole was situated adjacent to the south-western Pacific in the Lower Cretaceous, and the Australian inland seas of the Aptian and Albian stages were cool. Nevertheless, the record started there with *Kummelonautilus* and *Cimomia*. Even later, Western Australian seas were always warmer than coeval south-eastern Australian seas, though no deposits warmer than subtropical are known at any epoch. The cool epoch during the Oligocene reduced the Australian fauna *Eutrephoceras*. Only *Aturia*, which appeared in the Eocene, was present in the fossil record after the late Miocene chill which followed swiftly on the subtropical conditions of the upper Lower Miocene Burdigalian stage; this genus was still present in Victoria in the Upper Miocene (T. Darragh personal communication).

BIOGEOGRAPHY

The regional biogeography of Australian Ordovician nautiloids has been examined in detail, and allows an Australia-wide picture to be obtained for the Ordovician (Burrett & Stait 1985, 1987; Stait & Burrett 1987). However, a brief discussion of the affinities of the fauna from the Cambrian system is warranted as the North China province (*vide* Chen, J.-Y., Zou, Chen, T.E. & Qi 1979a, 1979b; Chen, J.-Y. 1980) included the Georgina Basin, north-western Queensland, from Cambrian into early Ordovician.

The five genera identified in the Cambrian of Australia (*Protactinoceras*, *Acaroceras*, *Quishugoceras*, *Ectenolites* and *Paraplectronoceras*) also occur on the North China platform. The extremely diverse Upper Cambrian fauna of North China is reduced in Australia, despite the close juxtaposition of the two areas (Burrett & Stait 1987).

The Australian Ordovician are best considered as two groups for biogeographical purposes: the basal Ordovician to lower Middle Ordovician faunas, and the middle Middle to Upper Ordovician faunas. This subdivision is made as only the Tasmanian sequences contain nautiloids throughout the Ordovician. Central and Western Australian, and Queensland sequences do not extend past the lower Middle Ordovician. Later deposition was confined to central New South Wales sequences, which do not contain nautiloids until the upper Middle Ordovician, and Tasmania.

North China and north-western Queensland are closely matched as centres of early nautiloid development, from Upper Cambrian through Gasconadian. By basal Ordovician (Gasconadian) time, the distribution of rich faunas had widened to include Eurasia and North America, but a subdivision into local faunas followed, in a time-span widely regarded as Arenig, equal to upper Middle and Upper Canadian (respectively Jeffersonian and Cassinian) and Whiterock (upper Lower Ordovician).

During the upper Lower Ordovician, Australian nautiloids were divided into eastern Australian and western Australian provinces, separated by a barrier through central Australia (Stait & Burrett 1987) and probably by a climatic barrier to the north. The nautiloid faunas of the Canning and Amadeus Basins are extremely similar, but very different from the fauna in the Georgina Basin. However, in the early Middle Ordovician a sea-way formed across Australia (Larapintine Sea; see Fig. 1.96C) and nautiloid faunas were very similar overall, including Tasmania.

The middle Middle to Upper Ordovician can be subdivided also. In the middle Middle Ordovician a series of small, carbonate fringing platforms formed on the submerged Molong High, central New South Wales (Webby & Packham 1982). Although a shallow-water carbonate platform was also present in Tasmania at this time there were very few similarities between the nautiloid faunas of the two areas (Stait & Burrett 1987). The Tasmanian sequence at this time was dominated by the nectobenthic Gouldoceratidae which were evidently unable to cross the deep water barrier. Tasmanian nautiloid faunas became highly endemic during the Middle and Upper Ordovician, probably as a result of their increased isolation from other shallow-water sequences.

Detailed Australia-wide studies of the post-Ordovician Palaeozoic nautiloid faunas have yet to be published. The faunas of the Devonian system are especially promising as they are widespread and diverse, and because elsewhere in the world the Devonian was a time of great diversity and rapid evolution in the Nautiloidea.

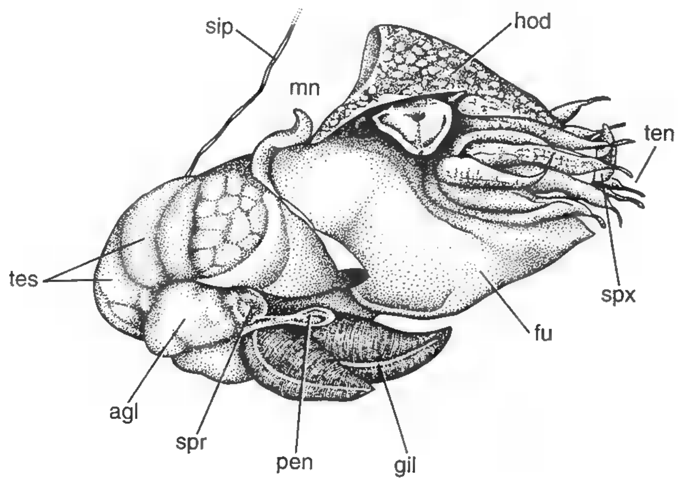

Figure 12.11 *Nautilus pompilius* (Nautilidae) extracted from the shell, part of mantle and right gills cut away to show male reproductive structures and major morphological features. **agl**, accessory glands; **fu**, funnel; **gil**, gills; **hod**, hood; **mn**, mantle; **pen**, penis; **sip**, siphuncle; **spr**, spermatophore sac; **spx**, spadix; **tes**, testis; **ten**, tentacles. (After Haven 1977) [D. Wahl]

The soft-part anatomy is primitive in comparison with that of other living cephalopods (Figs 12.1, 12.11; Pl. 21.2). *Nautilus* lacks chromatophores, tentacular sucker discs, and ink sac, and has a 13–element radula, jaws with calcite denticulation, four gills, an eye without a lens, 90 tentacles and a prominent spadix.

Knowledge of *Nautilus* is derived from diverse sources, including trapping data, aquarium and scuba-based observations, telemetric tracking, remote camera sequences, and shell radioisotopes (see Saunders & Ward 1987a for review). The animals range from near-surface to *ca* 500 m depth, but their optimal range seems to be 150–300 m. Factors controlling the upper limits include predation by teleost fishes and water temperature. The upper optimal temperature limit seems to be 21°C, and temperatures exceeding 25°C are lethal. These two factors explain why most shallow-water sightings of *Nautilus* are nocturnal and during cold months. Maximum depth limits are determined by shell implosion (*ca* 800 m) and chamber flooding (*ca* 300–400 m).

Males typically outnumber females by 5:1. The large eggs are laid singly or in groups of two or three. Growth is slow, and animals may live for years after maturity is reached at an estimated 5–15 years of age.

Superfamily NAUTILOIDEA

Family Nautilidae

The only living genus of this ancient and once-abundant subclass of externally shelled cephalopods is *Nautilus*. Until recently, knowledge of these enigmatic living fossils was severely limited by their inaccessible habitat. They were thought to be quite rare, and to occur at only a few remote Pacific island sites. They are known now to occur throughout much of the Indo-Pacific, where they seem to thrive as scavengers and opportunistic predators on deep reef slopes, competing successfully with deep-water crustaceans and fishes (Saunders 1987; Saunders & Ward 1987a).

The presence of living *Nautilus* in Australia was long suspected, on the basis of drift shells and a few beach-stranded specimens (for example, Iredale 1944; Cotton 1957a, 1957b), but living populations have been documented recently. *Nautilus pompilius* and *N. stenomphalus* occur together on the Great Barrier Reef off Queensland (Saunders & Ward 1987b), and a population of *N. pompilius* is now known from Rowley Shoals, 400 km NNE of Port Hedland, Western Australia. These two very disjunct occurrences, combined with the presence of drift shells elsewhere in Australia, suggest that *Nautilus* may be a ubiquitous component of Australian deep reef slopes. This account summarises what is known of the genus in Australia. For more detailed information, the monographic treatments of Owen (1832), Griffin (1900), Willey (1902, anatomy and physiology); Kummel (1964, fossil record); Stenzel (1964, natural history and morphology); Saunders & Landman (1987) and Ward (1987, natural history and physiology) should be consulted.

The shell of *Nautilus* is compressed and involute (*N. pompilius*) to umbilicate (*N. macromphalus*) and even slightly perforate (*N. scrobiculatus*). An umbilical callus may be present. Shell sculpture consists of sinuous growth lines with delicate to moderately strong, longitudinal lirae in some species. Shell colouration is variable. Typically, irregular red- to yellow-brown stripes radiate from the umbilicus. These cover the entire shell in juveniles, but in adults they are restricted to the dorsal, chambered portion of the adult shell. The adult aperture also shows deep hyponomic and ocular sinuses and a thickened, blackened margin. Typically, the shell has 32 septa that are perforated centrally by orthochoanitic septal necks accommodating a small siphuncle. The suture includes shallow lateral, umbilical, and dorsal lobes. Males have larger and broader shells than females when mature.

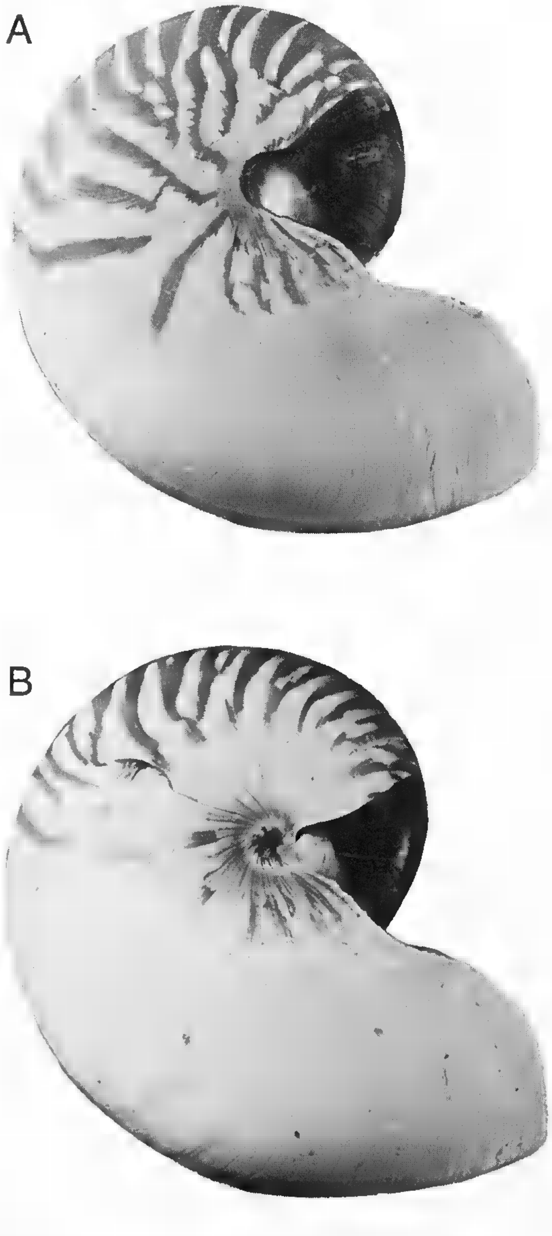

Figure 12.12 Shells of *Nautilus* species (Nautilidae) caught alive on Carter Reef, Queensland, at depths of 250–440 m. A, *Nautilus pompilius*. B, *Nautilus stenomphalus*; note the reduced colour pattern and the open umbilicus characteristic of *Nautilus stenomphalus*. [W.B. Saunders]

Catholic in diet, *Nautilus* species locate food with highly developed chemosensory cells located on the inner surface of the tentacles. The jaws are powerful, and are armed with heavy calcite elements that permit them to break and cut through bone and thick carapaces. The crop can distend greatly to accommodate food equal to 20% of the body weight. Crop contents indicate that decapod crustaceans are standard fare, but echinoid fragments, fish bones, coleoid beaks and *Nautilus* tentacles have also been observed. Live fishes may be taken as prey if they are confined, as shown by partly eaten teleosts and sharks in *Nautilus* traps, but it is doubtful whether fishes can be caught in open water.

Nautilus is highly mobile; tagged animals have moved over 150 km in one year, and telemetric tracking has recorded movement exceeding 1 km/day. An individual is capable of moving over its entire depth range (*ca* 0–500 m) in a single day. Telemetric devices show that the animals move into shallow water at night, and return to deeper water during twilight. However, deep-water camera studies show that the animals are not exclusively nocturnal, but remain active during daylight (Carlson, McKibben & DeGruy 1984; Saunders 1984; Ward, Carlson, Weekley & Brumbaugh 1984).

Living species are confined to the Indo-Pacific (*ca* 30°S to 30°N, *ca* 90° to 185°W), but fossil forms were cosmopolitan. The geologic range of *Nautilus*, like its origin, is poorly known. The genus seems to have been established by the early Tertiary (Eocene), but it is unknown from the late Tertiary. It probably evolved from the widespread and long-ranging (Triassic to Tertiary?) genus *Cenoceras* (Teichert & Matsumoto 1987). The genus is absent at many sites where it would be expected, for example, in Yap (Western Caroline group) and in Tonga, where physical factors such as water temperature are not limiting. The present distribution is thought to be a product of vicariance, and biotic interactions, most notably competition and predation by fishes and *Octopus* (Saunders 1987; Saunders, Spinosa & Davis 1987).

The genus includes five well-established species which can be distinguished on shell differences, and soft-part morphology in some instances (Saunders 1987), and two others of doubtful validity. Electrophoretic analyses of allozymes of the five species have been partly completed (Woodruff, Mulvey, Saunders & Carpenter 1983; Woodruff, Carpenter, Saunders & Ward 1987), and indicate a general genetic agreement with the morphologically based taxonomy given here. The Australian species of *Nautilus* include *N. pompilius* and *N. stenomphalus*.

Nautilus pompilius is the most widely distributed species and is best known from the Philippines. Living populations occur between American Samoa and the Andaman Islands, but shells drift as far as Madagascar and Kenya. The southernmost occurrence is Australian, and a single live specimen was found off Japan. Other occurrences include the Papua New Guinea region, Vanuatu and Fiji (House 1987; Saunders 1987).

Drifted shells are fairly common on Queensland beaches, but the only documented live-caught specimens were trapped at 250–440 m depth off Carter Reef, 20 km north-east of Lizard Island, Great Barrier Reef (Saunders & Ward 1987b). Specimens were collected at about 400 m depth by shrimp trawlers operating 7–60 km east of Mermaide Reef, Rowley Shoals, off Western Australia.

The shell has a minute umbilicus which, with rare exceptions, is filled with a callus (Figs 12.12A, 12.13A). The usual shell colouration comprises irregular, branching reddish stripes which radiate from umbilicus to venter, although colouration is variable in Australian populations (compare Fig. 12.13A, B). At maturity, shell size and animal weight are highly variable geographically. Mean shell diameter and shell body weight are 165 mm and about 850 g in animals from the Philippines. Specimens from the Great Barrier Reef are slightly smaller (mean shell diameter 155 mm, mean weight about 630 g), and shell stripes do not extend to the umbilicus in some specimens.

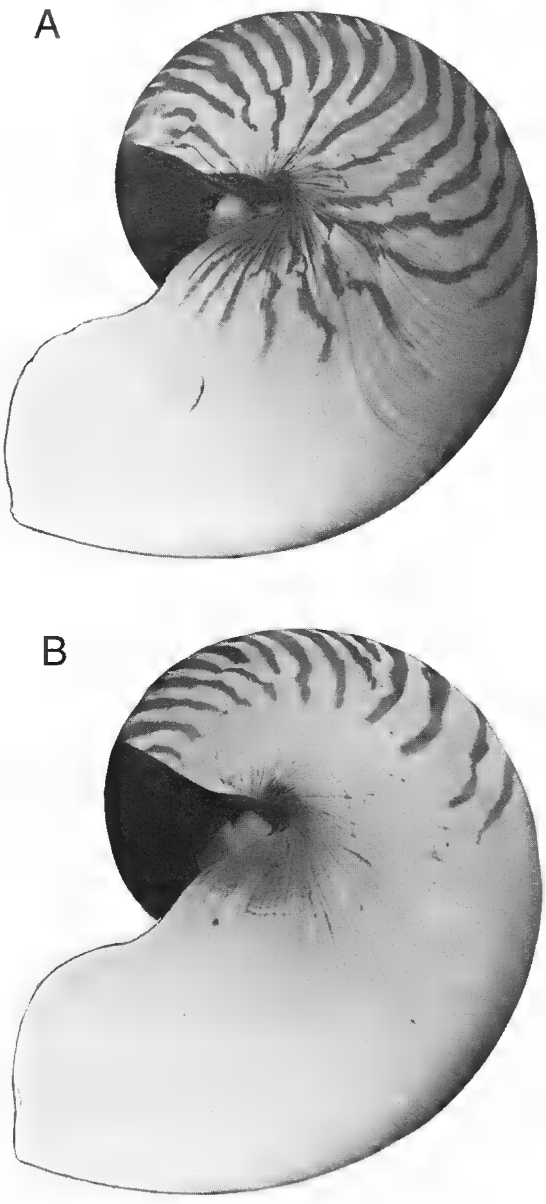

Figure 12.13 Colour variation in shells of live-caught *Nautilus pompilius* (Nautilidae) from Mermaide Reef, Rowley Shoals, Western Australia. A, typical colour pattern. B, greatly reduced colour pattern of the *repertus* form of *Nautilus pompilius*. [W.B. Saunders]

The Western Australian population includes the largest specimens known, with a mean shell diameter and mean weight of 222 mm and 1675 g, respectively. Shell striping varies from the typical form to reduced yellowish stripes that leave the umbilicus and much of the flanks white. Iredale (1944) described *N. repertus*, citing the large size (*ca* 228 mm), white umbilical region, and orange-brown colour bands as distinguishing features observed on two drifted specimens from Rottnest Island and Pelsart Island, Houtman Abrolhos, Western Australia. However, this does not seem to be adequate to distinguish the species, given the intergradation present, and the considerable range in variation in both shell size and colour pattern in *N. pompilius* (Saunders & Davis 1985; Saunders 1987; Swan & Saunders 1987). A similar specimen with soft parts was subsequently found near Yorke Peninsula, South Australia (Cotton 1957a, 1957b) and similar large drift shells have been reported from Queensland (Saunders & Ward 1987b).

The high proportion of *N. repertus*-type colour patterns and the unusually large size of the Western Australia specimens appear to be unique (Fig. 12.13B), although the reduced colour pattern said to distinguish *N. repertus* is present, albeit rarely, in most other populations of *Nautilus*, and the large shell size is matched by specimens from Ambon. Biochemical and genetic analysis of these specimens could shed light on the validity of this species.

The first and only known living specimens of *Nautilus stenomphalus* were trapped off Lizard Island, Great Barrier Reef, Queensland, at *ca*. 300 m depth, in 1984 (Pl. 21.2). Until then the species was known only from drift shells (Saunders 1986; Saunders & Ward 1987b). As most drift shells ascribed to this species occur in this region, its range may be limited to the Great Barrier Reef (Fig. 12.12B).

Nautilus stenomphalus lacks an umbilical callus, and the shell colouration is reduced and lacking in the umbilical region (Fig. 12.12B), although it is similar in size and weight (165 mm diameter, 700 g) to *N. pompilius*. The hood is covered with elevated, regular papillae in a unique pattern (Pl. 21.2). The gradation between *N. pompilius* and *N. stenomphalus* populations at Lizard Island is interpreted as hybridisation (Saunders & Ward 1987b). The two species can be distinguished if both shell and soft parts are available, but it may not be possible to distinguish them on the basis of shell characteristics alone.

Drift shells of *Nautilus macromphalus*, a species known as live animals only from New Caledonia and the adjacent Loyalty Islands, have been recorded as far away as Lizard Island, Queensland. *Nautilus scrobiculatus* is the rarest and most distinctive species of *Nautilus*, and was first seen alive in 1984 in Manus, Bismarck Archipelago, Papua New Guinea (Saunders, Davis & Knight 1987). It may range from the Solomon Islands to Indonesia. Although tagged drift shells of *Nautilus belauensis* have been found in the Philippines (Saunders & Spinosa 1979), presently this species is known only from Palau.

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Registration numbers of material photographed for illustrations are: Fig. 12.12, *Nautilus pompilius*, USNM 816710; *N. stenomphalus*, USNM 816711; Fig. 12.13, *N. pompilius* WAM 481–88, WAM 543–88.

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SUBCLASS COLEOIDEA

CHAPTER 13

DEFINITION AND GENERAL DESCRIPTION

Coleoids are cephalopods with an internal shell or without a shell. With the exception of *Nautilus*, all living cephalopods belong to the subclass Coleoidea. They have four or five pairs of appendages which bear suckers. All members of the group have only one pair of gills and one pair of nephridia.

HISTORY OF DISCOVERY

The name Coleoidea was introduced by Bather in 1888 for those cephalopods in which 'the protoconch is typically preserved by an external shell deposited by the mantle; the shell comes to be enveloped by the mantle, and may partly, even wholly, disappear'.

Coleoids were first recorded from Australian waters by Supercargo J. Van Roosenbergh in a letter to the directors of the Dutch East India Company, after he sighted quantities of cuttlebones in Shark Bay, Western Australia in 1627 (Alexander 1914). The first taxonomic descriptions of Australian coleoids are those of Lesueur (1821). He described several species from the Shark Bay area under the names *Sepia minima*, *S. peroni*, *S. boscii* and *S. varietas*. The original descriptions lack details and illustrations, and the species to which these names refer remain uncertain.

Quoy & Gaimard (1832) reported the zoological results of Dumont d'Urville's voyage on *l'Astrolabe* (1826–1829). They described four species from south-eastern Australia: *Sepia bilineata* and *Sepioteuthis australis* from Westernport, *Sepiola lineolata* from Jervis Bay and *Octopus superciliosus* from Bass Strait. In 1849, Gray added 11 species to the Australian list.

Though the *Challenger* Expedition (1873–1876) collected at only a few stations in Australian waters, Hoyle (1885) described ten new Australian species from expedition material. Brazier's (1892) first comprehensive list of Australian cephalopods included 20 octopod species, 19 cuttlefish species, eight myopsid squid species, five oegopsid squid species, as well as four *Nautilus* species.

The cephalopod collections made by the F.I.S. *Endeavour* in south-eastern Australia between 1909 and 1914 were described by Berry in 1918. Of the 13 species reported, eight were previously undescribed. Subsequently, no major report on Australian cephalopods was published until Iredale and Cotton embarked on their studies of Australian cuttlefishes. In a series of articles (Iredale 1926a, 1926b, 1940, 1954; Cotton 1929, 1931, 1932), 35 new species or subspecies were described, all based on beach-collected cuttlebones, and often on a single specimen. The soft parts of the animal were never described.

In 1940, Cotton & Godfrey published their monograph on 36 cephalopod species from South Australia. Unfortunately this work has confused the teuthological studies in Australia, as the authors did not give specimen references, and most of the specimens examined by the authors are no longer extant in the South Australian Museum. Further, the authors often copied the descriptions of Berry and others uncritically, and the true identity of the cephalopods they described may never be known.

In her studies of the planktonic cephalopod larvae from eastern Australian waters, Allan (1945) reported on 21 species, including two new species and several new records for Australia.

The next major work on Australian cephalopods was Adam's (1979) report on the Sepiidae in the Western Australian Museum collections. He described the species of *Sepia* from Western Australia, among them three new species, and new records of two eastern Australian species.

The interest in cephalopod fisheries in Australia in the late 1970s, especially those for squids, stimulated increased research efforts on Australian cephalopods. This interest and the greater awareness of the importance of cephalopods in the marine ecosystem resulted also in active expansion of the cephalopod collections. Since 1979, many papers on Australian cephalopods have been published.

The annotated checklist of the cephalopods from Australian waters by Lu & Phillips (1985) is the first comprehensive one since the publication of Brazier's checklist in 1892. They listed 222 nominal species from 35 families and 62 genera, among them four *Nautilus* species, 80 sepioid species, 15 myopsid squid species, 78 oegopsid squid species, 44 octopod species, and *Vampyroteuthis infernalis*. Many other articles on Australian coleoids have been published since 1979, for example by Lu (1982), Lu & Dunning (1982), Tait (1982), Lu & Tait (1983), Machida (1983), H.K. Smith (1983), Winstanley, Potter & Caton (1983), Lu, Roper & Tait (1985), Lu & Phillips (1985), Roper & Hochberg (1987, 1988), Stranks (1988a, 1988b, 1990), Zeidler & Norris (1989) and Stranks & Lu (1991).

MORPHOLOGY AND PHYSIOLOGY

In the course of coleoid evolution, the visceral hump has elongated and the funnel, used for jet propulsion, has developed from the posterior end of the foot. The morphological ventral surface has become the functional anterior end, and consequently, the functional body axes have shifted completely. The apex of the visceral hump, morphologically the dorsal surface, has become the posterior end of the animal functionally. In subsequent descriptions in this volume, the functional orientation of the animal is used, whereby arms and head are considered anterior, fins posterior, and the funnel ventral.

The exterior of a coleoid can be divided into an anterior head and a posterior body region. Anterior to the head are eight arms, and in squids and cuttlefishes, two additional tentacles. The arms and the tentacles bear suckers in one (on arms only) to many longitudinal rows. The suckers are muscular, and are equipped with chitinous rings in squids and cuttlefishes. In some squids, these rings are modified to form hooks. The mouth is located in the centre of the crown of arms. Posterior to the arms is a pair of large eyes, located on each side of the head. The eyes are covered by a cornea in sepioids, octopods and some squids. The muscular funnel lies ventral to the head.

The body, comprising the muscular mantle enveloping the internal organs, is elongate in squids, oval in sepioids and globose in octopods (Pls 17–21). All coleoids, except the incirrate octopods, have a lateral fin on each side of the mantle.

The internal shell lies dorsally in the body, under a layer of skin or mantle muscles. It is a calcareous structure with many chambers in *Spirula* and cuttlefishes, in which it is called a sepion (Figs 13.1B, 13.3). The shell of squids and some sepioids is a thin, feather-shaped plate of chitin, called a gladius or pen. In the finned (cirrate) octopods, the cartilaginous internal shell is saddle- or horseshoe-shaped. The internal shell of the benthic octopods (family Octopodidae) is reduced to two slender, cartilaginous rods. Some sepioids and the pelagic octopods lack a shell.

Thin skin covers the animal. The epidermis is a single layer of columnar epithelium with numerous mucous cells. It overlies the dermal layer of muscular fibres, chromatophores, iridocytes and connective tissue matrix. The combination and proportion of different pigments in the chromatophores are species specific. The chromatophores permit colour changes for background matching and visual communication (Pls 17.1–5, 20.1, 20.2).

The muscular system of the mantle in coleoids is well developed. Beneath the skin, the muscular layer is sandwiched between the outer and inner tunics of connective tissue fibres. In the squid genus *Loligo*, the thick muscular layer consists mainly of circular muscle fibres divided into regular bands by thin partitions of radial muscle fibres.

The mantle is the primary organ of locomotion in coleoids. Water is pumped in and out of the mantle cavity by alternate contractions of circular and radial muscle fibres in the mantle. The muscular funnel can be directed forward or backward, so that the animal can swim in either direction. Fins are more important as stabilisers but also act as propellers. Jet propulsion is important in squids as a means of locomotion. However, octopods can also swim by jet propulsion (Pl. 19.3), an alternative to their more common method of locomotion of creeping on the substratum, using the suckers on the arms for attachment (Pl. 19.2).

Deep-sea cirrate octopods, which have deep webs connecting the arms (for example, *Opisthoteuthis*; Fig. 13.31; Pl. 19.1), move by pulsating like a jellyfish, by the conventional jet propulsion, or by drifting passively like a drogue (Roper & Brundage 1972).

The coleoid mantle cavity is the large space bounded by the visceral mass and the mantle wall. The prominent, paired gills attach dorsally to the mantle by membranes and are ventilated by water in the cavity. The cavity receives excretory products.

The coleoid coelom is spacious. An incomplete septum partially separates the pericardial cavity from the perivisceral cavity. The pericardial cavity of sepioids and teuthoids encloses the branchial hearts at the base of the gills, but in octopods the pericardial cavity extends only to the base of the branchial hearts. In cranchiid squids, the large coelom is filled with ammoniacal fluid and serves as a buoyancy tank.

Initially, coleoids process food by means of a pair of beak-like jaws resembling those of a parrot. The beak with its strong muscles forms the buccal mass which is located at the centre of the circle of the arms and can protrude and rotate with great dexterity. The buccal cavity is filled with the odontophore carrying the radula, the salivary papillae and a pair of lateral lobes (Bidder 1966). Food is bitten and torn into small pieces and swallowed with the aid of the tongue-like action of the radula. The beaks and radula are chitinous, sclerotised structures (Hunt & Nixon 1981). In *Spirula* and some deep sea octopods, the radula is rudimentary or absent.

Cephalopod radulae are conservative in the number of teeth per row and tooth structure. Each radular row consists of a central tooth, flanked on each side by three lateral teeth, and a marginal plate which may be absent in some taxa; the radula row of *Ctenopteryx sicula* is unusual in having only two lateral teeth on each side. Teeth vary in structure quite widely across the subclass, from unicuspidate and dagger-like to multicuspidate or comb-like. However, too few radulae have been described or illustrated for a useful interpretation of these differences, even with the addition of radulae for 33 genera in 31 families recorded from Australian waters (see Figs 13.3–13.30, 13.32–13.38). Some of the variation may be phylogenetic in origin, but other factors such as diet may have an equal or greater influence.

The coleoid digestive tract is U-shaped. The descending branch, lined with a chitinous cuticle, includes the oesophagus and the stomach. In octopods, the posterior end of the oesophagus is expanded, forming a crop. The ascending branch includes the caecum and the short intestine, which is lined with a ciliated and glandular epithelium. The anus at the end of the intestine is situated just posterior to the funnel in the coleoids (Boucaud-Camou & Boucher-Rodoni 1983).

Coleoids have a single submandibular (sublingual) gland, and paired anterior and posterior salivary glands. The submandibular gland has been found in all Coleoidea examined. It is a median glandular mass underlying the salivary papillae; its function is unknown. The anterior salivary glands are located at the back of the buccal mass, and open onto the inner face of the lateral lobes. The posterior salivary glands, at the anterior end of the large midgut gland, have a long, common duct, lying adjacent to the oesophagus, which opens at the tip of the salivary papillae. Cirromorph octopods lack both anterior and posterior glands, and the latter are absent in *Spirula*. Various digestive enzymes are known from the secretions of the anterior and posterior salivary glands of *Octopus* and *Sepia* (reviewed by Boucaud-Labou & Boucher-Rodoni 1983). Additionally, toxins have been found in the secretions of the posterior salivary glands, at least in octopods and *Sepia*. These toxins are used to paralyse and kill the prey (Ghiretti 1960). Maculotoxin is found in the blue-ringed octopus, *Hapalochlaena maculosa* (Pl. 19.2). This neurotoxin, which resembles tetrodotoxin from some pufferfishes, paralyses the non-striated muscles and causes respiratory failure in vertebrate victims. At least one fatal case in humans has been reported (Halstead 1959; Sheumack, Howden, Spence & Quinn 1978; Sutherland 1983).

When an octopus attacks its prey, saliva containing digestive enzymes and toxin, is injected through the opening made by the beaks. The saliva serves to paralyse, kill and liquefy the soft parts of the prey. Toxins have not been isolated from the salivary secretion of any squid (Nicol 1966; Bidder 1966).

The coleoid midgut gland consists of two unequal parts arranged in series and served by the same ducts. The larger, anterior one is the brown digestive gland or 'liver' and the posterior one the 'pancreas'. Hence, the midgut gland has often been called the 'hepatopancreas'. The digestive gland is often brownish due to the presence of carotenoid pigments. In addition to digestive functions, the digestive gland also has some excretory functions, and is the storage site for energy reserves. The pancreas is always creamy white in colour. It is enclosed in the digestive gland capsule in octopods, and in the kidney sac in the Teuthoidea and Sepioidea. It has both excretory and digestive functions (see Bidder 1966; Boucard-Camou & Boucher-Rodoni 1983 for detailed reviews).

Food is passed, by peristaltic muscular action, from the buccal cavity through the oesophagus to the stomach, or into the crop in octopods. In the stomach the food is partly broken down by the action of enzymes from the digestive gland and perhaps from the salivary glands. The contents of the stomach are periodically released into the caecum where the food is mixed with additional enzymatic secretions, digestion is completed and a major part of absorption also takes place. The anterior portion of the caecum contains a series of spiral ciliated folds. These form a sorting area from which the larger non-digestible particles are diverted back to the stomach, then into the intestine. In *Sepia* and octopods, the digested food, a suspension of fine particles, enters the digestive gland through the 'pancreas', where absorption occurs. Food does not reach the digestive gland in *Loligo*, and absorption takes place chiefly in the caecum and the intestine (Bidder 1966).

The septal gland has developed into an ink gland and ink sac in all coleoids, except some octopods and *Vampyroteuthis*. The ink gland, located on the dorsal wall of the ink sac, produces the black or brown pigmented ink, which is stored in the reservoir, the ink sac. This sac discharges through a long duct into the rectum near the anus. The terminal ampulla is controlled by two circular sphincters. Discharged inkacts as a decoy to distract the attention of potential predators and, because of its alkaline nature, may also serve to deter potential predators. The ink gland has no known function in coleoid digestive processes.

Cephalopods are the only invertebrates that have an enclosed circulatory system capable of maintaining a high blood pressure. In coleoids, the system consists of a systemic heart with two auricles and a single ventricle, two branchial hearts, one at the base of each gill, an extensive arterial and venous system and an extensive capillary network.

Oxygenated blood returns from each gill via an efferent branchial vessel to an auricle and thence to the single ventricle. Three large arteries carry oxygenated blood from the ventricle. The dorsal aorta branches to supply the visceral mass and the head region, and the abdominal aorta and genital artery supply the mantle and fins, and the gonad respectively. Blood is supplied to tissue capillaries through several small branches of the major arteries.

Deoxygenated blood returns from the head region through a series of capillaries and small vessels to the large anterior vena cava, The latter divides into two branches near the kidney, each of which penetrates the kidney sac and enters the muscular branchial heart. The right branch of the vena cava also receives blood from the gonads. A pair of mantle and a pair of abdominal veins return blood from the mantle and viscera. The contraction of the branchial heart increases the blood pressure and its velocity, sending blood through the afferent branchial vessel to the capillaries of the gills.

The pigment haemocyanin binds oxygen during transport in the blood of coleoids (and *Nautilus*). Coleoids remove a very high proportion of oxygen on each circuit of the vascular system. *Loligo* can remove up to 93% of available oxygen, and even a resting octopus removes about 80% of the oxygen. The bluish colour of the transparent blood when oxygenated reflects the presence of copper molecules in haemocyanin (Wells 1983).

The coleoid excretory system consists of the renal appendages (kidney) contained in the renal sacs, the branchial heart appendages (pericardial glands), the renopericardial duct, and the digestive gland appendages (pancreas). Each renal sac opens to the mantle cavity through a small nephridiopore. The afferent branchial vessel carrying the deoxygenated blood enters the renal sac before reaching the branchial heart. The renal appendages are evaginations of the afferent branchial vessel and are the main excretory organs. Waste is secreted into the renal sacs. The filtrate is then passed from the branchial hearts and the appendages into the pericardial cavity, which is connected to the renal sacs by the renopericardial canals. The renopericardial canals open near the nephridiopores.

Some resorption of glucose and amino acids by the renopericardial canals and most organs in the coelom occurs. Ammonia is the principal excretory product. Gill surfaces and the digestive glands are also sites of nitrogenous waste disposal. In some squids, the nitrogenous waste is diverted and stored in the coelom or the body tissues as an aqueous solution of ammonium chloride, which is used to achieve neutral buoyancy. It has been calculated that as much as 40% of all ammonia produced in the life of a *Helicocranchia pfefferi* is retained in the coelom (Denton, Gilpin-Brown & Shaw 1969; Martin 1983).

All coleoid cephalopods are dioecious and in most species it is possible to use external characteristics to distinguish males from females when sexually mature. In some species, the single white testis of the male or the paired white nidamental or accessory nidamental glands of the female are prominent through the ventral mantle in the living animal. The hectocotylus, characteristic of the male in most species, may be prominent as a modification, reduction or loss of arm suckers and frequently as a modification by reduction or shape change of the whole arm on one or both sides. In many species, size differences can be used to separate the sexes.

Three components of the female reproductive system are generally present throughout the group: a single ovary, paired nidamental glands which produce a protective jelly to coat the eggs, and single or paired (in the Oegopsida and Octopoda), thin-walled and convoluted oviducts with a glandular portion near their openings. Adult females of some species which lay single eggs (for example, octopods, some oegopsids) lack nidamental glands. Loliginids also have accessory nidamental glands. Some teuthoids have glandular pouches in the buccal region which act as seminal receptacles, and in sepioids and octopods, the distal end of the oviduct is modified to serve this function.

The ovary is attached by a mesentery to the dorsal wall of the coelom at the apex of the mantle, directly beneath the gladius or sepion when present. Mature ova shed from the ovary pass forwards into the oviduct where they are stored free until spawning. The oviducal glands, when present, are white globular structures near the anterior opening of the oviducts. The paired nidamental glands are prominent as white elongate structures, bifurcated anteriorly, and situated ventrally on the midline forward of the branchial hearts. With maturity, these glands enlarge considerably, eventually almost protruding from the mantle cavity.

Five components of the male reproductive system can be recognised: the median testis, the vas deferens, the complex spermatophoric organ and the spermatophoric, or Needham's, sac which continues anteriorly as a muscular 'penis'. Spermatophores are transferred to the female during copulation, using the hectocotylised arm or arms.

The testis is a flattened elongate white organ, situated in an analogous position to the ovary in females, although somewhat displaced to the right side as the animal matures. Mature sperm collect in its central lumen, and are carried by the ciliated vas deferens into the spiral spermatophoric organ, where spermatophores are formed by secretions from the wall. These complex structures consist of a sperm mass, a cement body and an ejaculatory apparatus encased by several membranes and tunics. The vas efferens transfers the fully formed spermatophores one at a time into a spermatophoric sac. In some species, the angle of attachment (backwards and upwards) provides for their alignment in parallel rows with their aboral, non-opening end pointed distally. The penis, lying to the left of the anus, is a muscular extension of the spermatophoric sac through which small bundles of spermatophores are passed during copulation.

Complex courtship displays precede and often accompany mating in some shallow-water coleoids. These displays may involve the males in rapid and spectacular changes in colour pattern and arm posturing. R.E. Young (1975a) suggested that oceanic species may use their photophores in sexual attraction.

Coleoid cephalopods display a variety of methods of egg deposition and some species are believed to retain the eggs within the mantle or in a chamber formed by the webbed arms. Some oegopsids lay solitary planktonic eggs while others embed large numbers of eggs in layers of jelly to form large sausage-shaped masses (up to 1 m in length). Myopsids lay small numbers of eggs in finger-like capsules which are attached to the substratum, sometimes over vast areas (Pls 18.6–18.8). Sepioids lay single eggs with outer jelly or parchment-like coatings attached to hard substrata or corals and plants. Benthic octopod eggs are laid singly and generally cemented either singly or in small groups to the substratum where they are brooded (Pls 19.2, 20.3, 20.4). The pelagic *Argonauta* female secretes an elaborate egg case from the web of its dorsal arms (the paper nautilus shell) and attaches the eggs, cemented into strands, to the upper whorl (Pls 21.3–21.5).

Semelparity (death after a single reproductive season) appears to be a general phenomenon in coleoid cephalopods. After the gonad has been depleted, the animals undergo degenerative changes and death follows quickly. In only one species of benthic octopus has repeated copulation, spawning and brooding of clutches been observed (Rodaniche 1984).

Most coleoids hatch as miniature versions of the adults (Pls 18.8, 20.3), with the notable exception of ommastrephids and cranchiids. In ommastrephids, the young form a rhynchoteuthion stage, and the majority of cranchiid species undergo great ontogenetic changes in morphology (Voss, N.A. 1980). Most coleoids have planktonic young stages, for which the terms 'larvae' and 'juvenile' have been used traditionally. Recently, a new term 'paralarva' has been introduced as a 'general term for the planktonic young of cephalopods that meet certain ecological, and in some cases, morphological criteria' (Young, R.E. & Harman 1988). A young coleoid can be both a larva and a paralarva, or a juvenile and a paralarva (Young, R.E. & Harman 1988).

NATURAL HISTORY

Coleoids are active predators. In the sea, they usually consume crustaceans, fishes and other molluscs. The coastal, benthic cephalopods such as octopods or sepiolids usually live on shrimps, prawns and crabs, and pelagic cephalopods normally feed on pelagic crustaceans. Other prey found in coleoid stomachs include polychaetes, cephalopods, and, in some octopods, gastropods and bivalves (Boucaud-Camou & Boucher-Rodoni 1983). The nature of the prey changes with age, for example, from small crustaceans to larger crustaceans, fishes and cephalopods. In captivity, coleoids will usually eat the same prey they hunt in the wild. They can be fed prey they do not encounter in nature, such as *Artemia* or *Gammarus*, and may accept pieces of fishes, crustaceans, and a variety of freshwater and terrestrial organisms (Boletzky & Hanlon 1983; Toll & Strain 1988).

Attacks on prey are initiated visually in coleoids, although tactile approaches are important in *Octopus* species (Young, J.Z. 1961; Messenger 1968; Wells 1978). The prey are captured by the arms and tentacles. Cuttlefishes, such as *Sepia officinalis*, capture their prey using the two long tentacles (Messenger 1968). In the North Atlantic ommastrephid, *Illex illecebrosus*, the arms are used in the initial attack (Bradbury & Aldrich 1969).

Economic Significance

Coleoid cephalopods form a small but increasing component of Australia's fisheries production. Species of commercial or potentially commercial importance belong primarily to four families: Sepiidae, Loliginidae, Ommastrephidae and Octopodidae.

The major increases in production which occurred between the mid 1970s and early 1980s were largely the result of Taiwanese demersal trawling in northern waters for loliginids and sepiids. The intermittent activity by Japanese, Taiwanese and, more recently, Korean squid-jigging vessels, targeted ommastrephids off the southern coast.

Until quite recently, most cephalopods taken by Australian coastal fishermen were sold for bait. However, during the last 10–15 years the proportion destined for human consumption has increased significantly. Annual consumption of cephalopods in Australia exceeds 3000 tonnes. Although production from all sources in our waters has greatly exceeded this amount on some occasions (over 10 000 tonnes in 1979–1980), most found its way to the home markets of the foreign fishing nations noted above (Dunning 1982). In 1989–1990, Australia imported in excess of 4000 tonnes of squids and octopuses.

Families Sepiidae and Loliginidae: Until recently, cuttlefishes and loliginid squids were caught in northern Australian continental shelf waters by Taiwanese pair trawlers. They are taken, incidentally, by Australian prawn trawlers, although when prawn catches are low, some fishermen trawl for loliginids as an alternative target species in inshore waters off southern Queensland. Off New South Wales, Victoria and South Australia, these cephalopods are generally caught incidentally in finfish trawls, beach seines and fish traps. During some seasons, broad-finned squids or calamaris form the basis for small fisheries in gulfs and bays along the southern coast, using seine nets and baited jigs on handlines (Winstanley *et al.* 1983).

Family Ommastrephidae: In addition to incidental catches from prawn and finfish trawlers, since 1971–1972 foreign jigging vessels have undertaken exploratory and joint venture fishing intermittently for ommastrephids during summer in continental shelf waters off southern Australia (Dunning 1982). In 1979–1980, 64 Japanese vessels took over 8000 tonnes from Bass Strait and the annual resource has been estimated at up to 50 000 tonnes (Harrison 1979). Less than ten foreign vessels fished in Bass Strait in the early to mid 1980s but summer catches have exceeded 2000 tonnes (Collins & Baron 1986).

Squid jigs consist of a coloured plastic shaft approximately 50 mm long supporting a double ring of barbless spikes. Approximately 20 to 30 of these jigs are used in a single vertical longline attached to a roller which is hauled and lowered by machine or by hand in the upper 50 to 70 m of the water column. A typical vessel carries at least 30 machines, each with a pair of jig lines.

Preliminary investigations of the fisheries potential of oceanic representatives of this family have also been undertaken using jigging vessels and surface drift nets but no estimates of their resource potential are available (Dunning *et al.* 1981).

Family Octopodidae: As with cuttlefishes and squids, the octopus marketed in Australia is largely the bycatch of coastal trawling and shellfish dredging operations. Experimental trapping using various pot types (including cylindrical traps made of PVC pipe) has been conducted in the Bass Strait region and off the southern Western Australian coast. However, sustained commercial fisheries have not yet been established (Winstanley *et al.* 1983).

BIOGEOGRAPHY

The Australian marine fauna consists of two distinct latitudinal elements separated by zones of intermixing. Wilson & Gillett (1971) termed these the fauna of the northern Australian region, the southern Australian region and the eastern and western overlapping zones. The northern Australian region is part of the Indo-West Pacific faunal region. It is characterised by high species diversity, and a large component of species with wide distributions in the Indian and western Pacific Oceans.

The fauna of the southern Australian region is characterised by low diversity and high species endemicity. The overlap zones are long stretches of coast between the northern and southern regions. There is a gradual replacement of tropical forms with temperate forms, and some local endemism (Wilson & Allen 1987).

The Australian neritic coleoid fauna generally conforms with this distributional pattern, and includes the families Sepiidae, Sepiolidae, Idiosepiidae, Sepiadariidae, Loliginidae and Octopodidae.

The distributional pattern of oceanic cephalopods is less clear-cut. Although the data are preliminary, the latitudinal gradient in species diversity of the form observed in the eastern North Atlantic (Clarke & Lu 1974, 1975; Lu & Clarke 1975a, 1975b) is not evident. This is supported by the results of Nesis (1979a), who classified the pelagic realm of the Australia-New Zealand region into equatorial, southern subtropical, peripheral, notal and Antarctic zones, based on the data on pelagic cephalopods.

The equatorial and the southern subtropical zones occupy the entire eastern, western and northern waters, and the peripheral zone includes the Great Australian Bight region and Tasmania. The notal zone comes close to the south-western corner of Australia but largely lies outside the Australian Fishing Zone (Nesis 1979a). The broad distributional ranges of many species have resulted in a diffuse pattern with respect to the latitudinal gradient in species diversity. The southward flow of the warm Leeuwin Current in the west and the warm East Australian Current (see Bunt 1987) are contributing influences. The Leeuwin Current flows eastwards at around Cape Leeuwin, bringing warm, tropical water to the Great Australian Bight, and resulting in the presence of tropical marine taxa in the Bight (Maxwell & Cresswell 1981). The East Australian Current flows eastwards at around 32°S, where warm-core anticyclonic eddies are formed which continue southwards to as far south as 40°S. Brandt (1983) suggested that these eddies may be responsible for the large-scale patchiness in pelagic distribution in the western Tasman Sea. These eddies may carry tropical species beyond their normal ranges. The catching of a juvenile *Spirula spirula* in the zooplankton off the south-eastern Tasmania may represent such a case (C.C. Lu personal observations).

FOSSIL HISTORY

Few Australian fossils of coleoids have been recorded. The family Belemnidae is represented by several species of *Dimitobelus* from the Cretaceous in South Australia (Ludbrook 1966). *Spirulirostra curta* (family Spirulirostridae) has been collected from the Muddy Creek Formation (Middle Miocene, Balcombian) in Torquay. *Notosepia cliftonensis* (family Sepiidae) has been collected from the Balcombian in Dingley and Hamilton, Victoria. The Museum of Victoria holds material of both species.

METHODS OF STUDY

Studies of Australian coleoids are not well advanced, because of the difficulties involved in capturing and maintaining coleoids. Recommendations on future studies in systematics and morphology, ecology and general biology, life cycles and culture, Australian squid fisheries biology and assessment were made by Roper, Lu & Hochberg (1983). These recommendations apply to the studies of living cephalopods of Australia and elsewhere.

CLASSIFICATION

The classification outlined in Table 13.1 and adopted here is based on that of G.L. Voss (1977, 1988a), with modifications to reflect the current state of knowledge. A slightly different classification can be found in Clarke & Trueman (1988), in which the order Sepioidea was split into the order Sepiida, comprising the Spirulidae, Sepiidae and Sepiadariidae, and the order Sepiolida, comprising the Sepiolidae and Idiosepiidae. Eleven of the 44 families, marked with an asterisk, are not known from Australian waters. The families Gonatidae, Psychroteuthidae, Neoteuthidae, Batoteuthidae and Cirroteuthidae are known from Antarctic waters, but are not treated further in this volume.

Table 13.1 Classification of the subclass Coleoidea. Families marked with an asterisk have not been recorded from Australia.

Subclass COLEOIDEA
- Order SEPIOIDEA
    - Family Spirulidae
    - Family Sepiidae
    - Family Sepiadariidae
    - Family Sepiolidae
    - Family Idiosepiidae
- Order TEUTHOIDEA
    - Suborder MYOPSIDA
        - Family Pickfordiateuthidae*
        - Family Loliginidae
    - Suborder OEGOPSIDA
        - Family Lycoteuthidae
        - Family Enoploteuthidae
        - Family Octopoteuthidae
        - Family Onychoteuthidae
        - Family Walvisteuthidae*
        - Family Cycloteuthidae
        - Family Gonatidae*
        - Family Psychroteuthidae*
        - Family Lepidoteuthidae
        - Family Architeuthidae
        - Family Histioteuthidae
        - Family Neoteuthidae*
        - Family Bathyteuthidae
        - Family Ctenopterygidae
        - Family Brachioteuthidae
        - Family Batoteuthidae*
        - Family Ommastrephidae
        - Family Thysanoteuthidae
        - Family Chiroteuthidae
        - Family Mastigoteuthidae
        - Family Promachoteuthidae*
        - Family Grimalditeuthidae
        - Family Joubiniteuthidae
        - Family Cranchiidae
- Order VAMPYROMORPHA
    - Family Vampyroteuthidae
- Order OCTOPODA
    - Suborder CIRRATA
        - Family Cirroteuthidae*
        - Family Stauroteuthidae*
        - Family Opisthoteuthidae
    - Suborder INCIRRATA
        - Family Bolitaenidae
        - Family Amphitretidae
        - Family Idioctopodidae*
        - Family Vitreledonellidae
        - Family Octopodidae
        - Family Tremoctopodidae
        - Family Ocythoidae
        - Family Argonautidae
        - Family Alloposidae*

Key to the orders of the subclass Coleoidea

1 (a) Suckers with chitinous ring, which is modified sometimes into a hook. Mantle cavity communicates with exterior by three openings 2

(b) Suckers lack chitinous ring. Mantle cavity communicates with exterior by one opening, rarely two 3

2 (a) Fins not joined posteriorly. Tentacular stalks retractile. Mantle edge near mantle cartilages straight .... Order Sepioidea

(b) Fins usually joined posteriorly. Tentacular stalks not retractile. Mantle edge near mantle cartilages with small projections or 'angles' .... Order Teuthoidea

3 (a) Additional pair of thread-like, retractile, suckerless tentacles. Gladius a wide thin plate .... Order Vampyromorpha

(b) No retractile thread-like filaments. Gladius a fin support of small cartilaginous rods, or absent .... Order Octopoda

Order SEPIOIDEA

Sepioideans have four pairs of arms and one pair of tentacles, all armed only with suckers. The tentacles are retractile, and may be retracted into special pockets at the bases of tentacles. The suckers are stalked, and each chitinous ring usually has a denticulate edge. The arms are commonly not connected by webs, or when present, the webs are shallow. Oval or kidney-shaped fins are always present, situated on the sides of the body, near the posterior end or extending along the entire mantle in the form of a marginal fin. They are not connected posteriorly. Funnel cartilages are simple. In some species, the mantle is fused with the head and, less frequently, with the funnel, but if so the mantle cavity communicates with the exterior by three openings, on the ventral side of body and each side of the head. The shell may be a calcareous plate, a calcareous spiral, a thin chitinous pen-like plate, or is absent. The mantle edge near the mantle cartilages is straight, and protruding 'angles' are lacking. The oviduct is unpaired, and accessory nidamental glands are present. When present, all radular teeth are unicuspidate. The following key to sepioid families is based on that of Nesis (1982).

Key to the families of the order Sepioidea

1 (a) Shell calcified 2
  (b) Shell chitinous or lacking 3

2 (a) Shell a spiral coil, round in cross-section, in posterior end of body (Fig. 13.1). Radula absent .... Spirulidae
  (b) Shell in form of thick oval or rhomboidal plate on dorsal side of mantle (Fig. 13.3A–D). Radula present .... Sepiidae

3 (a) Mantle elongate, slightly narrowed and bluntly pointed posteriorly (Pl. 18.4). Fins in rear half of mantle. A rough, oval attachment organ on postero-dorsal part of mantle (Fig. 13.8A) .... Idiosepiidae
  (b) Mantle oval, broadly rounded posteriorly. Fins located at or slightly posterior to mantle midlength. No attachment organ 4

4 (a) Web between third and fourth arms encircles bases of tentacles on outside and inside, forming a cutaneous sac. Fins with broad bases and slightly developed 'earlets' (Fig. 13.4A, B; Pls 18.1, 18.3) .... Sepiadariidae
  (b) Web between third and fourth arms envelops tentacle bases on outside only, without forming sac (Fig. 13.7F–I). Fins with short bases and well-developed 'earlets' (Fig. 13.6; Pl. 18.5) .... Sepiolidae

Family Spirulidae

Members of this monotypic family are small animals, the mantle length rarely exceeding 45 mm. The characteristic spirally coiled internal shell is located in the posterior end of the animal, and contains over 30 chambers in adults (Fig. 13.1). The mantle is thin and muscular. The funnel-mantle locking cartilage is simple and straight. The short arms are connected by a deep web. The fins are attached almost perpendicularly to the longitudinal axis of the body. A large photophore is located between the fins. Both ventral arms of males are hectocotylised.

The sole species was named by Linnaeus in 1758 as *Nautilus spirula*. It was transferred to the newly erected genus *Spirula* by Lamarck in 1801. Though the family Spirulidae has been credited to Owen (1836) by many authors (Chun 1915; Voss, G.L. 1977; Clarke & Trueman 1988), in fact Orbigny first used the family name 'Spirulees' in 1826. Owen (1836) initiated the current latinised spelling of Spirulidae (Naef 1922). Accordingly, the family Spirulidae should be attributed to Orbigny, 1826.

The first published Australian record was Péron's (1807) figure of *Spirulea prototypos*. Lamarck renamed the same specimen as *Spirula australis* in 1816, and in 1822 as *Spirula peronii*. Angas (1865) reported on a beached specimen from near Port Jackson under the name *Ammonia laevis*. Brazier (1892) synonymised all these names with *Spirula peroni* and in 1909 Hoyle recognised *Spirula spirula* as the valid name of the species.

The family is characterised by its chambered, internal shell, shaped like a ram's horn (Fig. 13.1B). Externally the mantle is cylindrical, with a pair of small, round fins attached transversely to the posterior end of the mantle. The anterior margin of the mantle has three pronounced projections on the dorsal midline and ventro-laterally on each side of the funnel-mantle locking cartilages. The large eyes are equipped with muscular eyelids, as in oegopsids. The arm length increases from dorsal to ventral arms and each arm bears four to six rows of small suckers. The non-expanded club on each long tentacle carries 16 rows of numerous small suckers. The arms are connected with a web, except between the ventral arms.

Live *Spirula spirula* take up a vertical position, head downwards, when at rest. They can swim downwards, head first, propelled in part by fluttering movements of the fins, which stretch up vertically, and a current created by the funnel, which points backwards (Schmidt 1922). In rapid dashes, *S. spirula* employs the typical jet propulsion of cephalopods (Kerr 1931), involving muscles of the mantle, funnel arms and fins.

Feeding activities have not been observed directly. The digestive system of *S. spirula* is similar to that of other coleoids, except that there is no radula (Kerr 1931).

Owen (1880) and Kerr (1931) reported in detail on the reproductive system of *S. spirula*. The ventral arms of mature males are modified into hectocotyli (Fig. 13.1A). The right arm is larger and thicker than the left arm. In the preserved specimen, the margins of the aboral surface are rolled aborally to form prominent flanges. The lateral sides of the arm are smooth and prominent. Suckers are absent on the oral surface. There is a spoon-like organ at the distal end of the arm. The extreme tip of the arm extends into a sharp point flanked on each side by a claw-like point. The left ventral arm is more slender than its counterpart and lacks flanges. The tip of the arm is modified into a very complex organ of unknown function. The hectocotylisation first occurs at a mantle length of 20 mm (Kerr 1931; Bruun 1943). The spermatophoric structure of *Spirula* differs little from that of other cephalopods (Kerr 1931).

The eggs are small. Chun (1915) reported the largest ovarian eggs to be about 1.7 mm. The newly hatched young are estimated to be about 4.2 mm (Naef 1923). Animals attain sexual maturity at about 30 mm mantle length (Schmidt 1922). The smallest young known, presumably newly hatched, have a mantle length of about 1.5 mm with two chambers (Lu, Guerra, Palumbo & Summers 1992).

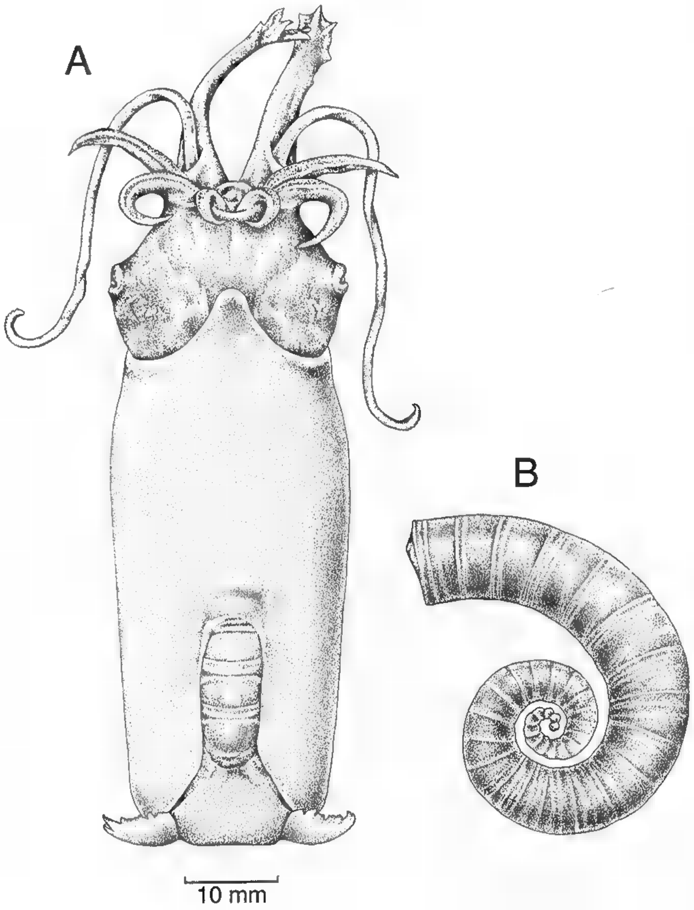


Figure 13.1 Family Spirulidae. *Spirula spirula*, the only living coleoid with a coiled shell: **A**, a male from the Coral Sea, dorsal view, showing the hectocotylised ventral arms; **B**, shell, lateral view. [K. Hollis]

Little is known about the life history of *Spirula*. No pelagic eggs have been identified. The capture of young at about 1000–1750 m suggests that females lay eggs on the bottom on the continental slope (Bruun 1943, 1955). Clarke (1970) suggested that in the North Atlantic, *S. spirula* hatches mainly in June or July and the animals grow to maturity after 12–15 months when mating and egg laying takes place. The life span is estimated to be about 18–20 months.

Spirula spirula is found in the open ocean. Bruun (1955) suggested that water temperature is the dominant factor in its distribution; all catches were in regions where the water temperature at 400 m is 10°C or more.

The animals undergo diel migration. During the day they are deeper than 550 m, with the centre of population at 600–700 m. During darkness, most animals occur at less than 300 m depth. Evidence suggests that the young larvae do not migrate immediately after hatching but adopt the migratory behaviour during early growth. The behaviour of old animals also changes; they appear to stay in deep water even at night (Clarke 1969). The animal controls its buoyancy by regulating the pressure of gas contained in the shell (Denton, Gilpin-Brown & Howarth 1967; Denton & Gilpin-Brown 1971).

No fisheries are based on this animal because of its relative scarcity and the small size as well as the tough and thin mantle. The beach-collected shells are sold in the shell trade.

Spirula spirula is found in the tropical and subtropical regions of all three major oceans. Around the Australian continent, this species has been captured in oceanic waters from Queensland to Tasmania, the Great Australian Bight and Western Australia. Shells have been collected from beaches around Australia.

Family Sepiidae

Members of this speciose family are small to medium-sized (although several species reach 0.5 m mantle length). They have a characteristic calcareous sepion, or cuttle (Fig. 13.3A–D), which is porous and finely laminated and located dorsal to the mantle beneath the skin. Sepiids are commonly called cuttlefishes, after this structure. The spine at the posterior end of the sepion may be absent in some species. The mantle is broad, or slender, robust, elongate-oval to circular in outline and slightly flattened dorso-ventrally.

The fins are narrow, lateral to the mantle and extend almost the whole length of the mantle. The posterior end of the fins is free, forming a lobe. The arms are equipped with two to four rows of suckers. The tentacles are retractable into a pocket on the ventro-lateral sides of the head. The tentacular clubs bear four to eight or more rows of suckers. The funnel-mantle locking apparatus is curved to angular in shape.

The study and naming of cuttlefishes dated back to Linnaeus who named the common cuttlefish of Europe *Sepia officinalis* in 1758. Many authors have contributed to the description and naming of this family since then, notably, Lesueur (1821), Férussac & Orbigny (1835–1848), Gray (1849), and more recently G.L. Voss (1963), Adam & Rees (1966), Roeleveld (1972), Roeleveld & Liltved (1985), Khromov (1987a, 1987b, 1987c, 1990) and Okutani, Tagawa & Horikawa (1987). Despite these numerous papers, detailed taxonomic revision has been limited; the monograph of Adam & Rees (1966) is still the most comprehensive on the family. Roeleveld's (1972) monograph clarified the Sepiidae of South African waters. Recently, Khromov (1987c, 1990) reported on his work on the classification and phylogeny of Sepiidae.

Despite the early description of the cuttlefishes from Australian waters (Lesueur 1821; Gray 1849), the taxonomy and biology of the Australian cuttlefishes are poorly known. Brazier (1892) listed 14 species of *Sepia* from Australia, including several names from the South African fauna. Two of the three species of *Sepia* described by Berry (1918) from southern Australia have not been recognised with certainty since the original description because sepions of the type material are missing or damaged.

From 1926 to 1954, Iredale (1926a, 1926b, 1940, 1954) and Cotton (1929, 1931, 1932) each described and named 29 and seven taxa of cuttlefishes, respectively, based solely on the sepions. Adam (1979) described 18 species of *Sepia* and clarified the status of many of Iredale and Cotton's taxa. Lu & Phillips (1985) and Lu (in press), summarised the status and distribution of the Sepiidae from Australian waters, incorporating Adam's (1979) findings and new data. Roper & Hochberg (1988) elevated the subgenus *Metasepia* to generic status, based on the colour pattern and locomotion of *Metasepia pfefferi* (Fig. 13.2A, B; Pl. 17.1). Lu (in press) recognised 26 species from Australian waters with three, known only from cuttlebones, designated as of uncertain status. All three genera, *Sepia*, *Metasepia* and *Sepiella*, are represented.

The sepiid body is flattened dorso-ventrally. The mantle may be elongate and slender, as in *Sepia braggi* (Fig. 13.2C), elongate-oval (for example, *Sepia rex*), broadly oval or nearly circular, as in *Metasepia pfefferi* (Fig. 13.2B; Pl. 17.1) and *Sepia apama* (Fig. 13.2D). The anterior dorsal margin of the mantle projects forwards. The fins are long and laterally attached to the mantle with free posterior lobes. The head is robust with prominent eyes. The eyes are covered by a transparent membrane and a conspicuous secondary fold on the eyelid. The eight arms are equipped with two or four rows of suckers. The tentacular club carries four to more than 20 rows of suckers, depending on species. The radular arrangement is illustrated in Figure 13.3E.

The sepion lies under the skin over almost the entire dorsal surface of the mantle. The shape of the sepion ranges from lanceolate to oval to rhomboidal (Fig. 13.3A–D). The dorsal side of the sepion is a calcareous plate called the dorsal shield. Ventrally the sepion is a series of numerous thin, narrow, oblique

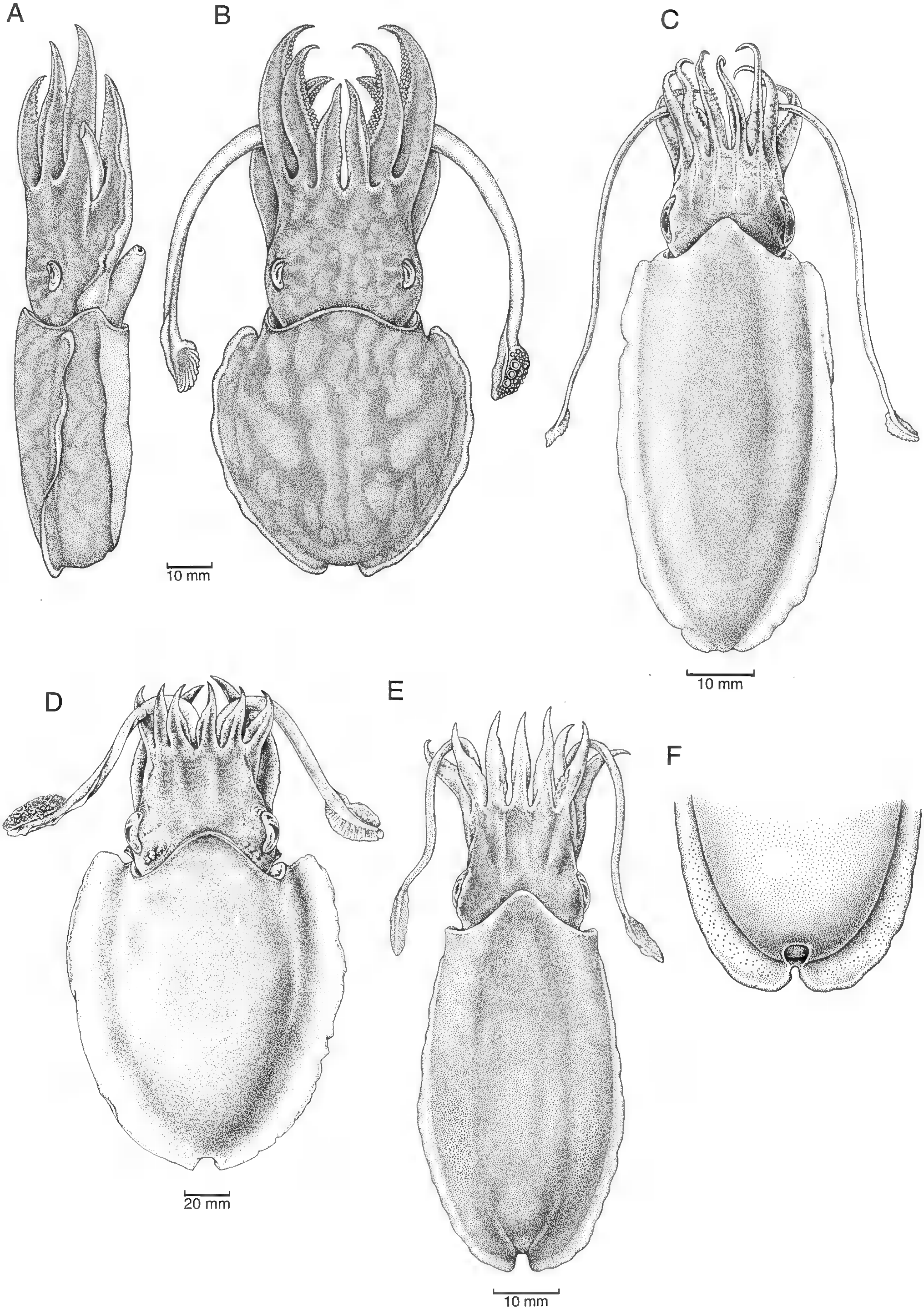


Figure 13.2 Family Sepiidae. A selection of Australian cuttlefishes. **A, B,** *Metasepia pfefferi.* **C,** *Sepia braggi* (65 mm mantle length). **D,** *Sepia apama* (150 mm mantle length). **E, F,** *Sepiella weberi.* **A,** lateral view. **B–E,** dorsal view. **F,** postero-ventral view, showing the posterior gland of unknown function. [K. Hollis]

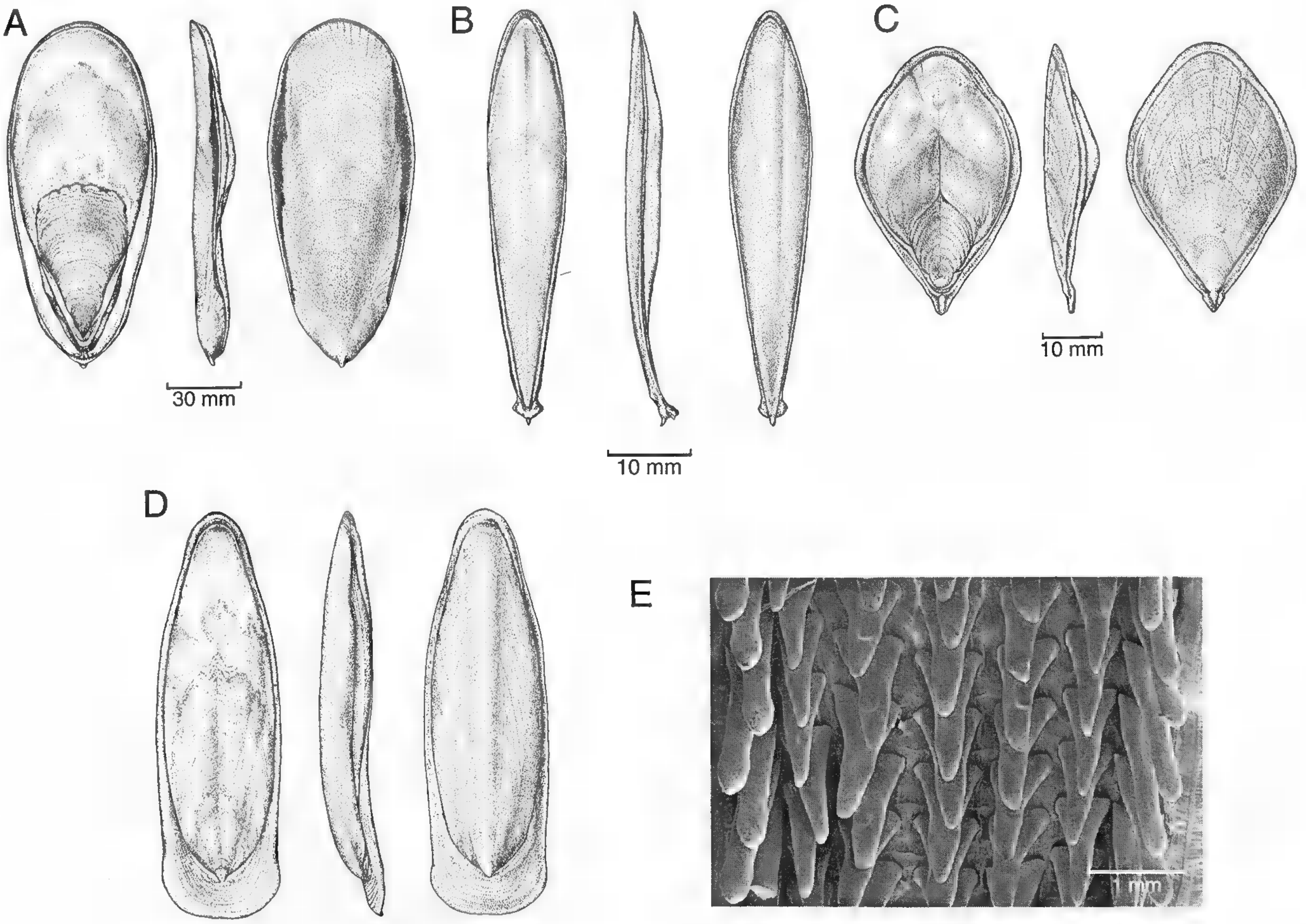


Figure 13.3 Family Sepiidae. **A–D**, shells of assorted Australian cuttlefishes, ventral, lateral and dorsal aspects: **A**, *Sepia apama*; **B**, *Sepia braggi*; **C**, *Metasepia pfefferi*; **D**, *Sepiella weberi*. **E**, portion of radula of *Sepia apama*, showing several tranverse tooth rows. [A–D, K. Hollis; E, C.C. Lu]

septa which are supported by numerous transverse calcareous rods. A spine present in most species at the posterior end of the sepion, is absent in the genus *Sepiella* and a few species of *Sepia*.

The sepion is the primary buoyancy organ of cuttlefishes (Denton & Gilpin-Brown 1961a, 1961b, 1973). The spaces or chambers between the thin septa contain fluid and gas, largely nitrogen. Each chamber is independent of others. The total gas space within the cuttlebone is that which brings the animal to neutral buoyancy. By regulating the relative amounts of fluid and gas in the chambers, the degree of buoyancy can be varied.

Jet propulsion is a common feature of all living cephalopods. Cuttlefishes are slower swimmers than squids which are more streamlined. Through their ability to attain neutral buoyancy, sepiids can hover in midwater, gently passing water over the gills. The fringing lateral fins function as stabilisers and the undulating movements along the fins in either direction give great turning manoeuvrability (Pls 17.2–17.4) (Clarke 1988).

Not all mature male cuttlefish species have hectocotylised arms. In those that do, hectocotylisation affects the left ventral arm by the reduction of size of certain suckers and development of transverse folds in the modified area. During mating the spermatophores are transferred by the hectocotylised arm from the penis to the seminal receptacle under the buccal mass of the female.

Interspecific variability in size at sexual maturity is considerable. Mangold-Wirz (1963) reported that male *Sepia officinalis* can be fully mature as small as 60–80 mm mantle length, while individuals as large as 100 mm mantle length may still be immature. Females exhibited the same phenomenon, maturing at sizes varying from 110–250 mm mantle length.

Similar variation has been observed in *Sepia pharaonis* from the Gulf of Carpentaria, where the mature males range from 34–145 mm mantle length and mature females range from 141–192 mm mantle length. The largest immature female measured 143 mm mantle length (Dunning *et al.* 1994; Lu unpublished data).

In keeping with body size differences, ovary size and egg numbers in *S. officinalis* vary. Smaller individuals have only 150 mature ovarian eggs whereas large individuals may have more than 500 eggs (Mangold-Wirz 1963). Including immature eggs at various stages of more than 1 mm in diameter, the total number of eggs in an individual varies from 500 to over 1000, depending on the size of the animal. The factors responsible for this variation in body size at maturity were found to be the combined effect of temperature and light (Richards, see Boletzky 1983a).

In *S. officinalis* spawning occurs soon after mating. Eggs are laid at regular intervals of 2–3 minutes over several hours. The egg is 25–30 mm in length and up to 12–14 mm in diameter. Each is fixed to any oblong object by means of a ring-shaped basal structure. The animal produces the ring using its armtips to draw the gelatinous envelope of the egg into a pair of processes. These are wound round the supporting object so that they stick together (Boletzky 1983a). A female may empty her ovary of mature eggs within a few days.

The length of embryonic development varies with temperature and ranges from 40–45 days at 20°C, to 80–90 days at 15°C. Hatchlings of *S. officinalis* are 6–9 mm mantle length and resemble the adults.

The normal life span of *S. officinalis* varies from 18–24 months, although some males may live longer. Mass mortality at the end of the spawning period occurs on the Atlantic Coast, but no comparable intensity has been reported in the Mediterranean. In Australia, mass mortality of *Sepia apama* has been observed in July/August off the coast of New South Wales (H. Battam personal communication). Examination of two of the individuals involved revealed the male (382 mm mantle length, 6.2 kg) was mature while the female (300 mm mantle length, 2.4 kg) was immature. The stomachs of both individuals were empty.

The growth of *S. officinalis* was studied by Richard (see Boletzky 1983a). There is positive correlation between temperature and early growth rate, and between maximum size and life span. Maximum size or age and early growth rate are negatively correlated, as are temperature and life span. From rearing experiments, Pascual (1978) concluded that higher food intake produces faster growth at higher temperatures. Efficiency of food conversion varied from 35–50% under normal rearing conditions, independent of temperature.

Bell (1979) estimated the growth rate of *Sepia apama* to be 10 mm per month and the animals take 10–12 months to reach adult size, based on data from a large collection of sepions from Victoria. The largest specimen, 460 mm in length, was estimated to be about four years old.

Sepiids prey on a wide variety of organisms. On the Tunisian coast, stomachs of *S. officinalis* contained various crustaceans, molluscs and fishes (Najai & Ktari 1974, in Boletzky 1983a). Prey included a species of *Penaeus* and other decapod crustaceans, isopods, copepods, ostracods, bivalves, gastropods, pteropods, octopods, decapod cephalopods, polychaetes, nemerteans and fishes.

Little is known about food of cuttlefishes in Australian waters. Recent examination of *S. pharaonis*, *S. elliptica* and *S. smithi* from the Gulf of Carpentaria revealed large numbers of individuals with crustacean remains in the stomachs (Lu unpublished data).

Various sepiid species have been found among the stomach contents of predators such as pygmy sperm whales, *Kogia breviceps*, and dwarf sperm whales, *Kogia simus*, in South Africa (Ross 1984), and Risso's dolphin, *Grampus griseus*, in the English Channel (Clarke & Pascoe 1985). Off Natal, *S. officinalis* formed 33% by weight of the prey of *Tursiops truncatus* (Cockcroft & Ross 1990). In Australia, they have been found in the stomach contents of long-finned pilot whales, *Globicephala melas*, and the Australian fur seal, *Arctocephalus pusillus doriferus*, in Tasmania (Gales, Pemberton, Lu & Clarke 1994).

Adam & Rees (1966) cautioned that far too little is known about the bathymetric distribution of sepiids to allow any general conclusions. They suggested that for the species with wide distributions, the bathymetric distribution appears to be related to the geographical distribution. *Sepia elegans* was found at depths of 20–250 m in European waters and 80–430 m off the West Africa coast. Similarly, *S. orbignyana* was found between the surface and 100 m on the European coast and from 116–430 m off West Africa.

Roeleveld (1972) studied the known bathymetric records of many South African sepiids and noted that few species have been recorded below 100 m off the southern coast of South Africa, where the continental shelf is wide. Off the east and west coasts, where the continental shelf is narrow, sepiids have been recorded as deep as 460 m.

Recently, *Sepia cultrata* was been reported from a depth of 60–600 m off Tasmania and exhibits strong diel migration from the bottom during the day to midwater at night (Lu & Roper 1991).

Sepia officinalis has been the subject of many behavioural studies. Colour changes and colour patterns have been described by Holmes (1940) and Boycott (1958). Boletzky (1972) and Messenger (1977) studied the prey capture and learning. Hanlon & Messenger (1988) examined colouration and concurrent behaviour in young cuttlefishes. Roper & Hochberg (1988) described the chromatic components and body patterns of *Metasepia pfefferi* (Pl. 17.1) and *Sepia papuensis* from Lizard Island, Australia, as well as a new type of locomotion termed 'ampling'. *S. latimanus* shows a wide range of colour patterns under different conditions (Pls 17.2–17.4).

The family Sepiidae includes numerous species of great economic importance. Cuttlefish catches in the major fishing areas in 1981 totalled 178 000 tonnes (FAO 1983; Roper, Sweeney & Nauen 1984), comprising 13.6% of the total world cephalopod catch. The catches for 1987 were 225 000 tonnes with the important species being: *Sepia officinalis*, *S. elegans* and *S. orbignyana* in the north-eastern Atlantic; *S. officinalis* and *S. hierredda* in the eastern central Atlantic; *S. officinalis*, *S. elegans*, *S. orbignyana* in the Mediterranean; *S. pharaonis*, *S. esculenta*, *S. brevimana* and *Sepiella inermis* in the western Indian Ocean; *Sepia lycidas*, *S. esculenta*, *S. madokai*, *S. lorigera*, *S. andreana* and *Sepiella japonica* in the north-western Pacific; and *Sepia pharaonis*, *S. esculenta* and *S. latimanus* in the western central Pacific (Guerra 1991). *Sepiella japonica* (known as *Sepiella maindroni* in China) is the most important cephalopod fishery species in Chinese waters with annual catches of 40 000–50 000 tonnes (Dong 1988).

In Australia, traditionally sepiids have not been fished for human consumption. This lack of commercial interest has resulted in a paucity of catch data. Liu & Yeh (1984) estimated the standing stock of cuttlefishes in the Arafura Sea, northern Timor, southern Timor Sea and North West Shelf at 2900, 1700, 2400 and 12 700 tonnes, respectively. There appears to be strong potential in cuttlefish fisheries, particularly on the North Shelf where *Sepia pharaonis*, an important species in commercial fisheries overseas, is predominant in the cuttlefish catches (Lu unpublished data). In eastern Australia, small quantities of cuttlefishes (132 tonnes for New South Wales, 14 tonnes for Victoria in 1978–1979) are taken mainly as a by-catch of prawn and mixed species trawl fisheries (Dunning 1982). The sepions are sold by the pet trade as the source of calcium for birds in captivity.

Various sepiid species occur on the continental shelf and upper slope of the temperate to tropical waters of the Old World. As a group, cuttlefishes are found from Japan, China, the Philippines and Indo-Malay region to Australia, eastward to Fiji and westward around the Indian Ocean to the eastern Atlantic as far north as the North Sea. Sepiids do not occur along the American coast or in New Zealand waters. The eastern-most Pacific records are for the Marshall Islands and Fiji. Adam & Rees (1966) stated that many of the Indo-Pacific species had only been found in very restricted areas but too little collecting had been done to afford a clear picture of their geographical distribution.

In South African waters, 17 of the 20 known species are endemic. One of the remaining three is a tropical species, one is Atlantic and the third has an interrupted distribution. The endemic group comprises east coast subtropical species, and temperate species occurring on the western and southern coasts and gradually diminishing along the east coast (Roeleveld 1972).

Although our knowledge of Australian sepiid distributions is far from complete, the fauna generally conforms with the distributional pattern outlined by Wilson & Gillett (1971), though the exact limits of each species do not necessarily conform with the limits of their zones.

Lu (in press) summarised the geographical distribution of Australian sepiids as follows.

Northern Australian Region: *Sepia cottoni*, *Sepia elliptica*, *Sepia latimanus*, *Sepia opipara*, *Sepia papuensis*, *Sepia pharaonis*, *Sepia smithi*, *Metasepia pfefferi*, *Sepiella weberi*.

Southern Australian Region: *Sepia apama*, *Sepia braggi*, *Sepia chirotrema*, *Sepia cultrata*, *Sepia dannevigi*, *Sepia hedleyi*, *Sepia novaehollandiae*, *Sepia rex*.

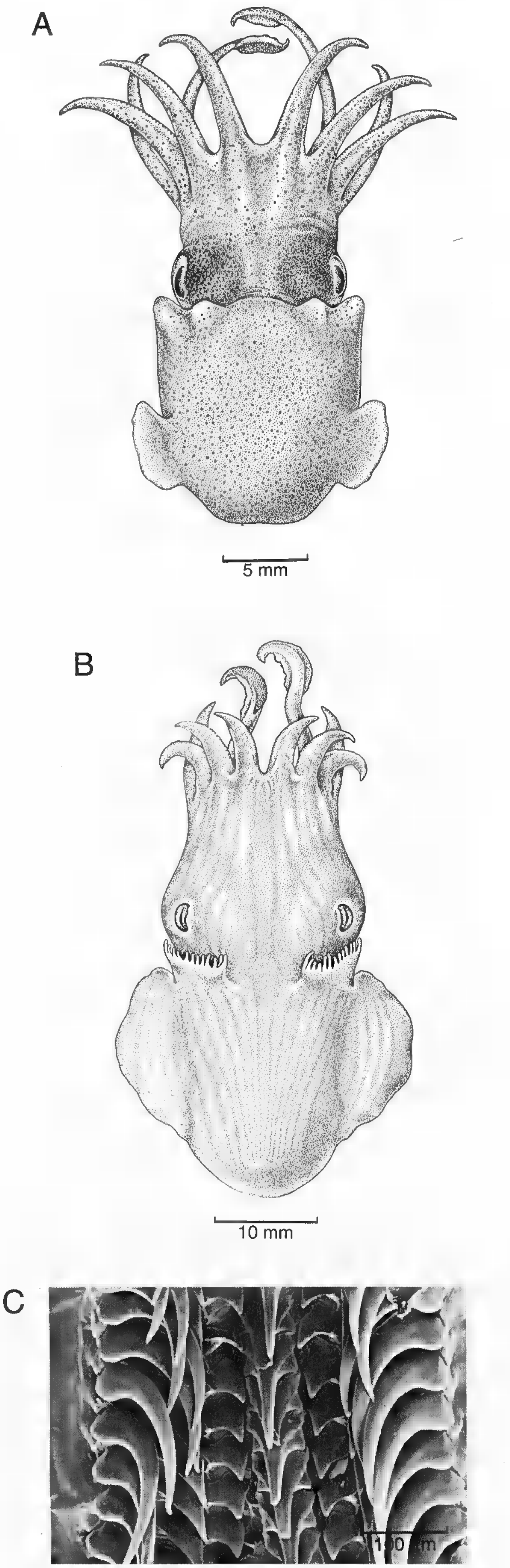


Figure 13.4 Family Sepiadariidae. **A**, **B**, endemic Australian species, dorsal view: **A**, *Sepiadarium austrinum*; **B**, *Sepioloidea lineolata*. **C**, portion of radula of *Sepiadarium kochi*, showing several transverse tooth rows.
[A, B, K. Hollis; C, C.C. Lu]

Eastern Overlap Zone: *Sepia mestus*, *Sepia plangon*, (extends to Gulf of Carpentaria), *Sepia rozella*, *Sepia whitleyana* (extends to Gulf of Carpentaria), *Sepia baxteri*, *Sepia mira*.

Western Overlap Zone: *Sepia irvingi*, *Sepia vercoi*, *Sepia reesi*.

Of the nine species listed for the northern Australian region, only *Sepia cottoni*, *Sepia opipara*, *Sepia smithi* and *Metasepia pfefferi* are known only from Australia at present; the other five species also occur elsewhere in the Indo-West Pacific region. The eight species listed for the southern Australian region are all known only from Australia. Similarly, none of the nine species listed for the eastern and western overlap zones is known to occur elsewhere.

Thus of 23 species reported from Australia (excluding the three species known only from sepions), 20 species are considered to be endemic to Australian waters, a figure supporting the assertion of Adam & Rees (1966) that the Australian fauna is one of the richest in endemic species.

Family Sepiadariidae

Sepiadariids have a short body, with narrow, ear-like fins attached to the sides (Fig. 13.4; Pls 18.1, 18.3). The arms are short and are connected by a wide web, particularly around the tentacular base. The mantle is fused with the head on the dorsal side and with the funnel on the ventral side in the genus *Sepiadarium*; it is connected (articulated) with the funnel by a unique locking apparatus in the genus *Sepioloidea* (Fig. 13.5). The funnel member of the locking apparatus is sole-shaped in outline with a broader, deeper anterior pit and a shallower, longer and narrower posterior groove; the form of the mantle cartilage complements the funnel member. There are two genera in the family: *Sepiadarium* and *Sepioloidea*.

The earliest record of any member of this family was that of Quoy & Gaimard (1832) who described *Sepiola lineolata* (now known as *Sepioloidea lineolata*) from Jervis Bay, New South Wales. Orbigny (in Férussac & Orbigny 1835–1848), recognised that it was different from *Sepiola* and transferred it to a new genus *Sepioloidea*. In 1881, Steenstrup erected the genus *Sepiadarium* to accommodate his new species, *S. kochi*, and grouped *Sepiadarium*, *Idiosepius*, *Sepioloidea* and *Spirula* in the family Sepio-Loliginei (subfamily Sepiadarii). Fischer (1882) erected and restricted the family Sepiadariidae to include only *Sepiadarium* and *Sepioloidea*.

The first Australian record of a *Sepiadarium* species is the description of *S. auritum* from the Monte Bello Islands by Robson in 1914. Berry (1921) described the additional species *S. austrinum* (Fig. 13.4A) from Gulf St Vincent, South Australia. Though Cotton & Godfrey (1940) recorded *S. kochi* from South Australia, recent collecting failed to confirm this record, and their record of *S. kochi* in South Australia must be regarded as erroneous. The presence of *S. kochi* in tropical northern Australia is confirmed, however (Lu & Phillips 1985; Lu unpublished data).

Sepiadariids are small, up to 40 mm mantle length, with a short, broad body. The narrow ear-like fins are attached to the sides of the body. The arms are connected by a deep web which envelops the tentacular stalk forming a sac into which the tentacle may retreat. The arms are equipped with two rows of suckers on the proximal part, increasing to four to eight rows distally in some species. In mature males, the left ventral arm is hectocotylised by the disappearance of suckers and transformation of sucker stalks into papillae and small lamellae. The gladius and luminous organs are absent.

The anterior dorso-lateral mantle margins are fringed in the Australian *Sepioloidea lineolata* and smooth in the remaining members of the family. In *S. lineolata* only, the dorsal mantle surface is characterised by a series of longitudinal stripes which are dark blue or, more often, brown coloured throughout life (Fig. 13.4B; Pls 18.1, 18.2; Dew 1959a). Numerous round, blunt papillae are scattered on the ventral mantle surface particularly towards its edges. In species of *Sepiadarium*, the dorsal mantle

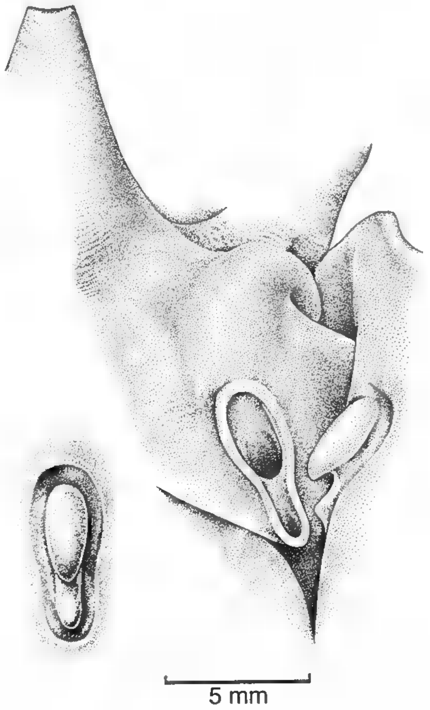


Figure 13.5 Family Sepiadariidae. Funnel-mantle locking apparatus of *Sepioloidea lineolata*. [K. Hollis]

surface is covered with large white chromatophores surrounded by many smaller red-brownish chromatophores (Pl. 18.3). These large white chromatophores are absent in *Sepioloidea*.

The mantle cavity in the New Zealand species *Sepioloidea pacifica* is divided medially by a thin septum. On the ventral surface of the visceral mass, the median anus with its small, paired anal flaps, opens near the base of the funnel. Paired renal apparatuses open on each side of rectum. Paired gills with branchial hearts are well developed and lie on each side of the visceral mass. Postero-medial to the branchial hearts lies the male reproductive system. Lateral to this on the left side is Needham's sac, and the penis passing forwards dorsal to the left afferent branchial vessel, to open within the base of the funnel. The testis lies to the right and posterior to Needham's sac. In the female, the paired oviducts open on each side in the mantle cavity (Dell 1952).

The mantle cavities of *Sepiadarium kochi*, *S. austrinum* and *Sepioloidea lineolata* resemble that of *S. pacifica*.

The digestive system of *Sepioloidea pacifica*, described by Dell (1952), differs little from that of other cephalopods. The buccal mass containing the beak is located at the centre of the head surrounded by the brachial crown. The radular arrangement in *Sepiadarium kochi* is illustrated in Figure 13.4C. From the buccal mass, the oesophagus passes through a groove between two lobes of the digestive gland, and leads to the ventrally situated stomach. A thin salivary duct runs from the postero-ventral aspect of the buccal mass ventral to the oesophagus. The salivary duct bifurcates in the vicinity of the digestive gland to drain from the paired posterior salivary glands. The posterior salivary glands are triangular, and are located on the anterior tip of the digestive gland. The stomach is a small muscular sac which leads dorsally to a thin-walled caecum. The short intestine and rectum run from the caecum antero-ventrally to open via the anus into the base of the funnel. The digestive gland is bilobed, somewhat flattened and partly divided by a median groove. Pancreatic tubules are formed around the dorsal surface of the caecum, along the digestive gland ducts and the posterior portion of the intestine.

The male reproductive system of *Sepioloidea pacifica* comprises a large testis which fills the posterior portion of the visceral mass. The thin, convoluted vas deferens links a median groove on the testis to a thick slightly coiled spermatophoral gland. A short tube leads from the spermatophoral gland to the accessory gland which in turn is linked by a longer tube to Needham's sac and the penis. In mature males, Needham's sac is packed with about 300 spermatophores which measure 4.0 mm in length and up to 0.36 mm in diameter. No information is available on the female reproductive system in *S. pacifica* or other members of the family.

Dew (1959a) described the eggs and the hatchlings of *Sepioloidea lineolata*, based on observations of eggs removed from a spawning site. The eggs (55 in all) were found on the underside of a rock in about 3 m of water, off Cronulla, New South Wales, and were removed and placed in an aquarium for observation. They were white and opaque, 10 mm in diameter, and attached individually to the rocks by a short stalk. Immediately prior to hatching, at one end of the egg a bulge formed and enlarged slightly. The bulge was finally ruptured by larval movement, and the hatchling shot out, posterior end of the mantle first. The eggs hatched over 16 days, indicating that the collected eggs were not of the same age. The young hatchlings, 9–10 mm long and about 4 mm wide were similar to adults in colour and shape (Pl. 18.2). They swam in short jerks for a few minutes after hatching and then settled to the bottom.

The young were negatively phototaxic. Upon settling, they dug into the sand as the adults do, by jerking downwards and forwards, then downwards and backwards. By repeating these movements several times, they quickly disappeared into the sand, leaving only their eyes showing. *Sepiadarium austrinum* collected from Port Phillip Bay also exhibited this behaviour in an aquarium (C.C. Lu unpublished data). Small amphipods and other small crustaceans were the preferred food of the young *Sepioloidea lineolata*. They stalk and capture their prey in the same way as the adults.

Provided that sufficient prey and sand are available, Australian members of this family, at least, appear to be maintained easily in aquaria. They should make good laboratory animals for studies of behaviour and physiological processes.

There is no commercial fishery based on any member of the family, and none has any economic significance.

Sepiadariids are benthic dwellers on the continental shelf in the Indo-West Pacific and around Australia and New Zealand. The genus *Sepioloidea* with the two described species, *S. lineolata* and *S. pacifica*, as well as several other unnamed species is known only from Australia and New Zealand. The generic identity of a sepiadariid found in the stomach of *Alepisaurus ferox* from the Solomon Sea has yet to be confirmed (Okutani & Tsukada 1988). *Sepiadarium* includes five described species and one undescribed species occurring through the Indo-West Pacific northwards to Japan. Four species, *S. kochi*, *S. auritum*, *S. austrinum* and an unnamed species are found in Australia; all but *S. kochi* are endemic.

Family Sepiolidae

Sepiolids are small, being less than 100 mm mantle length. The mantle is short with a rounded posterior end (Fig. 13.6; Pl. 18.5). The anterior dorsal mantle margin may be fused with the head or articulated by nuchal cartilages. The large head is as wide as or wider than the mantle. The large, lateral fins are kidney-shaped, with well-developed anterior lobes. The tentacles are retractable and each bears a well-defined club (Fig. 13.7A–E). The short arms lack protective membranes. When present, the gladius is chitinous and rudimentary; it is absent in some genera. Luminous organs are present on the ink sac in most members of the family. One or both dorsal arms, or a latero-dorsal arm, is hectocotylised in males. Only the left oviduct is developed. There are numerous genera and species, placed in three subfamilies: Rossiinae, Sepiolinae and Heteroteuthinae.

Naef (1923), Sasaki (1929) and G.L. Voss (1955, 1956, 1963) have treated regional faunas in some detail, namely the Mediterranean, the Japanese, the Caribbean Sea and the Gulf of Mexico, and the Philippines, respectively. Joubin (1902) provided the only major taxonomic revision of this large and diverse family on a worldwide basis.

Pfeffer (1884) described the first Australian member of this family from Bass Strait as *Sepiola tasmanica* (now *Euprymna tasmanica*; Pl. 18.5). Brazier (1892) included *Sepiola rondeletii*, *Inioteuthis stenodactyla*, and *Inioteuthis tasmanica* in his catalogue of cephalopods from Australia, although the basis for inclusion of *Sepiola rondeletii* is not clear. The last two taxa are species of *Euprymna*. Berry (1918) described *Rossia australis* from the Great Australian Bight, and Allan (1945) described *Heteroteuthis serventyi* from New South Wales. Lu & Phillips (1985) recorded an undescribed species of *Iridoteuthis* and *Sepiolina nipponensis* from Australia for the first time, together with an undescribed *Sepiola* species. Adam (1986) described *Euprymna hoylei* from northern Western Australia. Reid (1991) reviewed the Australian Rossiinae and described a new species, *Neorossia leptodons*, from south-eastern Australia.

Australian members of the subfamily Rossiinae, *Rossia australis* (Figs 13.6B, 13.7B, G) and *Neorossia leptodons*, are medium-sized animals, rarely exceeding 60 mm mantle length. The large, semicircular fins have conspicuous anterior lobes, sometimes reaching beyond the mantle margins, and poorly defined posterior lobes. The mantle margins are connected with the head dorsally by the spade-shaped nuchal cartilage and ventrally by the funnel-mantle locking cartilages. The funnel locking cartilages are oval and deeply grooved.

The head is large, and the prominent eyes have free lower eyelids. The radular arrangement in *Euprymna tasmanica* is illustrated in Figure 13.7K. The large funnel reaches the level of the centre of the eyes. The short arms bear two series of suckers. The suckers are spherical with minute apparatus. They are similar on all the arms of females, and gradually increase in size from the base and from the tip towards the middle of the arm. In males, both dorsal arms are hectocotylised (Fig. 13.7G). On these arms, the basal six to eight pairs of suckers are very small, followed distally by about six pairs of much larger suckers; more distal suckers decrease in size towards the arm tips. A slightly swollen pocket of soft, spongy, colourless glandular tissue is located on the ventral face of these arms, opposite the sixth to the ninth pairs of suckers. A deep longitudinal groove is located a little above the middle of the organ, and a deeper pocket lies between the margin of the gland and the sucker-bearing face of the arm. The suckers on the main portion of the remaining arms of the males are greatly crowded and much larger than the corresponding suckers of the females.

The tentacles are long and slender, tipped with an elongate club about a quarter of total length of the tentacle (Fig. 13.7B). The club is not expanded and numerous minute suckers cover its oral aspect.

The rudimentary gladius is chitinous, slender, lanceolate and shorter than the body. The surface of the body is smooth. The chromatophores are several shades of reddish brown.

The subfamily Sepiolinae is represented in the Australian waters by several species of *Euprymna* (Fig. 13.6C) and *Sepiola* (Fig. 13.6A). All resemble *Rossia australis* in external features, except that the anterior dorsal mantle margin is fused with the head by a muscular band. The nuchal cartilage is absent and the funnel-mantle locking cartilages are simple, straight lines. The arm suckers in most species are biserial, though in all but one non-Australian species of *Euprymna* they are tetraserial. The club suckers are in four, eight, 10 or more series, according to genus (Fig. 13.7E, J). The shell is absent in the genus *Euprymna*, and rudimentary in *Sepiola*, *Rondeletiola*, *Sepietta* and *Inioteuthis*.

The subfamily Heteroteuthinae is represented in Australian waters by the several members of the genera *Heteroteuthis* (Fig. 13.6F), *Iridoteuthis* (Fig. 13.6E) and *Sepiolina* (Fig. 13.6D). None has been studied and reported on in any detail. The anterior dorsal mantle margins either articulate with the head by the nuchal cartilage (*Heteroteuthis, Nectoteuthis*) or are completely fused with the head (*Iridoteuthis, Sepiolina* and *Nectoteuthis*). The forward extension of the ventral mantle margin varies from extensive, covering the funnel and part of the head (*Iridoteuthis* and *Nectoteuthis*), to moderate (*Heteroteuthis*), and slight (*Stoloteuthis* and *Sepiolina*).

In all, the first three pairs of arms are united by a deep web. The arm suckers are in two series. The fins are large. The shell is absent. All members have rich colouration with metallic sheen. In the mantle cavity, a forked median mantle adductor muscle forms the anterior support of the median mantle septum. Most members of the family have luminescent organs on the ink sac.

Nothing is known about the luminescent organs of any of the Australian sepiolids. Sepiolids which have them are members of the genera *Heteroteuthis*, *Iridoteuthis*, *Sepiolina*, *Sepiola* and *Euprymna*. Herring (1988) reviewed the knowledge on these organs in cephalopods. The luminescent organs in sepiolids are paired organs, being paired, separate, ear-shaped organs in *Sepiola* and *Euprymna* and being fused into a single, round-shaped entity in *Heteroteuthis*, *Nectoteuthis*, *Iridoteuthis*, *Stoloteuthis* and *Sepiolina*. It is generally accepted that bacterial luminescence is involved in the photophores of sepiolids, despite luminescent bacteria not having been identified or cultured *in vitro* in some genera such as *Heteroteuthis* and *Sepiolina*.

Euprymna morsei and *Heteroteuthis* species have been reported from the stomach contents of lancetfishes *Alepisaurus ferox* captured in the Solomon Sea (Okutani & Tsukada 1988).

The reproductive systems of three Australian sepiolid species described by Reid (1991) resemble those described and figured by Naef (1923) for females of several species of Mediterranean sepiolids, and the male *Sepiola rondeletii* described and figured by Marchand (1907). The hectocotylised arms of representatives of five genera are illustrated in Figure 13.7F–J.

In males, the testis is on the left side of the visceral mass below and close to the caecum. The proximal deferent canal connects distally to the testis, and opens into three seminal vesicles. The most distal seminal vesicle (SV III) joins a ciliated canal and a narrow tube. The ciliated canal opens into the genital sac and the tube connects the seminal vesicle III with the accessory gland and accessory gland appendage. The latter joins the posterior end of the Needham's sac via the distal deferent canal. The Needham's sac is large and leaf-shaped with a large tongue-shaped lobe on its posterior end. The genital orifice opens into the anterior end of mantle cavity. The posture adopted by *E. tasmanica* during copulation is shown in Plate 18.5.

In females, the ovary is located at the posterior end of the mantle cavity. In the mature animal, the large ovary displaces other organs in the mantle cavity. The ovary opens via a single, thick-walled oviduct at the anterior end on the left side. The opening of the oviduct is modified as a seminal receptacle, and often bears spermatophores embedded in the inner edge of the opening. The accessory nidamental glands lie distal to the pair of tear-shaped nidamental glands, located antero-ventral to the ovary.

In aquaria, *Euprymna tasmanica* lays eggs individually, attached to the substratum and to the adjacent eggs in the clutch (English 1981). Each egg is coated with a tough, opaque gelatinous capsule. They are similar to those described for *Sepiola robusta* by Boletzky (1983b). Development took approximately 29 days at 20°C.

Nothing is known about the eggs of Australian Rossinae and Heteroteuthinae. *Rossia palpebrosa* of the North Atlantic was reported to lay eggs in sponges (Akimushkin 1963; Aldrich & Lu 1967), *R. macrosoma* laid eggs in bivalve shells (Boletzky & Boletzky 1973), and *R. pacifica* attached the eggs singly or in small groups to seaweed or other objects on the bottom in the north-eastern Pacific (Hochberg & Fields 1980).

Most benthic sepiolids (Rossinae and Sepiolinae) bury themselves in soft substrata during the day. The 'burrowing' process has two phases. In the first phase, the animal blows jets of water on the sand while it gradually settles down. In the second phase, the dorso-lateral arms are stretched out over the surface to gather sand

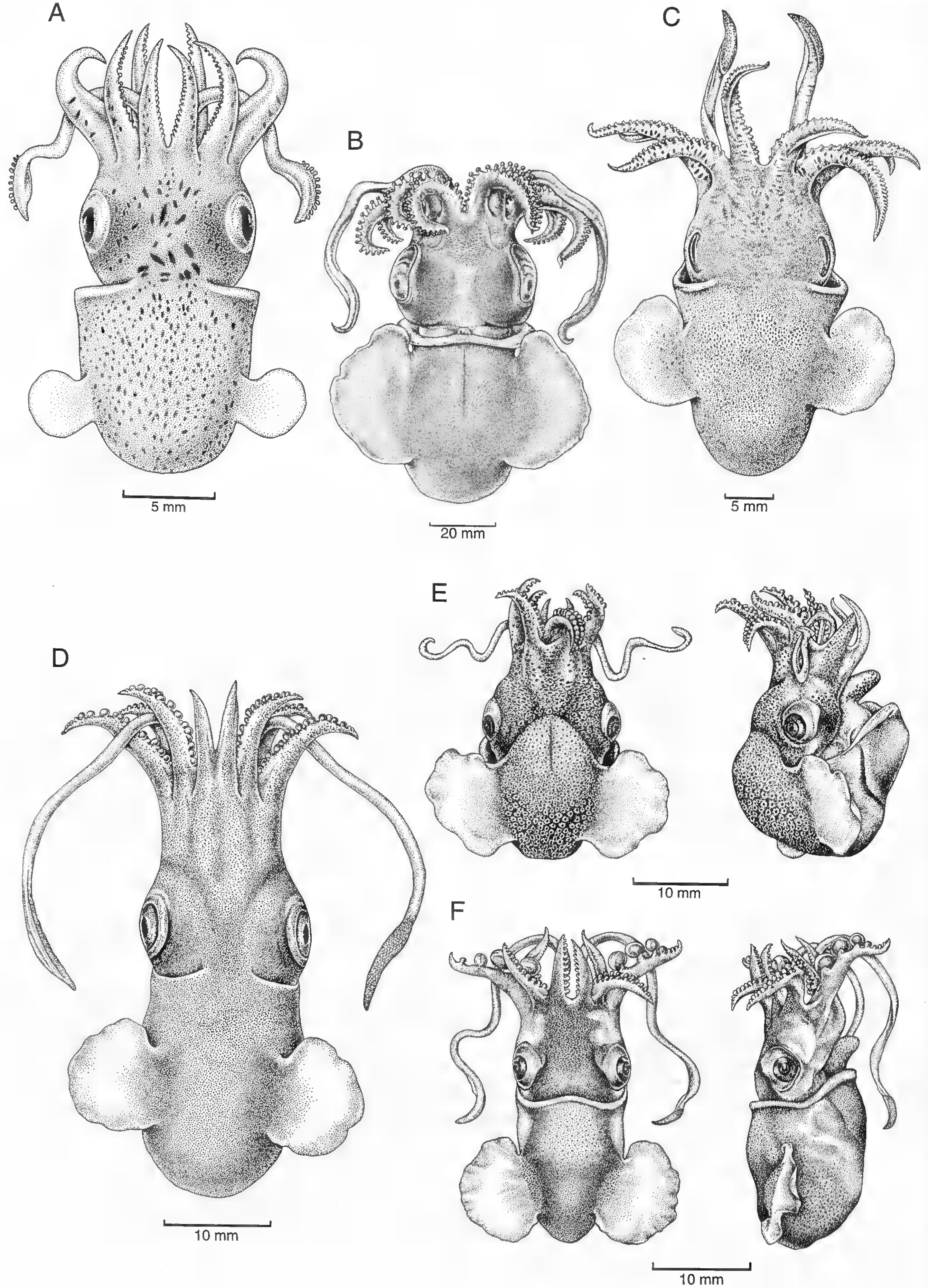


Figure 13.6 Family Sepiolidae. These small squids are primarily benthic on the continental shelf, or in mid-water over the slope. **A–D**, dorsal view: **A**, *Sepiola* sp.; **B**, *Rossia australis*; **C**, *Euprymna tasmanica*; **D**, *Sepiolina nipponensis*. **E**, **F**, dorsal and lateral view: **E**, *Iridoteuthis* sp.; **F**, *Heteroteuthis serventyi*. [K. Hollis]

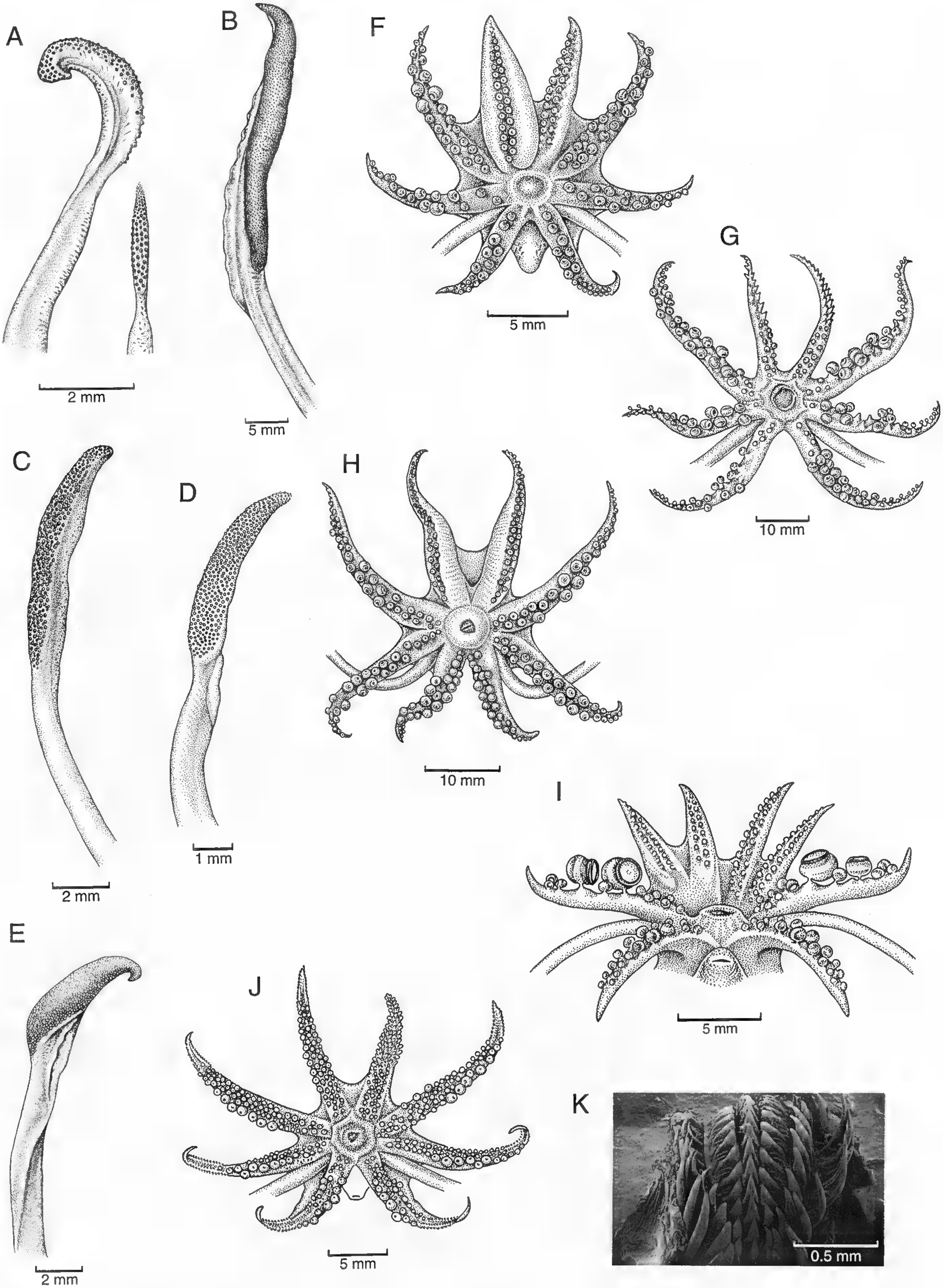


Figure 13.7 Family Sepiolidae. **A–E**, male tentacular clubs. **F–J**, arm crowns, showing hectocotylised arms. **A**, **F**, *Iridoteuthis* sp. **B**, **G**, *Rossia australis*. **C**, **H**, *Sepiolina nipponensis*. **D**, **I**, *Heteroteuthis serventyi*. **E**, *Euprymna tasmanica*. **J**, *Euprymna* cf. *morsei*. **K**, portion of radula of *Euprymna tasmanica*, showing several transverse rows.
[A–J, K. Hollis; K, C.C. Lu]

particles to completely cover the animal. This behaviour has been observed in four species of *Sepiola* and three species of *Sepietta* (Boletzky & Boletzky 1970; Bergstrom & Summers 1983). Newly hatched *Euprymna tasmanica* settle immediately and adopt the benthic mode of life of adults. In aquaria, day-old juveniles initiated burying behaviour, but no successful burying was achieved prior to death at three days old (English 1981).

The benthic sepiolids are generally easy to maintain in the laboratory. They are small animals, requiring little aquarium space. It has been suggested that they are ideal laboratory animals for behavioural, physiological and genetic studies (Arnold, Singley & Williams-Arnold 1972; Boletzky 1983b).

Nothing is known about food and feeding of Australian sepiolids. Data on non-Australian sepiolids are derived largely from diets offered in laboratory rearing experiments. Boletzky, Boletzky, Frösch & Gätzi (1971) reared six Mediterranean sepiolid species: young animals were fed on mysids (*Leptomysis mediterranea*); older juveniles and adults were fed *Leander* species. Bergstrom & Summers (1983) also successfully cultured *Sepietta oweniana* in aquaria. The juveniles were fed mysids (*Praunus flexuosus* and *P. inermis*), amphipods (*Ericthonius*) and large copepods; on rare occasions cannibalism also occurred. Adults were fed *Praunus flexuosus* and the shrimps *Palaemon elegans*, *Thoralus cranchii* and *Crangon crangon*.

Shrimps, crabs, small fishes and cephalopods form over 80% of the diet of *Rossia pacifica*, a species common in the North Pacific, in its natural environment (Brocco 1970; Hochberg & Fields 1980).

Their small size renders sepiolids of little commercial importance, although some species, such as *Sepiola birostrata*, *S. rondeletii*, *Euprymna berryi*, *E. morsei*, *Rossia macrosoma*, *R. pacifica* and *Neorossia caroli* are eaten locally (Roper *et al.* 1984). No Australian sepiolids are exploited commercially.

Family Idiosepiidae

The smallest known cephalopods are in the monogeneric Idiosepiidae. The maximum size of mature males is 17 mm mantle length, and females attain 22 mm in mantle length. The mantle is elongate and slightly pointed at the posterior end. An oval attachment organ is located on the dorsal surface of the mantle (Fig. 13.8). The fins are small, kidney-shaped, attached laterally at the posterior end of the mantle and slightly oblique to the longitudinal body axis. The anterior edge of the mantle is not fused with the head; the nuchal cartilage is lacking. The head is prominent with large, bulbous eyes that are covered by a cornea. The funnel-mantle locking cartilage is peg-like in all except the southern Australian *Idiosepius notoides*, which has a simple, straight cartilage. The short arms bear two rows of suckers. The slender tentacles are short and retractile. The tentacular clubs are not expanded; they support two to four rows of suckers. Both ventral arms of mature males are hectocotylised, the modification involving loss of suckers on most of the arms and the tips of the left ventral arms become bilobed.

Idiosepius pygmaeus, the first-named member of the Idiosepiidae, was first described by Steenstrup in 1881 from specimens collected in a surface net at 4°20′N 107°20′E in 1869, as well as a specimen from Zamboango. Several other species have been described and named, all from the Indo-West Pacific region. The first Australian idiosepiids were recorded by Berry (1921) with his description of *Idiosepius notoides* (Pl. 18.4), from South Australia. Allan (1945) reported the presence of *Idiosepius pygmaeus* in Australia. Cotton & Godfrey (1940) also recorded *I. paradoxus* from Australia. Lu & Phillips (1985) questioned the validity of the records for *I. pygmaeus* and *I. paradoxus* as no specimen of either was available for examination. However, subsequent collections have confirmed the occurrence of all three species in Australian waters.

Idiosepiids lack an external shell and have a vestige of a chitinous internal shell. The animal has an oval adhesive organ on the dorsal surface of the mantle used for attachment to sea weed or seagrass blades (Fig. 13.8A). The organ is located chiefly in the integument layer and is glandular (Sasaki 1923). Adhesion is caused by a sticky substance secreted by the organ. Its external surface is uneven with irregularly arranged furrows and pits.

Natsukari (1970) reported on egg-laying behaviour, and embryonic development of *Idiosepius paradoxus* in western Japan. The females laid eggs once, sometimes again three days later. The total number of eggs laid by individual females ranged from 25–64. The females died one to two days after last laying.

Natsukari (1970) observed squids laying eggs in glass jars. The female adhered upside-down to the bottom of the glass jar. She ejected a single egg from the funnel and received it in her arms. She then steadied herself by grasping the bottom with the dorsal three pairs of arms and stuck the egg to the bottom using her tentacles. After sticking the egg, she slid backwards by hard flapping of her fins and repeated the egg laying process, taking about 30 sec each time. The egg is elliptical in shape, measuring 0.87–0.91 mm in length and 0.67–0.72 mm in width. Incubation of the eggs took 15–17 days at water temperatures of 18.5°–22.6°C.

Idiosepius species are considered to be excellent experimental animal because of the short generation span, ease of maintenance in aquaria and local abundance in some coastal waters.

Aquarium-kept *Idiosepius* species from the Sydney area laid eggs on the side wall of an aquarium, beneath pieces of aquarium tubing, or on the underside of seagrass leaves (English 1981). English suggested that in nature, this species lays its eggs on hard substrata such as bivalve shells or beneath blades of seagrass. The main breeding period is reported to be throughout the spring and summer. The species is reported to have a life span of approximately 12–15 months.

Jackson (1986) studied *Idiosepius* from northern Queensland and confirmed the occurrence of both *I. pygmaeus* and *I. paradoxus* in the area. Adult *Idiosepius paradoxus* were found to be planktonic while *I. pygmaeus* had a more nektonic life. The larval mode of life of both species is similar to that of the adults. The two species show some degree of niche separation. *Idiosepius pygmaeus* is adapted to an estuarine existence while *I. paradoxus* is part of the continental shelf plankton community. In tropical Australia, *I. pygmaeus* has a fast growth rate and a short life span. Males and females mature as young as 42 days and 60 days old, respectively; the oldest ages known are 67 days for males and 79 days for females (Jackson 1988; Jackson & Choat 1992). Using tetracycline as a marker, Jackson (1986, 1988) confirmed that one growth ring was laid down per day in the statoliths of *I. pygmaeus* held in aquaria.

The diet of *I. paradoxus* in Japan consisted chiefly of gammarids as large as its own body (Sasaki 1929). The prey were bitten on the back just at the point where the heart is located. The animal can extend its buccal mass fully the length of its first arm, and move it freely in all directions to eat out the soft flesh of the prey without breaking its external chitinous skin. The radular arrangement in *Idiosepius notoides* is illustrated in Figure 13.8F.

The family is distributed in the Indo-West Pacific from Japan to Australia, and South Africa. It has not been reported from Atlantic waters. The animals are commonly found in seagrass beds where they attach to the underside of leaves. Worldwide, seven species of the single genus *Idiosepius* are known. In Australian waters, *I. pygmaeus* and *I. paradoxus* are known from northern Queensland waters, but their southern limit of distribution is not known. *Idiosepius notoides*, an Australian endemic species, is known in southern Australian waters from the Albany area of Western Australia to southern New South Wales.

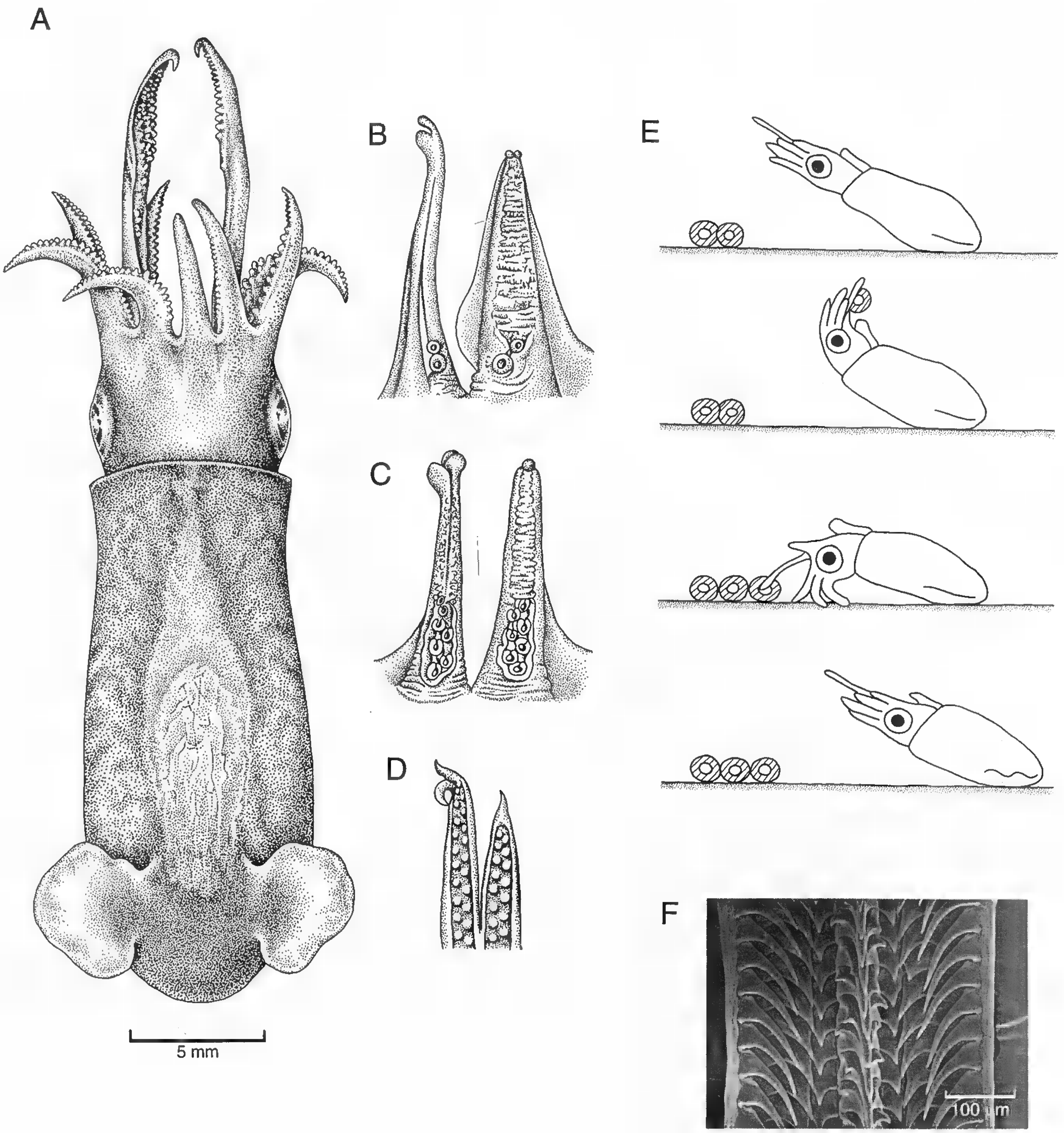


Figure 13.8 Family Idiosepiidae. Idiosepiids mature sexually at less than 20 mm total length. **A,** *Idiosepius notoides*, a southern Australian endemic, dorsal view. **B–D,** hectocotylised arms of three Australian species: **B,** *Idiosepius notoides*; **C,** *Idiosepius paradoxus*; **D,** *Idiosepius notoides*. **E,** egg laying in *Idiosepius pygmaeus*. **F,** portion of radula of *Idiosepius notoides*, showing several transverse tooth rows. (D, after Voss, G.L. 1963; E, after Natsukari 1970) [A–E, K. Hollis; F, C.C. Lu]

Order TEUTHOIDEA

Teuthoids have four pairs of arms and one pair of tentacles. These are always present in 'larvae', but may be absent in adults. Such specimens have a typical squid form. The tentacular stalks are not retractile. Arms are usually not connected by webs, or when present, the webs are generally shallow. The suckers are stalked, and have a chitinous ring, usually with a denticulate edge. In some species, sucker rings on the arms and/or the tentacular club may be modified into hooks. Fins are located at the posterior part of the body or along the entire mantle and, generally, merge along the midline or near the posterior end. Nuchal, mantle, and funnel cartilages are usually present. In some species, the mantle is fused with the head and, less frequently, with the funnel. If so, the mantle cavity communicates with the exterior by three openings, one on ventral side of body and two on sides of head. The non-calcified shell is represented by a thin, horny, pen-like or sagittate gladius. Small projections or 'angles' are located on the anterior edge of the mantle near the mantle locking cartilages. Between these the ventral mantle edge is slightly excavated. The central radular tooth is tricuspidate, or very rarely unicuspidate. The following key for the teuthoid families follows Roper, Young & Voss 1969. The family Walvisteuthidae (Nesis & Nikitina 1986) is not included.

Key to the families of the order Teuthoidea

1 (a)	Eye covered by a transparent cornea. Suborder Myopsida	2
(b)	Eye without cornea and in open contact with seawater. Suborder Oegopsida	3
2 (a)	Four rows of suckers on manus of tentacular clubs. Fins rhombic in outline. Medial posterior border of fins concave (Fig. 13.9; Pls 18.6, 18.9)	Loliginidae
(b)	Two rows of suckers on manus of tentacular clubs. Fins rounded, ear-like. Medial posterior border of fins convex	Pickfordiateuthidae
3 (b)	Funnel free from mantle, a funnel-mantle locking apparatus present	4
(b)	Funnel fused to mantle on each side, no funnel-mantle locking apparatus present	24
4 (a)	Funnel-mantle locking apparatus a simple, straight groove and ridge	5
(b)	Funnel-mantle locking apparatus not a simple, straight groove and ridge	18
5 (a)	Arms with hooks, or with suckers in four rows on the proximal half of the ventral arms	6
(b)	Arms without hooks, or with suckers in two rows on the proximal half of the ventral arms	8
6 (a)	Armature of arms in two rows	7
(b)	Armature of arms in four rows	Gonatidae
7 (a)	Tentacles present; fully developed clubs present (Fig. 13.11; Pl. 18.12)	Enoploteuthidae
(b)	Tentacles and clubs absent in adults (Fig. 13.13); clubs always rudimentary when present in 'larvae' or occasionally juveniles (*Taningia*)	Octopoteuthidae
8 (a)	Buccal membrane connectives attach to the ventral side of ventral arms	9
(b)	Buccal membrane connectives attach to the dorsal side of ventral arms	13
9 (a)	Hooks present on tentacular clubs (Fig. 13.14A, B; tentacles and clubs not described for *Chaunoteuthis*)	Onychoteuthidae
(b)	Hooks lacking on tentacular clubs	10
10 (a)	Cartilaginous scales present on mantle (Fig. 13.16; may be minute). Tentacular clubs with four longitudinal rows of suckers	Lepidoteuthidae
(b)	Cartilaginous scales lacking. Tentacular clubs with more than four longitudinal rows of suckers on some areas	11
11 (a)	Fins comb-like and nearly as long as the mantle, supported by strong, transverse, muscular ribs (Fig. 13.20A). Minute suckers on oral surface of buccal lappets	Ctenopterygidae
(b)	Fins not comb-like, less than half the body length, without supporting ribs. No suckers on buccal lappets	12
12 (a)	Tentacular clubs with six rows of suckers. Tail present, long and spike-like (greater than the fin length)	Batoteuthidae
(b)	Tentacular clubs with four rows of suckers on distal portion, numerous rows on proximal portion. Tail absent. (Fig. 13.21)	Brachioteuthidae
13 (a)	Eye with row of photophores on ventral surface. Buccal membrane with eight lappets. (Fig.13.10A, B)	Lycoteuthidae
(b)	Eye without photophores. Buccal membrane with seven lappets or less	4
14 (a)	Surface of mantle, head and arms covered with numerous photophores (usually large and distinct). (Fig. 13.18A, B)	Histioteuthidae
(b)	Surface of mantle and head without photophores; arms may have a few photophores	15
15 (a)	Oral surface of buccal lappets with minute suckers. (Fig. 13.19A)	Bathyteuthidae
(b)	Oral surface of buccal lappets without suckers	16
16 (a)	Many small to minute suckers (or suckers and knobs) at the proximal end of the manus	17
(b)	No cluster of small suckers at proximal end of the manus	Psychroteuthidae
17 (a)	Medial posterior borders of fins slightly convex. Carpal knobs in a single dorsal row or absent. Small size	Neoteuthidae
(b)	Medial posterior borders of fins concave (Fig. 13.17). Carpal knobs in a cluster alternating with carpal suckers. Attains gigantic size.	Architeuthidae
18 (a)	Funnel locking cartilage with a longitudinal and a transverse groove, ⊥-shaped or ⊣-shaped	19
(b)	Funnel locking cartilage oval, triangular or oval with inward projecting knobs	20

19 (a) Funnel locking cartilage with a longitudinal groove crossed by a transverse groove at its posterior end: ⊥-shaped. Fins less than 60% of mantle length (Fig. 13.22A–U; Pl. 18.11) .... Ommastrephidae
(b) Funnel locking cartilage with a longitudinal groove from which a shorter groove branches medially: ⊣-shaped. Fins more than 80% of mantle length (Fig. 13.23A, B) .... Thysanoteuthidae
20 (a) Funnel locking cartilage oval with one or two knobs directed toward the centre of the concavity 21
(b) Funnel locking cartilage oval or subtriangular, without knobs 22
21 (a) Club with four rows of suckers (Fig. 13.24A) .... Chiroteuthidae
(b) Club with more than 15 rows of minute suckers (Fig. 13.25A) .... Mastigoteuthidae
22 (a) Suckers on arms in four to six rows. Tail longer than mantle length (Fig. 13.27A) .... Joubiniteuthidae
(b) Suckers on arms in two rows. Tail less than 50% of mantle length, or absent 23
23 (a) Suckers on the tentacular clubs in four longitudinal rows. Mantle free dorsally. (Fig. 13.15A, B) .... Cycloteuthidae
(b) Suckers on the tentacular clubs in eight or more longitudinal rows. Mantle fused dorsally to head .... Promachoteuthidae
24 (a) Mantle free dorsally, articulates with head by ridge and groove. (Fig. 13.26) .... Grimalditeuthidae
(b) Mantle fused dorsally with head. (Fig. 13.28) .... Cranchiidae

Suborder MYOPSIDA

The eyes of myopsids are covered by a transparent membrane (cornea), except for a tiny hole, the 'lacrimal pore'. The mantle is muscular. The buccal connectives are seven-pointed and connect to the ventral arms on the ventral border. The funnel locking cartilage is simple and straight. Only the left oviduct is developed. Paired nidamental glands and accessory nidamental glands are present. One or both ventral arms are hectocotylised in males.

Family Loliginidae

Loliginids are characterised by a transparent cornea covering the eyes. The mantle locking apparatus is straight and simple. There are seven buccal lappets each with a few small suckers, and the buccal connectives attach to the ventral borders of the ventral arms.

The mantle is elongate, and tapered posteriorly. The fins are oval, elongate rhomboidal or heart-shaped, either terminal on the posterior end, or marginal. The fins range in length from about half to nearly the entire length of the mantle. The arms bear two rows of suckers. The tentacles are not retractile and suckers occur in four rows on the tentacular club. In the mature males (Fig. 13.9), the left ventral arm is hectocotylised, except in the genus *Loliolopsis*, in which both ventral arms are hectocotylised.

Eleven genera are recognised at present: *Loligo*, *Nipponololigo*, *Photololigo*, *Heterololigo*, *Sepioteuthis*, *Loliolus*, *Lolliguncula*, *Loliolopsis*, *Doryteuthis*, *Alloteuthis* and *Uroteuthis*. *Photololigo*, *Sepioteuthis* and *Loliolus* are found in Australian waters (Fig. 13.9).

The name Loliginidae was introduced by Orbigny in 1839 (Férussac & Orbigny 1835–1848) to include the extant squid genera *Sepioteuthis* and *Loligo* and the fossil genera *Teudopsis*, *Leptoteuthis* and *Beloteuthis*. The currently recognised genera appear to be stable, with the exception of *Loligo* and *Doryteuthis* for which definition and composition remain to be settled. Natsukari (1983, 1984) separated three new genera, *Nipponololigo*, *Photololigo* and *Heterololigo*, from the genus *Loligo*, thus restricting *Loligo sensu stricto* to those species distributed in the eastern Atlantic.

Quoy & Gaimard (1832) provided the first report of loliginids from Australian waters, when they described *Sepioteuthis australis* and *S. bilineata* from Westernport Bay, Victoria. Gray's (1849) description of *Loligo australis* from Newcastle, New South Wales, is brief and the type specimen has deteriorated to the point that the name cannot be applied with certainty to any loliginid in the area. *Loligo etheridgei*, described by Berry (1918) from an unknown Australian locality, has been regarded as a junior synonym of *Loligo chinensis* (now *Photololigo chinensis*; Fig. 13.9A) (Natsukari & Okutani 1975).

Lu & Tait (1983) concluded that two species of the genus *Sepioteuthis*, *S. lessoniana* and *S. australis* (Fig. 13.9H, K) occur in Australian inshore waters. Lu, Roper & Tait (1985) described the new species, *Loliolus noctiluca* (Fig. 13.9C) from Australia and reviewed the taxonomy of the genus. The taxonomic problems with the remaining Australian loliginids are currently under study (for example, Yeatman & Benzie 1993).

The loliginid shell or gladius is quill-shaped (*Loligo*, *Photololigo*, *Nipponololigo*, *Heterololigo*, *Doryteuthis*, *Sepioteuthis*), leaf-shaped (*Loliolus*) or long and slender with a long conus (*Alloteuthis*, *Uroteuthis* males). Some sexual dimorphism occurs in the gladius of some species. Cohen (1976) noted that the vane (the posterior portion of the gladius) is wider in females of *Loligo pealei*, *L. plei* and *L. roperi*, and suggested that the wider gladius in the female may support or protect the large mass of eggs in a ripe female. In males of *Alloteuthis subulata* and *A. africana*, the posterior end of the mantle develops into a longer tail than in females (20 mm in females, 60 mm in males in *A. subulata*). The gladii reflect this sexual dimorphism.

Jet propulsion is the most important method of locomotion in loliginids. Contraction of circular muscles in the mantle produces high hydrostatic pressure in the mantle cavity, resulting in a jet of water from the funnel and the movement of the animal in the opposite direction. Trueman & Packard (1968) measured the momentum produced by the efflux of jet water from the mantle cavity in *L. vulgaris*, and concluded that the swimming tensions derived from the maximum jet pressures were, in general, equivalent to the body weight. Cole & Gilbert (1970) calculated the velocity in *L. pealei* to be about 4 knots for an animal of about 250 mm body length, comparable to that of *L. vulgaris* (Packard 1969).

Loliginids, in particular *L. pealei* and *L. forbesi*, are widely used in neurophysiological research, their giant axons providing systems for experimentation. Giant axons are the large diameter nerve fibres which serve the rapid coordination of large groups of muscle in quick escape or withdrawal responses. In squids, the jet propulsion depends on the rapid contraction of the mantle muscles which is initiated through giant axon innervation of these muscles. Much of our knowledge on neurophysiology stems from research performed on the giant axon of squids, particularly of loliginids. Adelman & Gilbert (1990) reviewed the techniques in this research and listed the squid species having useful giant axons. No Australian loliginids have been used for neurophysiological investigations.

Mating behaviour and other aspects of reproduction of have been studied in many non-Australian loliginids. Arnold (1962, 1965) reported that male and female *L. pealei* and *Sepioteuthis sepioidea* form pairs, in which the male pursues and protects the female

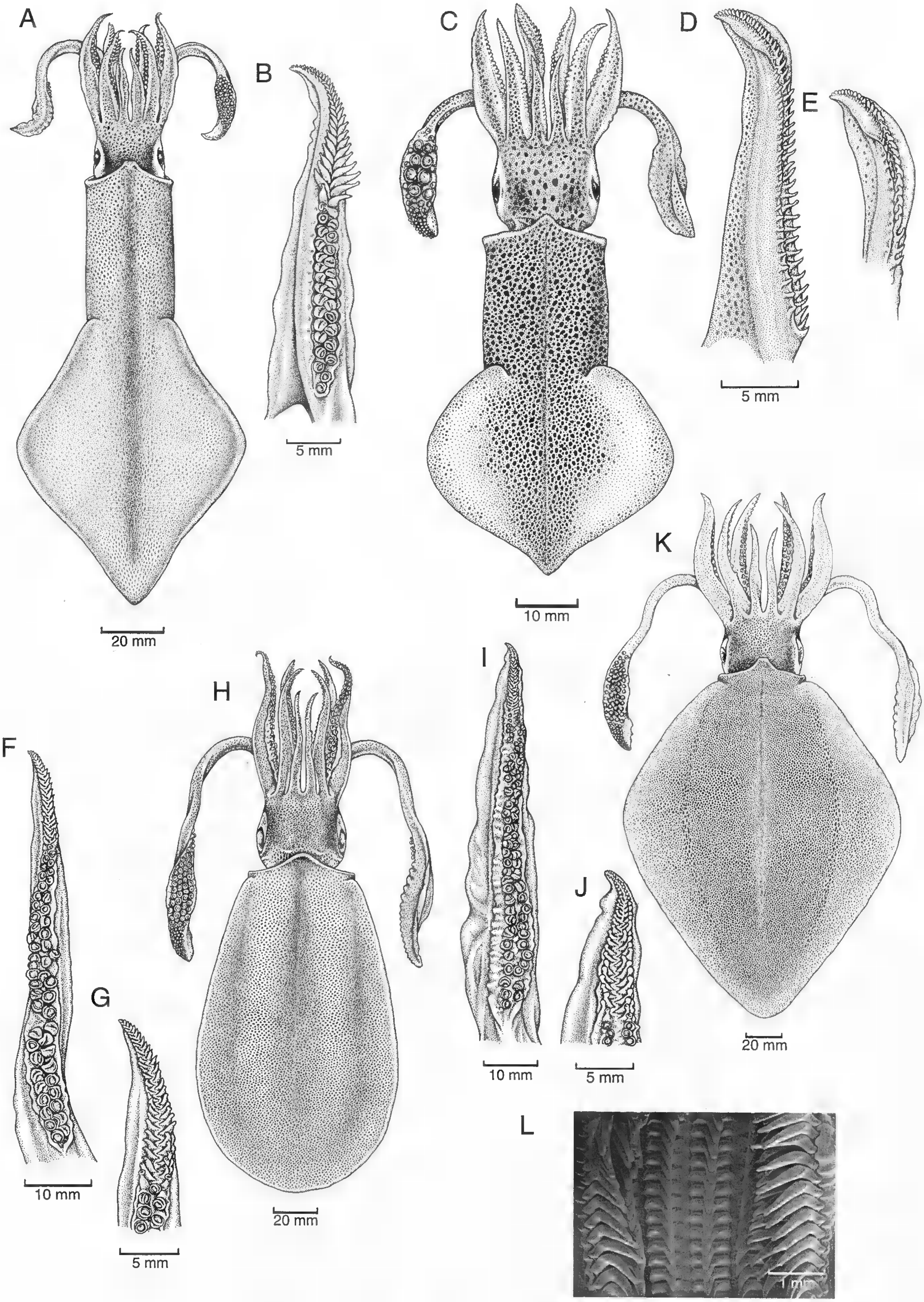


Figure 13.9 Family Loliginidae. Australian loliginids, members of a speciose group of common inshore squids. **A**, **B**, *Photololigo chinensis*: **A**, dorsal view; **B**, hectocotylised arm. **C–E**, *Loliolus noctiluca*: **C**, dorsal view; **D**, hectocotylised arm; **E**, detail of arm tip. **F–H**, *Sepioteuthis lessoniana*: **F**, hectocotylised arm; **G**, detail of arm tip; **H**, dorsal view. **I–K**, *Sepioteuthis australis*: **I**, hectocotylised arm; **J**, detail of arm tip; **K**, dorsal view. **L**, portion of radula of *Sepioteuthis lessoniana*, showing several transverse tooth rows. [A–K, K. Hollis; L, C.C. Lu]

from other males. Courting is initiated by an aggressive male who selects a female and swims parallel to her while displaying his courtship colour pattern. Typically, the females show little initial response. Later, the female responds by swimming parallel to the male and displaying her own courtship pattern. Similar courting behaviour has been observed in *S. lessoniana* in Japan (Segawa 1987) and *Loligo opalescens* in California (Hurley 1977).

Mating behaviour of *L. pealei*, *L. opalescens* and *S. lessoniana* has been described. Two postures were observed in *L. pealei*. A head-to-head posture preceded transfer of spermatophores to the buccal seminal receptacle of the female (Drew 1911; Arnold 1962). In the second pose, the mating squids are parallel to each other when the male grasps the female around the mantle behind the head, dips his hectocotylised arm into his own mantle cavity and picks up the spermatophores. He transfers them to the female via her funnel and cements them to the inside of the mantle near the oviduct (Arnold 1962).

A male *Loligo opalescens* copulates with a female by grasping her from below and inserting his right ventral arm into her mantle. The right arm is withdrawn just before the hectocotylised left ventral arm carrying spermatophores is inserted in its place (Hurley 1977). The head-to-head mating position also occurs in *L. opalescens* (Fields 1965). Mating in *S. lessoniana* is similar to that described above except the head-to-head posture was not observed (Segawa 1987).

At spawning, the eggs pass from the oviduct out through the funnel. The eggs are enveloped in secretions from the oviducal and nidamental glands (Pls 18.6, 18.7). The number of eggs in each egg capsule varies between species. The egg capsule of *L. opalescens* is 60–90 mm long, and contains an average of 156 eggs (Yang, Hixon, Turk, Krejci, Hulet & Hanlon 1986). Those of *S. sepioidea* contain only two to four eggs (LaRoe 1971). Similarly, *S. lessoniana* has only two to nine eggs in each capsule (Pls 18.7, 18.8) (Choe & Ohshima 1961) and *S. australis* (as *S. bilineata*) of New Zealand has two to six eggs (Larcombe & Russell 1971). In southern Australia, this last species also produces capsules containing up to six eggs each (Smith, B.J., Black & Shepherd 1989). The egg mass comprises many egg capsules.

Egg laying in *L. pealei* is initiated by visual stimuli. Arnold (1962) found that the presence of a naturally laid egg mass or an artificial egg mass made of water-filled polyethylene tubing induced animals to lay egg capsules; several females often contributed to the same egg mass. Several *S. australis* have also been observed to lay eggs on the same egg mass (Larcombe & Russell 1971).

Females of *Loligo opalescens* and *L. bleekeri* die after spawning, resulting in a mass mortality in the spawning area (Fields 1965; Hamabe 1973a). This phenomenon has not been observed in other species.

From commercial catch data, Fields (1965) estimated that *L. opalescens* spawns and dies at three years of age. He inferred also that the life span is one to four years, and that most live about three years. Spratt (1978) estimated the life span to be about one to two years, from the growth rings in the statoliths. Laboratory rearing indicates that *Loligo opalescens* is capable of spawning at one year of age (Hixon 1983).

Studies of growth rings in the statoliths led Jackson (1990a) to conclude that *S. lessoniana* reaches sexual maturity in less than 100 days in the tropical waters of northern Queensland. All the specimens studied (75–213 mm mantle length and 75–184 mm mantle length for males and females, respectively) were less than six months old. Using tetracycline staining techniques, Jackson (1990a, 1990b) established that daily growth rings are formed in *S. lessoniana*, *Photololigo chinensis* and *Loliolus noctiluca* under laboratory conditions. *Loliolus noctiluca* and *Photololigo chinensis* reach adult size in less than 200 days (Jackson & Choat 1992).

A wide range of food is eaten by loliginid squids. Crustaceans, polychaetes, fishes and cephalopods have all been found in the stomach contents of loliginids. *Loligo opalescens* of California prey on euphausiids, calanoid copepods, cumaceans, mysids, shrimps, anchovies and squids (Fields 1965; Karpov & Cailliet 1978). Fields (1965) and Karpov & Cailliet (1978) described the food preference differences of *L. opalescens* that are associated with growth, habitat, sex and reproductive maturity. Vovk (1972) reported that euphausiid and decapod crustaceans are eaten by smaller *L. pealei* and that larger squids eat fishes and other squids.

Many loliginid species have been reared successfully in captivity. Boletzky & Hanlon (1983) reviewed the extensive literature on rearing of loliginids including *S. lessoniana*, *S. sepioidea*, *L. vulgaris*, *L. opalescens*, *L. pealei*, *Doryteuthis bleekeri*, *Lolliguncula brevis* and *L. panamensis*. All have been reared on diets of crustaceans and fishes. Among the species occurring in Australian waters, *Loliolus noctiluca*, *Photololigo chinensis* and *S. lessoniana* have been reared in captivity on live sergestid shrimps (*Acetes sibogae australis*), juvenile penaeid prawns, and fishes of the families Ambassidae, Mugilidae, and Sillaginidae (Jackson 1990a, 1990b). The radular arrangement in *Sepioteuthis lessoniana* is illustrated in Figure 13.9L.

Prey detection and capture in loliginids is visual. Kier (1982, 1985) divided the attack into three phases: attention, positioning and strike. In the attention phase, the head of the squid turns rapidly so that the arms and tentacles are pointed towards the prey and the eyes are directed forward. During the positioning phase the squid swims towards the prey with the arms held together in a tight cone-shaped arrangement with the tips of the tentacles protruding just beyond the arms. During the strike phase the arms flare out from the previous tight cone and the tentacular stalks extend rapidly in a straight trajectory, with the tentacular clubs reaching the prey in approximately 15–35 milliseconds. The clubs strike the prey and attach to it with the suckers. The tentacles then contract, pulling the prey within the reach of the arms. The arms then converge around the prey and subdue and orientate the prey for ingestion.

Loliginids are preyed on by many vertebrates, among them fishes, seabirds and marine mammals. *Loligo opalescens* was preyed on by 19 fish species, 13 seabird species and eight marine mammal species in Monterey Bay (Morejohn, Harvey & Krasnow 1978). *Loligo vulgaris* was also eaten by cetaceans, sharks, tunas and seabirds (Worms 1983). In Australian waters, *S. australis* has been found among the stomach contents of pilot whales *Globicephala melas*, bottlenose dolphins *Tursiops truncatus* (Gales, Pemberton, Clarke & Lu 1992), hammerhead sharks (Dunning *et al.* 1993), as well as the Australian fur seal, *Arctocephalus pusillus doriferus* (Gales *et al.* 1994). Beaks of *Loliolus noctiluca* have been identified from the stomach of an Australian fur seal found in Port Phillip Bay (Lu unpublished data).

The distributions of loliginids are influenced by temperature and salinity, like those of other cephalopods. Some loliginids have been reported to tolerate salinity far below the normal salinity of sea water. *Lolliguncula brevis* is known to inhabit water with a salinity of 20–30‰, and is recorded from salinities as low as 17‰ (Gunter 1950; Laughlin & Livingston 1982). *Loliolus noctiluca* has been captured from waters with bottom salinity of 24‰ and surface salinity of 17.5‰ at a temperature of 11°C (Lu *et al.* 1985).

Loliginid squids are important in fisheries, and account for approximately 9% of the world cephalopod catches (Roper *et al.* 1984). According to FAO data, the world catch of loliginids in 1990 was 103 609 tonnes. In Australia, about 300 tonnes of *S. australis* are sold on the domestic market annually (Dunning 1982). In northern Australian waters, where several loliginid species occur, 2000–3000 tonnes of squids were captured annually by Taiwanese trawlers prior to the declaration of Australia's 200 mile fishing zone (Dunning 1982; Dunning *et al.* 1994). Liu & Yeh (1984) estimated the standing stock of loliginids in the southern part of the Arafura Sea, the northern Timor Sea, the southern Timor Sea and the North West Shelf to be 39 400, 19 300, 700, and 4500 tonnes respectively.

Various loliginid species inhabit the shelf and upper slope of the world's oceans, except the Arctic and Antarctic regions. *Loliolus noctiluca* (Fig. 13.9C) is known only from the inshore waters of eastern Australia including Tasmania, the Gulf of Carpentaria, and the Gulf of Papua (Lu *et al.* 1985). *Sepioteuthis australis*, an endemic, is known only from southern Australia and northern New Zealand (Lu & Tait 1983). *Sepioteuthis lessoniana* (Fig. 13.9H) is a widely distributed Indo-West Pacific species known from northern Australia. Several species of *Photololigo* occur in northern Australian waters (Yeatman & Benzie 1993; Dunning *et al.* 1994). The south-eastern limit of the distribution of this genus is around Newcastle, New South Wales, on the east coast. The southern limit on the west coast has yet to be determined. The taxonomy of *Photololigo* requires clarification before discussion of the biogeography of the group is useful.

Suborder OEGOPSIDA

In members of this order, the eyes lack a cornea and the lens is in direct contact with seawater. The mantle may be muscular or semi-gelatinous. The buccal connectives are six-, seven- or eight-pointed and connect to the ventral arms on either the dorsal or the ventral border. The funnel locking cartilage may be simple or complex and modified, or may be fused with the mantle. Both oviducts are developed. Paired nidamental glands are present, except in Enoploteuthinae; accessory nidamental glands are absent. If the hectocotylus is present, one or both ventral arms are modified.

Family Lycoteuthidae

This family of small to medium-sized squids, less than 200 mm mantle length, is characterised by a simple, straight funnel locking cartilage, biserial sharp-toothed suckers on the arms and tetraserial suckers on the tentacular clubs (Fig. 13.10). The buccal connectives attach to the dorsal border of the ventral arms and light organs are present on the viscera, at the apex of the mantle and on the ventral surface of the eyes in some genera. Sexual dimorphism is pronounced in some genera, in which males have brachial photophores and larger, more numerous, mantle photophores. The posterior mantle and the dorso-lateral arms are elongate in males. The four genera are divided into two subfamilies. The Lampadioteuthinae include only the genus *Lampadioteuthis*, and the Lycoteuthinae contain *Lycoteuthis*, *Selenoteuthis* and *Nematolampas*. These subfamilies are distinguished by the number of light organs on the eyes, four compared with five, respectively (Roper *et al.* 1969; Toll 1983).

Pfeffer (1912) described a specimen of *Lycoteuthis diadema* from south of Western Australia. *Lycoteuthis diadema* and *L. lorigera* were recorded for the first time from south-eastern Australian waters by Lu & Phillips (1985). No lampadioteuthine species have been recorded from Australian waters.

The considerable sexual dimorphism apparent in this relatively rare family (Fig. 13.10) resulted in taxonomic confusion until additional specimens of both sexes were examined recently (Toll 1983). Male *L. diadema* diverge from the typical oegopsid pattern in having paired genital ducts (Voss, G.L. 1962), although whether this is characteristic of all lycoteuthids awaits the examination of further specimens. No information regarding the life history of any lycoteuthid is available from Australian waters or elsewhere.

Recent studies of the feeding biology of a continental slope fish, *Macruronus novaezelandiae* (blue grenadier), around Tasmania have shown that lycoteuthids are a significant part of the diet of this species (Bulman & Blaber 1986). Around New Zealand, petrels commonly feed on lycoteuthids (Imber 1975) and these squids are also preyed upon by sperm whales and dolphins elsewhere (Clarke 1966). Lycoteuthids elsewhere are known to feed on pelagic crustaceans and fishes, including myctophids (Voss, G.L. 1962). The radular arrangement in *Lycoteuthis lorigera* is illustrated in Figure 13.10C.

G.L. Voss (1962) considered that *L. diadema* in the Gulf of Mexico occurs predominantly at depths of 300–600 m, with larvae in the upper 50 m. Its recent occurrence in demersal trawl catches off eastern Tasmania suggests that this species may be on or close to the seabed during part of the day. Extensive diel vertical migration is characteristic of the genus *Selenoteuthis* elsewhere and is suspected by Roper & Young (1975) to be typical of the family. Of the four recognised genera, only *Lycoteuthis* occurs in Australian waters; this genus has a worldwide distribution in subtropical oceanic waters. *Lycoteuthis diadema* and *L. lorigera* are known from off southern New South Wales and eastern Tasmania. Further clarification of their Australian distribution awaits the collection of additional specimens.

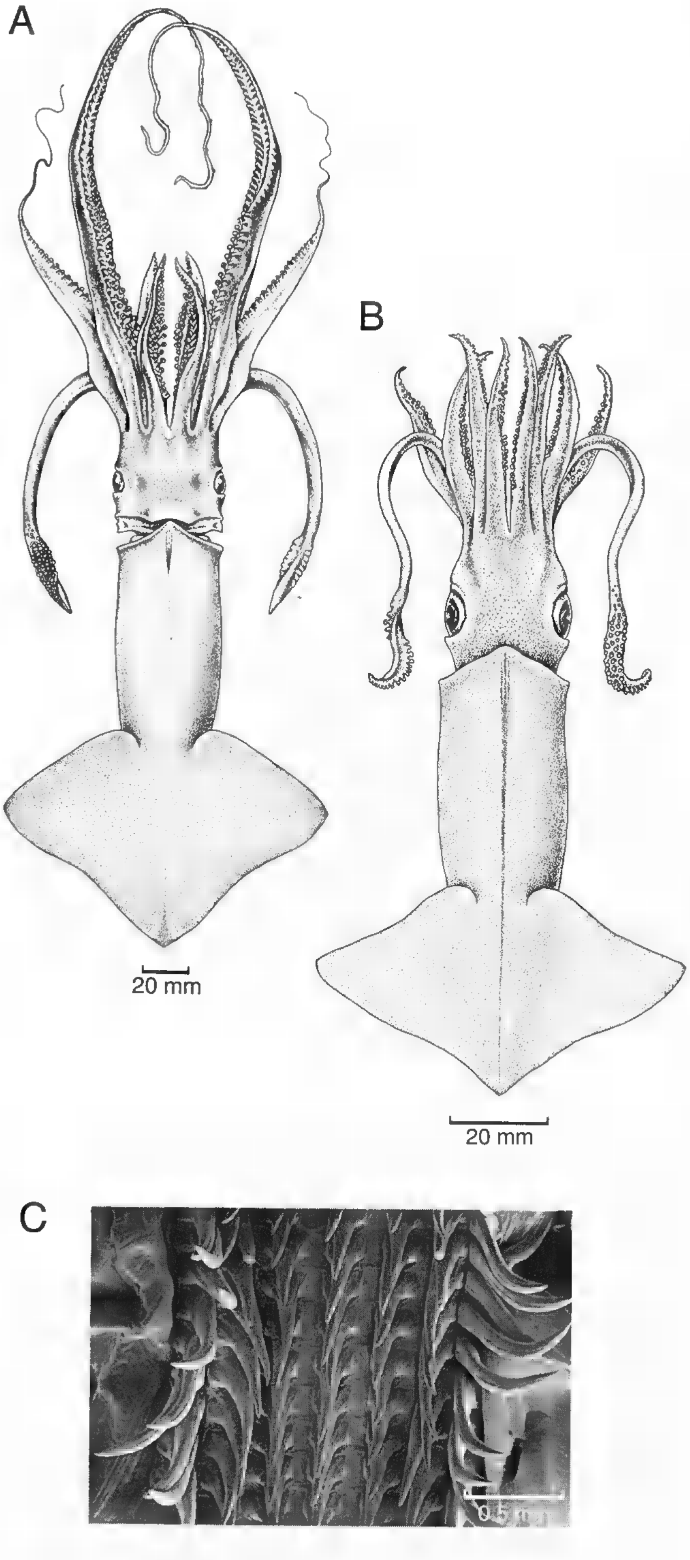


Figure 13.10 Family Lycoteuthidae. *Lycoteuthis lorigera*, a benthopelagic species common on the continental slope waters: **A**, male, dorsal view; **B**, female, dorsal view; **C**, portion of radula, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

Family Enoploteuthidae

The family Enoploteuthidae is represented in Australian waters mainly by an abundance of small to medium-sized mesopelagic species, all generally of less than 150 mm mantle length (Fig. 13.11A–E). Enoploteuthids are characterised by a simple, straight funnel locking apparatus, sharp-toothed suckers or suckers and hooks arranged in biserial rows on the arms and four rows on the tentacular clubs. Buccal connectives attach to the dorsal border of the ventral arms and light organs are present in adults of all genera. One or both of the ventral arms are hectocotylised in males. Three well-defined subfamilies designated by Pfeffer (1912) have become widely accepted (Roper *et al.* 1969; Riddell 1985), and are used in this treatment; these subfamilies were elevated to family level by Clarke & Trueman (1988).

The Enoploteuthinae have many small photophores on the ventral surface of the mantle, head and arms and large photophores on the eyeballs. Adults are not more than 150 mm mantle length.

In the Pyroteuthinae, photophores are present on the viscera and eyeballs, and embedded in the tentacles. Adults are not more than 60 mm mantle length.

The Ancistrocheirinae lack photophores on the eyeballs but have regularly spaced large bead-like photophores on the ventral and lateral surfaces of the mantle, head and tentacles. Adults are not more than 500 mm mantle length.

Berry (1918) described the first enoploteuthid recorded in Australian waters, *Enoploteuthis galaxias*, from material collected during the trawling investigations of the F.I.S. *Endeavour* in Bass Strait (Fig. 13.11A, F; Pl. 18.12). Paralarvae of three additional species were described from the New South Wales coast by Allan (1945), and Nesis (1979a) provided an overview of the zoogeography of the common oceanic representatives of this family from the Australian region. Clarke (1980) and Clarke & MacLeod (1982) recognised ancistrocheirine squids in the diets of sperm whales from south-western Australia and the Tasman Sea respectively. At least eight species were recorded by Brandt (1983) from an East Australian Current warm-core eddy. Lu & Phillips (1985) provided the most recent Australian checklist.

Hooks are strongly developed on the arms of all Australian enoploteuthids and on the tentacular clubs of all genera, except *Pterygioteuthis*, in which sucker rings only are present with slender pointed teeth on their distal margins. Fin shape varies among the subfamilies. In the Enoploteuthinae, the lanceolate subterminal fins have slightly concave posterior borders (Fig. 13.11A). In the Ancistrocheirinae, the large fins with slightly convex posterior margins extend almost the entire length of the mantle. The semi-gelatinous posterior tip of the mantle in these subfamilies is extended posteriorly in several species. The fins of pyroteuthine squids are nearly circular in outline with the sharp conus of the gladius obvious at the posterior tip of the mantle (Fig. 13.11D, E). The lateral arms are keeled in many enoploteuthine and pyroteuthine species. The arrangement, size and number of light organs in enoploteuthids are genus and species specific characteristics and their structure and function have been studied intensively in the same and closely related species elsewhere. These structures may provide concealment from potential predators through counter-illumination, the obliteration of the animal's silhouette through bioluminescence from below (Young, R.E. 1977, 1983). Radulae from species in each subfamily are illustrated in Figure 13.12.

Reproductive organs are typically oegopsid, except in the Enoploteuthinae which lack nidamental glands, and have the oviducal glands strongly developed. Hectocotylisation in males shows considerable variation between species. In the Enoploteuthinae (Fig. 13.11F), Ancistrocheirinae and in the genus *Pyroteuthis*, enlarged protective membranes are evident distally on the edges of the hook-bearing surface of the ventral arms of mature males. Hooks are modified in *Pyroteuthis* with the development of a secondary cusp. All hooks are replaced in *Pterygioteuthis* by a single chitinous plate housed in a fleshy pocket midway along the oral surface of the ventral arm. Spermatophores are transferred to the nuchal crest region of females in some species, but no structures for their storage have been described (Roper *et al.* 1969; Riddell 1985).

No comprehensive life history data are available for enoploteuthids from Australian waters. Most squids deposit their eggs in masses. However, some female enoploteuthids release individual eggs into the plankton. Around Hawaii, eggs and larvae of enoploteuthine species closely related to those in Australian waters are common in near surface waters, although spawning locations are unknown (Young, R.E. & Harman 1986). Preliminary studies provide some indication of reproductive patterns in Australasian waters. Brandt (1983) found multimodal size distributions for *Abraliopsis gilchristi* and *Pterygioteuthis gemmata* from an eddy off the New South Wales coast. However, in this same study only a unimodal distribution was evident for *P. giardi*, perhaps indicating that congeners do not necessarily display similar reproductive patterns. In slope waters off New South Wales in the summer months, mature female *Ancistrocheirus* sp. have been recovered from the stomachs of sharks (Dunning & Stevens unpublished data) and probable spawning populations of *Enoploteuthis galaxias* have been sampled in demersal trawls (Dunning & Brandt 1985).

Riddell (1982) concluded from size frequencies and data on reproductive condition that *Pyroteuthis margaritifera* and *Pterygioteuthis gemmata* spawn during a single restricted period in summer in New Zealand waters and the largest mature females were larger than the males, as appears to be generally the case in enoploteuthids. In contrast, *Abraliopsis gilchristi* is believed to have a protracted summer spawning season. A trimodal size distribution in *Abralia astrolineata* suggested that the population may have three discrete spawning periods during the year. Off southern Japan, *A. andamanica* also displays a multimodal size distribution, and spawning apparently occurs in late summer to early winter (Kubota, Koshiga & Okutani 1982). Mature females of this species were caught off the Australian North West Shelf in late winter (Dunning & Lindholm unpublished data).

Females of enoploteuthine and pyroteuthine species that mature at about 50 mm mantle length are capable of producing between 10 000 and 20 000 eggs, typically with a maximum diameter of 1.2 mm (Kubota *et al.* 1982; Riddell 1982). Ripe eggs of mature *Ancistrocheirus* are large for oegopsids, reaching 3 mm over the long axis (Dunning unpublished data). Growth rates of enoploteuthid squids have not been studied although the preponderance of large females seen in populations of many species perhaps suggests that males have shorter life spans than females (Kubota *et al.* 1982; Riddell 1982; Brandt 1983).

Enoploteuthids are among the most commonly caught squids in midwater trawls. This abundance in the epipelagic and mesopelagic zones is reflected in their prevalence in the diets of tunas and lancetfishes, sharks and marine mammals (Rancurel 1970; Rancurel 1976; Wolff 1982; Okutani & Tsukada 1988; Dunning *et al.* 1993). Small enoploteuthids feed predominantly on pelagic crustaceans, particularly euphausiids, and larger individuals also take fishes and smaller squids (Riddell 1982). Representative radular arrangements are illustrated in Figure 13.12 for the three subfamilies.

Elsewhere, enoploteuthids are known to be diel vertical migrators and also show ontogenetic descent. Larval enoploteuthine squids are most abundant at depths of 100–150 m during the day, and at 30–50 m at night (Young, R.E. & Harman 1986). Adults occur at depths of 300–600 m during the day, migrating to the upper 150 m at night (Roper & Young 1975).

Although no enoploteuthids are fished in Australian waters, two species grow large enough to be of commercial interest. Individuals of an *Ancistrocheirus* species attain lengths in excess of 400 mm mantle length, but this species is unlikely to find local market acceptance because of the semi-gelatinous texture of its mantle. *Enoploteuthis galaxias* reaches 110 mm mantle length,

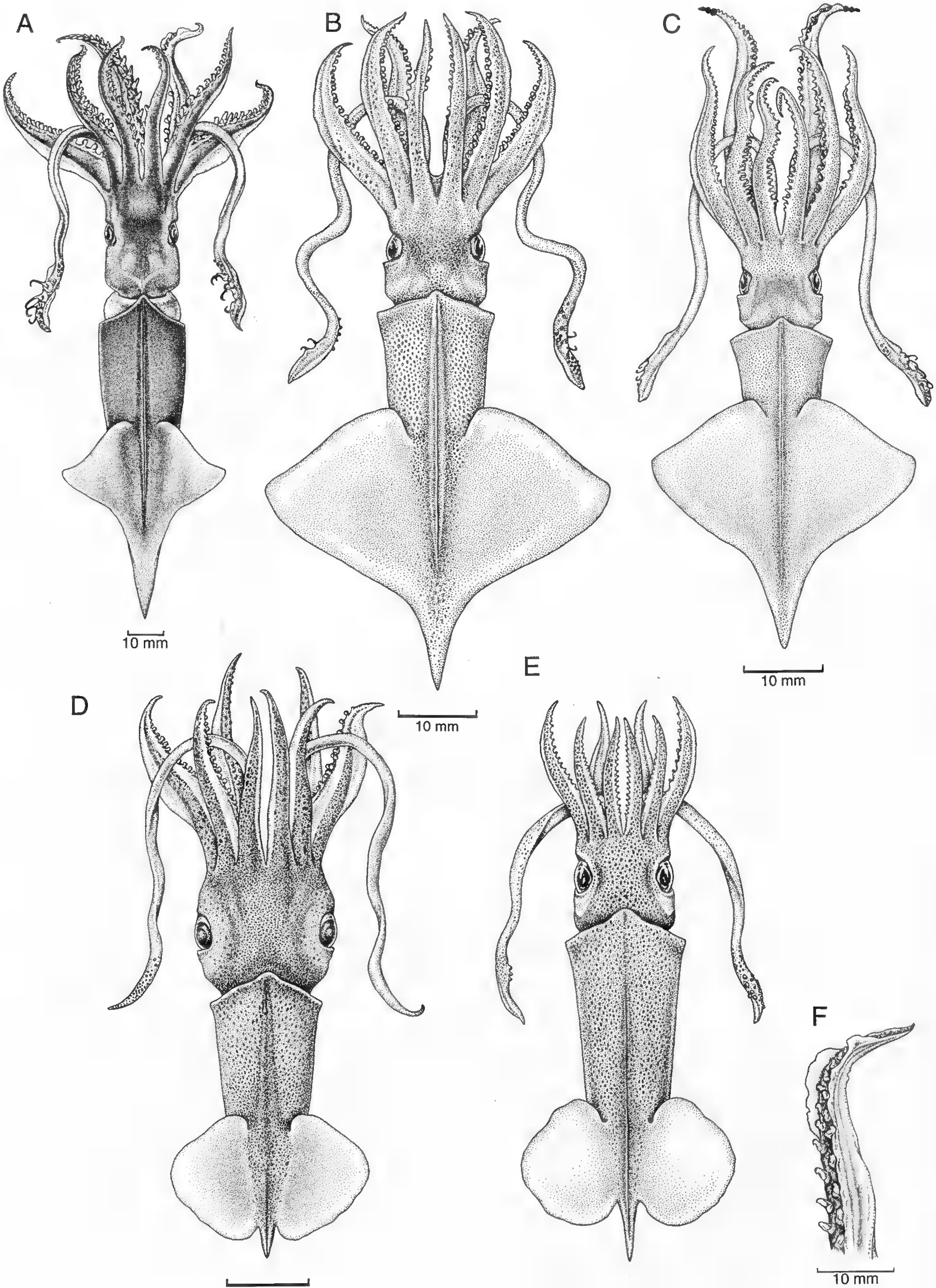


Figure 13.11 Family Enoploteuthidae. Members of this diverse, abundant family of oceanic squids occur from the surface to the bathypelagic zone. **A–E**, dorsal views: **A**, *Enoploteuthis galaxias*; **B**, *Abralia andamanica*; **C**, *Abraliopsis gilchristi*; **D**, *Pyroteuthis margaritifera*; **E**, *Pterygioteuthis gemmata*. **F**, hectocotylus of *Enoploteuthis galaxias*. [K. Hollis]

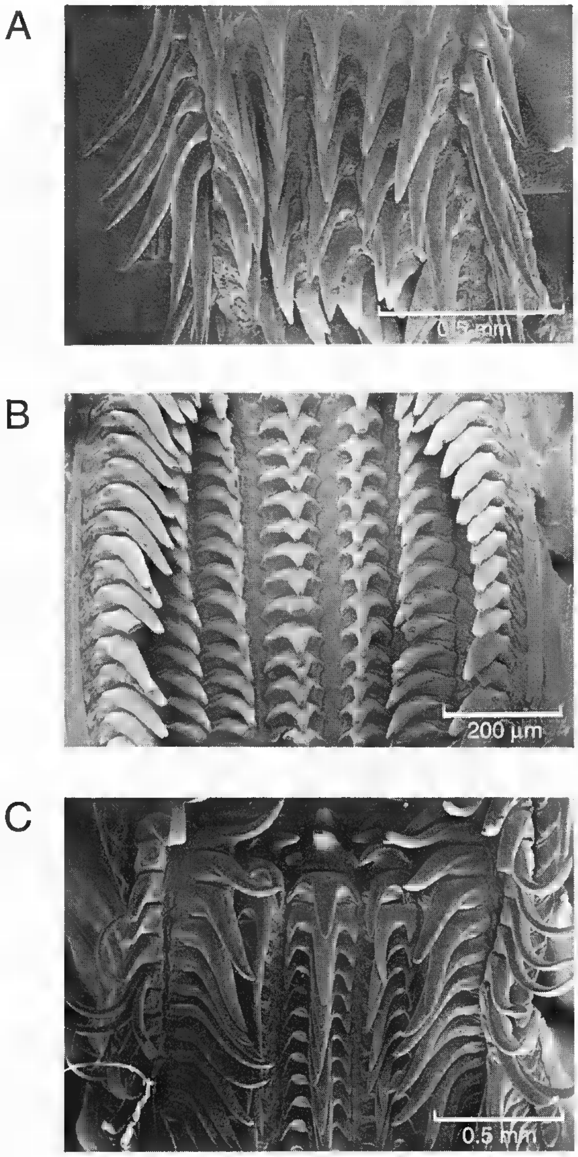


Figure 13.12 Family Enoploteuthidae. Representative enoploteuthine, pyroteuthine and ancistrocheirine radulae, showing several transverse tooth rows. **A**, *Enoploteuthis galaxias*. **B**, *Pyroteuthis margaritifera*. **C**, *Ancistrocheirus lesueuri*. [C.C. Lu]

similar to that of the commercially important enoploteuthid of Japanese waters, *Watasenia scintillans*, and is occasionally abundant in demersal trawl catches off the eastern Australian coast (Dunning & Brandt 1985).

None of the 12 species recorded from Australian waters is endemic, although *Enoploteuthis galaxias* appears to be restricted to southern Australia and New Zealand. Nesis (1979a) assigned nine pelagic enoploteuthid species from the Australian region to tropical, subtropical and peripheral groups. The distributional boundaries of these major groupings are defined largely by the Tropical and Subtropical Convergences. However, none of these species has been the subject of detailed study.

Enoploteuthids of all life stages are caught readily in good condition in sampling nets and, because of their size, can be kept in onboard aquaria. They have proven to be ideal subjects for the laboratory study of bioluminescence in Hawaiian waters (Young, R.E. 1983).

Family Octopoteuthidae

The family Octopoteuthidae includes two genera of medium-sized to large squids, up to more than 1000 mm mantle length, characterised by a broad, straight funnel locking apparatus and very broad fins extending almost the length of the mantle. The arms bear biserial hooks and sometimes small biserial suckers at their tips. The tentacles, which in all larvae carry a few distal club suckers, are lost in adults (Fig. 13.13). Buccal connectives attach to the ventral borders of the ventral arms. Several small, spindle-shaped photophores are present on the tips of all eight arms in the genus *Octopoteuthis*. A single very large photophore is present at the tip of each dorso-lateral arm in the monotypic genus *Taningia*. Hectocotylisation in males is unknown (Roper *et al.* 1969). Species within the genus *Octopoteuthis* are poorly delineated, and the genus is badly in need of revision (Lu & Phillips 1985).

The genus *Octopoteuthis* was recognised first from the south-western Pacific by Rancurel (1970). Nesis (1979a) also reported *T. danae* from the Australian region. Further records of octopoteuthids are provided by Clarke (1980) from material in sperm whale stomachs from off Albany, Western Australia, and Zeidler (1981) reported large moribund *T. danae* from off South Australia.

In larval *Octopoteuthis* body proportions change rapidly during growth up to 15 mm mantle length. Eyes which appear stalked initially, become sessile at mantle lengths of 10–15 mm. By this size, most specimens have lost their tentacles also (Stephen 1986). The mantle of some *Octopoteuthis* species has a thick gelatinous layer over the pigmented skin-like layer; it is especially thick over the tail region. Clarke (1980) suggests that longitudinal grooving in the anterior mantle jelly is characteristic of females in at least one species and that this area of the mantle is where spermatophores are lodged by the males. Clarke (1967) estimated that a female of a species of *Taningia* of 1400 mm mantle length carried 250 000 ovarian eggs. No life history studies of octopoteuthids have been made in Australian waters or elsewhere. The radular arrangement in *Octopoteuthis sicula* is illustrated in Figure 13.13B.

Octopoteuthids form a significant part of the diet of sperm whales off south-western Australia and in the Tasman Sea (Clarke 1980; Clarke & MacLeod 1982). They are included also in the diet of lancetfishes in the Coral Sea (Rancurel 1970; Okutani & Tsukada 1988) and of hammerhead, blue and tiger sharks off eastern Australia (Dunning *et al.* 1993).

From their numbers in stomachs of individual sperm whales, Clarke (1980) concluded that *O. rugosa* is a schooling species, but that *Taningia* may be solitary or form only small groups. Small specimens of *Taningia* species occur in the upper 200 m, while adults are more abundant in depths of more than 1000 m, suggesting that ontogenetic descent may occur (Clarke 1967). Roper & Young (1975) concluded that larvae of *Octopoteuthis* species off California are distributed in a narrow depth band from 200–400 m during the day, and spread throughout the upper 500 m at night. However, Stephen (1986) was unable to find conclusive evidence of diel variation in the depth distribution of *Octopoteuthis* larvae collected primarily from the North Atlantic.

Until their taxonomy has been clarified, the distribution of octopoteuthid species in Australian waters will remain poorly known. *Octopoteuthis megaptera* is considered to occur from tropical waters to as far as 36°S off the east coast and to Cape Leeuwin in the west (Nesis 1979a). *Taningia* occurs as far south as 44°S.

Members of this family have soft gelatinous bodies and have no commercial fisheries potential, although some reach very large sizes. They are readily damaged during capture in sampling nets, and therefore are unsuitable for laboratory study.

Family Onychoteuthidae

Onychoteuthids are medium-sized to very large oceanic squids, up to 2 m mantle length, with a strong, muscular torpedo-shaped mantle (Fig. 13.14). The family is characterised by a simple, straight funnel locking cartilage, biserial and sometimes smooth suckers on the arms and biserial hooks. There are two rows of marginal suckers on the tentacular clubs in the immature stages. The buccal connectives attach to the ventral border of the ventral arms and visceral light organs are present in the genus *Onychoteuthis*. Hectocotylisation is not evident in males of this family (Roper *et al.* 1969).

Onychoteuthis rutilis, described by Gould (1852) from off Sydney, New South Wales, was the first-recorded onychoteuthid from Australian waters. Allan (1945) assigned onychoteuthid larvae from off New South Wales to this species. Additional species have been recorded from the Australian region by Rancurel (1970, 1976) and Nesis (1979a). The most recent checklist of Australian onychoteuthids includes all genera except the Antarctic *Kondakovia* (Lu & Phillips 1985). Animals assigned to the genus *Onykia* are now known to be immatures of a *Moroteuthis* species (Tsuchiya & Okutani 1991).

The large muscular fins are generally rhomboidal. In some species of the genera *Moroteuthis* and *Ancistroteuthis*, fins and mantle are attenuated posteriorly. In contrast to the typically muscular mantle of other genera, *Chaunoteuthis* has a soft gelatinous body. Numerous distinctive dorsal pleats are present in the neck region in *Onychoteuthis* and *Chaunoteuthis*, and the skin of *Moroteuthis* and *Kondakovia* often contains subcutaneous papillae and ridges. Lateral arms have swimming keels in some of the larger species.

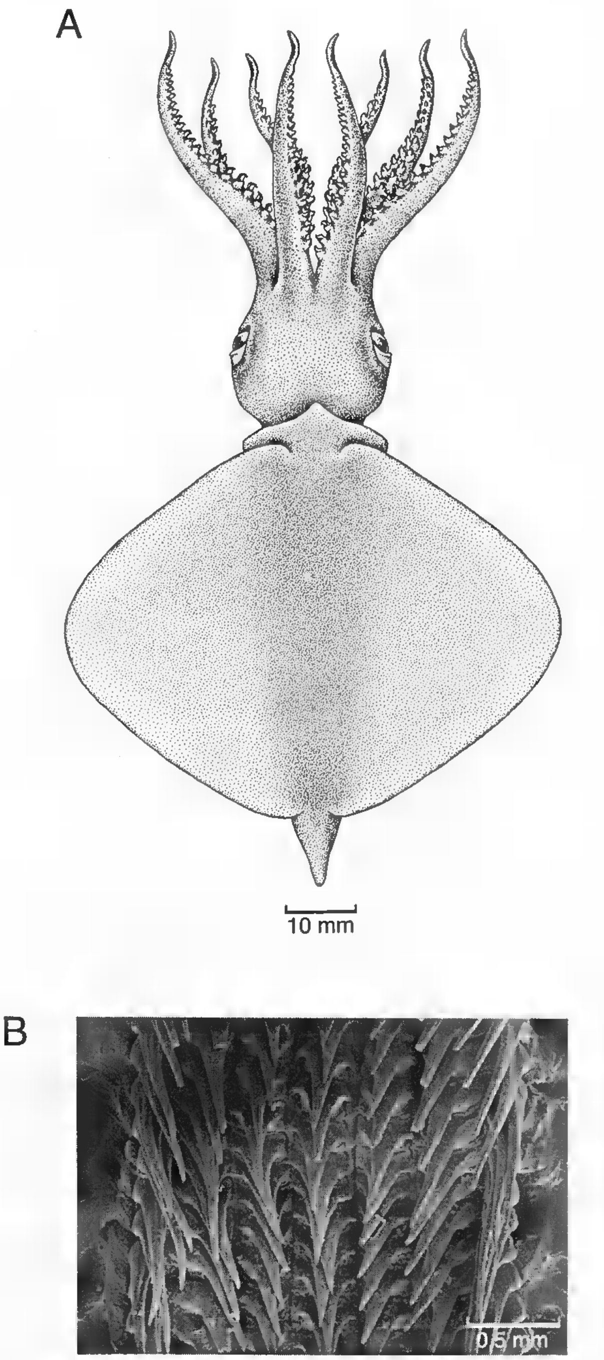


Figure 13.13 Family Octopoteuthidae. The large fins, biserial hooks on all arms and absence of tentacles in adults are typical of the family. A, *Octopoteuthis sicula*, dorsal view. B, portion of radula of *Octopoteuthis sicula*, showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

Reproductive organs are typically oegopsid and vary little within the family. Hectocotylisation has not been observed in any male onychoteuthid, although Gilly, Horrigan & Fraley (1986) noted that male *Moroteuthis* from off California had only a prominent fleshy keel on the ventral arms. Spermatophores appear to be introduced into the mantle of female *Onychoteuthis* and *Moroteuthis* from the elongate penis, through a longitudinal cut made midway between the head and fins of the female using the beak or perhaps the tentacular hooks. Mature copulated females of *O. borealijaponica* off Japan display a bright orange colour over the viscera and mantle (Clarke 1980; Murata, Iishii & Osaka 1982).

Age and growth of onychoteuthids in Australian waters have not been studied. Indeed the biology of only one species in this family, *O. borealijaponica*, is relatively well known. Reaching over 300 mm mantle length, this species inhabits temperate waters of the north-western Pacific, and apparently spawns from late autumn to winter in warmer subtropical waters to the south. Larvae have been found in the upper 150 m of the water column but not at the surface. The growth rate of adults is up to 20 mm per month and the life span approximately one year. Generally females are larger than contemporary males (Okutani & Murata 1983). *Moroteuthis* is believed to spawn in submarine canyon areas on the upper continental slope off California (Gilly *et al.* 1986). From examination of material collected from sperm whale stomachs, Clarke (1980) concluded that *M. robsoni* spawns in the austral autumn on the lower continental slope (2500 m) off South Africa. Clarke suggested that the young grow to more than 500 mm mantle length over a period of approximately two years, before a single spawning is followed by a wasting of the body musculature and death.

Onychoteuthids are oceanic forms, occasionally encountered in continental slope waters where they may be caught in demersal trawls. Elsewhere they feed on a broad range of fishes, crustaceans including krill, squids and other pelagic molluscs, and are at least partially cannibalistic. The radular arrangement in *Moroteuthis robsoni* is illustrated in Figure 13.14C. Known predators include lancetfishes and tunas, pelagic sharks, whales, dolphins, seals and albatrosses (Rancurel 1970; Rancurel 1976; Clarke 1983; Okutani & Tsukada 1988; Dunning *et al.* 1993).

Onychoteuthids form schools. Juvenile *Onychoteuthis* are able to leap above the surface to escape predators, as do ommastrephids, and sometimes are found on the decks of vessels. Off Japan, *O. borealijaponica* appears to make a north-south migration from feeding grounds to the warmer spawning grounds (Okutani & Murata 1983), although whether such migrations are typical, even of temperate onychoteuthids, remains to be confirmed. Little information regarding the vertical distribution of any onychoteuthid species is available. Immatures of *Moroteuthis* species share with the much larger ommastrephid, *Ommastrephes bartrami*, and some epipelagic octopods, the deep blue dorsal day colouration characteristic of the neuston generally (Roper & Young 1975).

The presence of immature *Moroteuthis* in the stomachs of lancetfishes and yellowfin tunas further confirms their epipelagic distribution (Rancurel 1970; Fujita & Hattori 1976; Rancurel 1976). Clarke & Lu (1974) recorded juvenile *Onychoteuthis banksi* from 100–1250 m in the North Atlantic.

In Australian waters, onychoteuthids are not fished commercially, although sometimes members of the genus *Moroteuthis* are caught incidentally in demersal trawls in continental slope waters (300–600 m) off both the north-western and southern coasts (Dunning & Brandt 1985). In Subantarctic waters off New Zealand, they make up a significant proportion of the trawled squid catch (Roberts 1978). The flesh of *Moroteuthis robsoni* caught off California proved to be unpalatable (Clarke 1966).

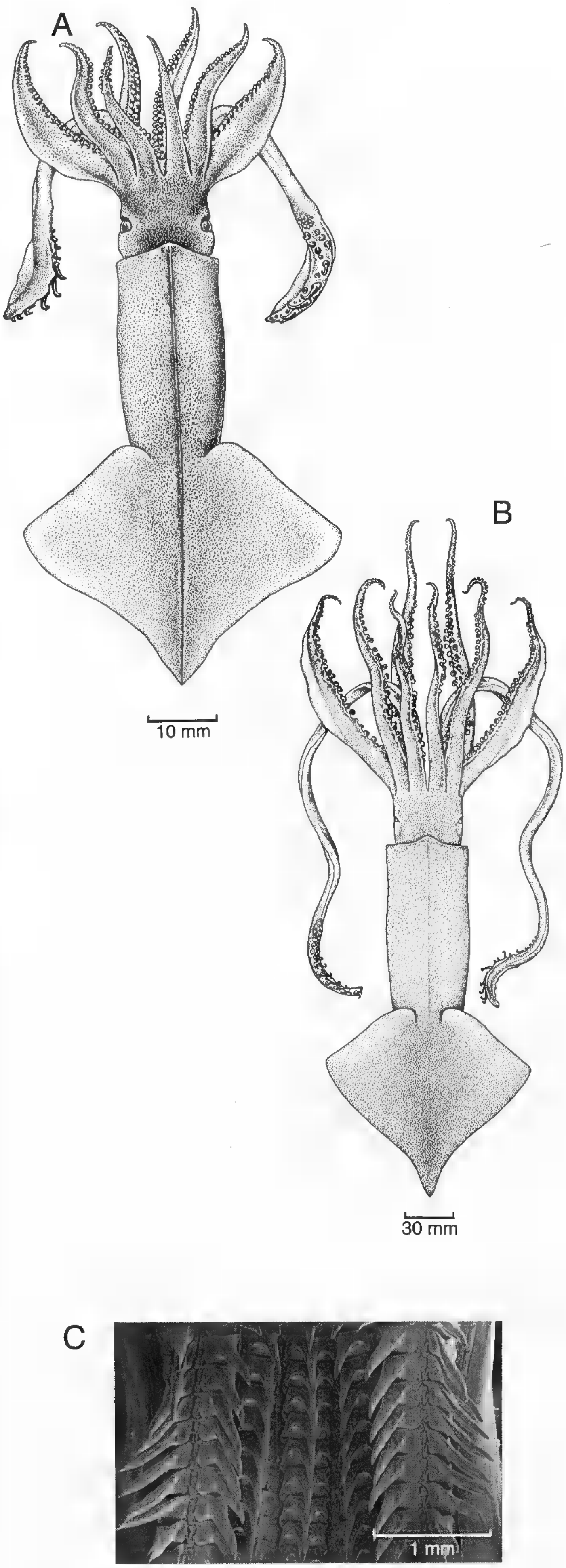


Figure 13.14 Family Onychoteuthidae. These oceanic squids are medium-sized to large epipelagic, mesopelagic or benthic inhabitants of the bathyl zones. **A**, *Onychoteuthis banksi*, dorsal view. **B**, *Moroteuthis loennbergi*, dorsal view. **C**, portion of radula of *Moroteuthis robsoni*, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

Onychoteuthid squids occur in all oceans. With the exception of *Kondakovia*, all currently recognised genera occur in Australian waters but generally their distributions are poorly defined. Nesis (1979a) considered *Onychoteuthis* to be a very eurythermal, mesopelagic and epipelagic tropical species, in waters as far south as 44°S. Fossil statoliths of late Pliocene *Moroteuthis* have been found in California (Clarke & Fitch 1979), although none has yet been discovered in Australia.

As was noted for ommastrephids, collection and laboratory maintenance of these muscular, highly mobile molluscs present major difficulties and have not been attempted in Australian waters. Large scale commercial trawls are necessary to catch the larger adults although larvae have been collected successfully using large tow nets and hand-held scoop nets.

Family Cycloteuthidae

The poorly known family Cycloteuthidae includes two genera of medium-sized to large squids, generally less than 500 mm in mantle length (Fig. 13.15). These apparently mesopelagic species have rarely been encountered in Australian waters. Cycloteuthids are characterised by a subtriangular funnel locking cartilage. The toothed or smooth suckers are arranged biserially on the arms and tetraserially on the tentacular clubs. Buccal connectives attach to the ventral border of the ventral arms, and light organs are present in adults around the eyes, on the ventral mantle and at the arm bases in some species. Fins extend anteriorly for more than 70% of the mantle length in adults. In the genus *Cycloteuthis*, the mantle is elongate posteriorly, forming a distinct tail (Fig. 13.15A) and the ink sac bears a single light organ. In *Discoteuthis*, a tail is lacking, the fins are very large and round (Fig. 13.15B), and mantle photophores only are present. No mature males of any cycloteuthids have been described in the literature, and the form or even the presence of hectocotylisation is unknown (Young, R.E. & Roper 1969a).

This family was described first from Australian waters by Clarke (1980), who found specimens of *Cycloteuthis akimushkini* (perhaps a junior synonym of *C. sirventyi*) among the stomach contents of sperm whales caught off Albany, Western Australia. Later, *Cycloteuthis* and beaks assigned tentatively to *Discoteuthis* were also found in whales from the Tasman Sea (Clarke & MacLeod 1982). Lu & Phillips (1985) recorded *Discoteuthis discus* from off the south-eastern Australian coast.

The mantle of cycloteuthids is not strongly muscular. A central layer of gelatinous connective tissue lies between thin inner and outer layers of strong, circular muscle. The head is also covered with moderately thick semi-gelatinous tissue (Clarke 1980). In contrast to the superficially similar octopoteuthids, the fins of *Discoteuthis* are separate (Fig. 13.15B) and insert directly onto the shell sac of the gladius. Those of *Octopoteuthis* are fused and continuous across the dorsal midline, and pass over the shell sac. Corresponding differences in the structure of the gladius also occur. That of *Octopoteuthis* is thin and fragile, compared to the very thick, rigid supporting structure of *Discoteuthis* (Young, R.E. & Roper 1969a).

No studies of cycloteuthid life history have been undertaken in Australia or elsewhere, because they are rarely captured. Cycloteuthids form part of the diet of sperm whales in the Australian region (Clarke 1980; Clarke & MacLeod 1982) and elsewhere (Clarke 1983). The radular arrangement in *Discoteuthis laciniosa* is illustrated in Figure 13.15C.

The few records of this family from Australian waters and elsewhere are uninformative about their vertical distribution. Elsewhere all three species recognised by R.E. Young & Roper (1969a) have been captured in the upper 200 m at night.

Cycloteuthids have not been recorded in sufficient abundance in Australian waters to indicate any commercial fisheries potential or to assess adequately their geographic distribution.

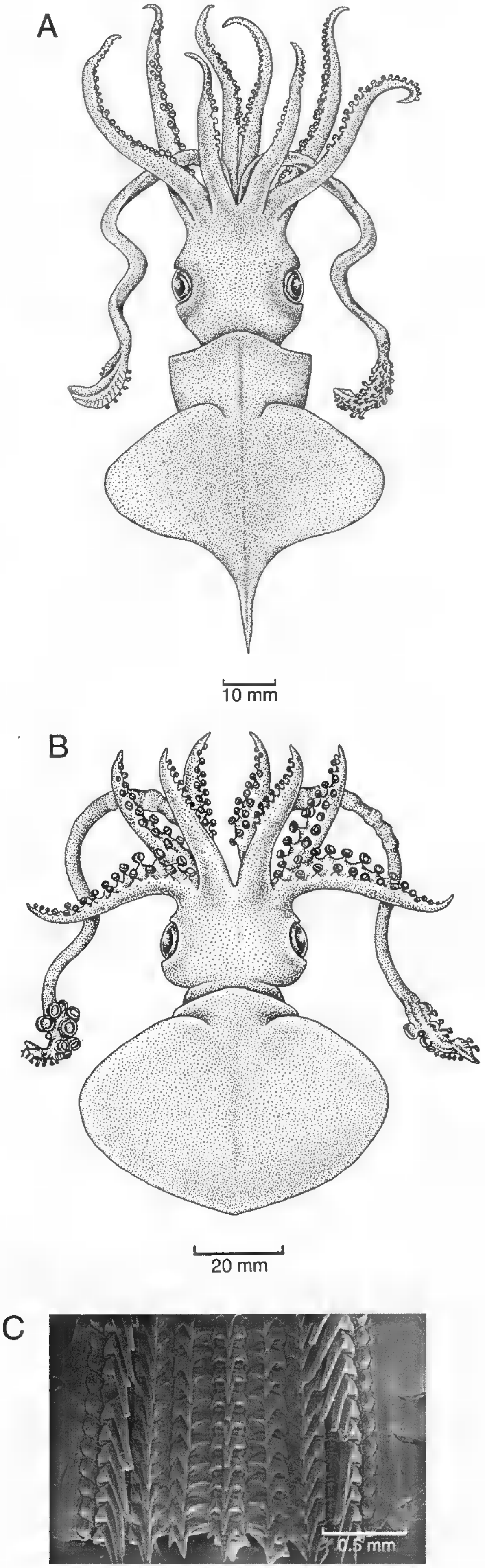


Figure 13.15 Family Cycloteuthidae. A, *Cycloteuthis sirventyi*, dorsal view. B, *Discoteuthis discus*, dorsal view. C, portion of radula of *Discoteuthis laciniosa*, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

Family Lepidoteuthidae

Lepidoteuthids are characterised by the presence of distinct 'scales' on the mantle and a simple, straight funnel locking apparatus. Suckers are generally toothed, and form two rows on the arms and four rows on the tentacular clubs. Adult *Lepidoteuthis grimaldii* lack tentacles. Buccal connectives attach to the ventral border of the ventral arms, and light organs are absent. Hectocotylisation in males has not been described (Roper *et al.* 1969).

The family Lepidoteuthidae currently includes three genera of medium-sized to large oceanic and continental slope species, up to 1.0 m mantle length (Fig. 13.16), but the taxonomy of the group requires revision. Clarke (1980) considered this family to contain only the genus *Lepidoteuthis*; *Pholidoteuthis* and *Tetronychoteuthis* were assigned to a separate family Pholidoteuthidae. In addition, Clarke suggested that the two currently recognised species in the genus *Tetronychoteuthis* may be growth stages of *Pholidoteuthis boschmai*. Based on studies of the 'scales', Roper & Lu (1989, 1990) also pointed out that the present grouping is not natural, and that use of the terms 'scales' or 'cartilaginous scales' for these structures is inaccurate and inappropriate. Roper & Lu (1990) introduced the term 'dermal cushions' to refer to these structures in *Lepidoteuthis grimaldii* (Fig. 13.16D) and *Pholidoteuthis adami*; the dermal structures on *Tetronychoteuthis* species (Fig. 13.16B) were referred to as tubercles.

A single specimen of *T. dussumieri* (Fig. 13.16A) was described by Pfeffer (1912) from south of Western Australia. Allan (1945) assigned juvenile specimens caught in plankton nets off New South Wales to *T. massyae*, a species which Pfeffer (1912) considered might represent a juvenile form of *T. dussumieri*. Rancurel (1970, 1976) reported both *Tetronychoteuthis massyae* and *Lepidoteuthis grimaldii* (Fig. 13.16C) from the stomachs of lancetfishes (*Alepisaurus*) caught in the Coral Sea, and lepidoteuthids were among the stomach contents of sperm whales from south-western Australia and the Tasman Sea respectively (Clarke 1980; Clarke & MacLeod 1982). Lu & Phillips (1985) included three lepidoteuthid species in their checklist.

The nature of the 'dermal cushions' and 'tubercles' varies with the genus. The large dermal cushions of *Lepidoteuthis grimaldii* are diamond-shaped to hexagonal in form, and arranged like fish scales but lacking bony structure. Internally, they are highly vacuolated and contain numerous chambers of irregular size and shape separated by thin membranous walls. The dermal cushions of *Pholidoteuthis adami* are irregularly rounded to roughly pentagonal in outline. Internally, they are vacuolated, consisting of continuous, thin-walled, irregularly shaped chambers. The tubercles of *Tetronychoteuthis massyae* are stellate, minute and tightly packed. Each tubercle is roughly mushroom-shaped in profile, with a slightly concave central disc and a thick base. Internally the tubercle consists of very dense material interspersed with small vacuoles of varied size and shape. Roper & Lu (1990) suggested that the dermal cushions of *Lepidoteuthis grimaldii* and *Pholidoteuthis adami* may serve to store less dense solution containing ammonium ions, and thereby function together with the mantle as a buoyancy mechanism. The tubercles on *Tetronychoteuthis massyae* are thought to maintain laminar flow along the boundary layer during locomotion by reducing hydrodynamic drag.

The small number of specimens available in collections has precluded any comprehensive studies of lepidoteuthid life history either in Australia or elsewhere. The presence of lepidoteuthids in stomachs of lancetfishes, yellowfin tunas and sperm whales (Rancurel 1970, 1976; Clarke 1980; Clarke & MacLeod 1982; Okutani & Tsukada 1988) has been noted above. These squids are also preyed upon by pilot whales, dolphins, deep-sea sharks and scabbard fish (Clarke 1966). The radular arrangement in *Lepidoteuthis grimaldii* is illustrated in Figure 13.16E.

Pholidoteuthis species have been caught in demersal trawls in continental slope waters, but only during the day. Therefore, it seems likely that this species leaves the near-bottom waters and disperses into midwater at night (Roper & Young 1975). Clarke

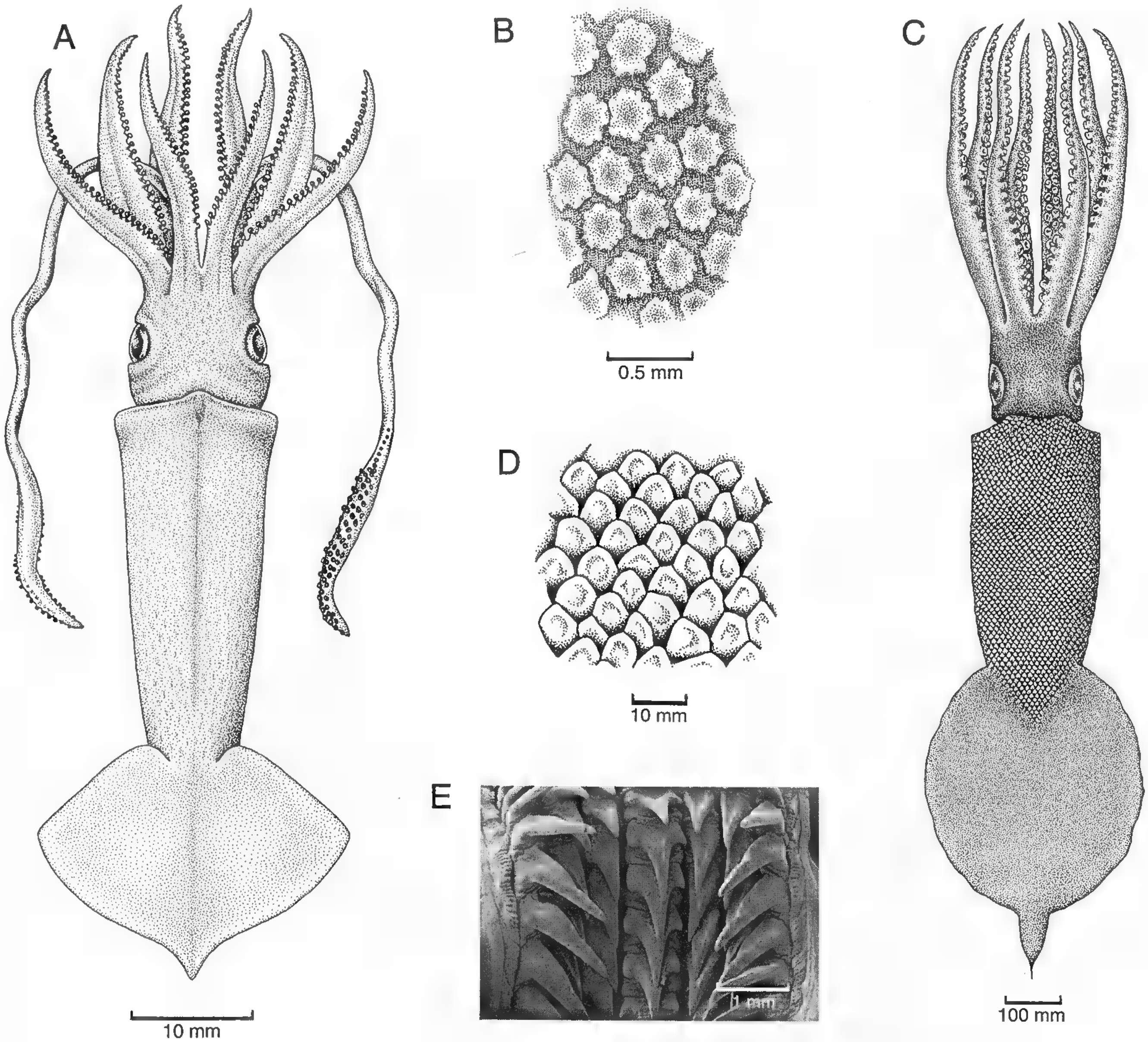


Figure 13.16 Family Lepidoteuthidae. These large squids are characterised by 'scales' on the mantle. **A, B,** *Tetronychoteuthis dussumieri*: **A,** dorsal view; **B,** section of mantle surface enlarged to show tubercles. **C–E,** *Lepidoteuthis grimaldii*: **C,** dorsal view; **D,** section of the mantle surface enlarged to show dermal cushions; **E,** portion of radula, showing several transverse tooth rows. [A–D, K. Hollis; E, C.C. Lu]

(1980) suggests that large individuals of *Pholidoteuthis* species may be solitary or occur in small groups. In the Gulf of Mexico however, schools of *P. adami* have been observed at the surface at night (Clarke 1966).

Although lepidoteuthids grow large enough to be of commercial interest, they have not been recorded in sufficient abundance in Australian waters to indicate any commercial fisheries potential, and too few specimens are available in existing collections to clarify their geographic distribution.

Family Architeuthidae

The 19 nominal species of giant squids within the monotypic family Architeuthidae are poorly defined and some workers have suggested that all specimens can be assigned to as few as three species (Roper & Boss 1982). The genus *Architeuthis* is characterised by a muscular mantle, short oval fins (Figs 13.17, 11.2) and a simple straight funnel locking cartilage. Suckers bearing many small, sharp teeth occur in two rows on the arms. A distinct cluster of small suckers and knobs is present at the proximal end of the tentacular club and larger quadriserial suckers occur distally. Two longitudinal rows of alternating suckers and pads are present along the tentacular stalks. Photophores have not been described from any specimen and both ventral arms are described as being hectocotylised in mature males (Knudsen 1957; Kjennerud 1958; Roper *et al.* 1969; Roper & Boss 1982).

A specimen of an *Architeuthis* species stranded in eastern Victoria, and assigned by Allan (1948) to *A. kirki*, was the first record of this family from Australian waters. A larval *Architeuthis* was caught in a midwater trawl in the upper 20 m off the central New South Wales coast in October 1981 and a live juvenile female was taken in this same region in the upper 300 m in January 1982 (Lu 1986).

Adults of species of *Architeuthis* are the largest living cephalopods (Fig. 11.2). They weigh more than 1 tonne, and have mantle lengths exceeding 4.5 m (Clarke 1966). A relatively high concentration of ammonium ions in the muscles of the mantle, head and arms provides buoyancy (Clarke, Denton & Gilpin-Brown 1979). The oxygen carrying capacity of the haemocyanin in the blood of *Architeuthis* is much less than that of other active oceanic squids, such as ommastrephids (0.3 *versus* 1.6–1.9 mM O_2). As haemocyanin's affinity for oxygen has a pronounced sensitivity to temperature, this low carrying capacity may limit the distribution of adults to low water temperatures. Their encounters with warm currents may result in suffocation and may explain the strong correlation of strandings in some areas with warm water inflow (Brix 1983).

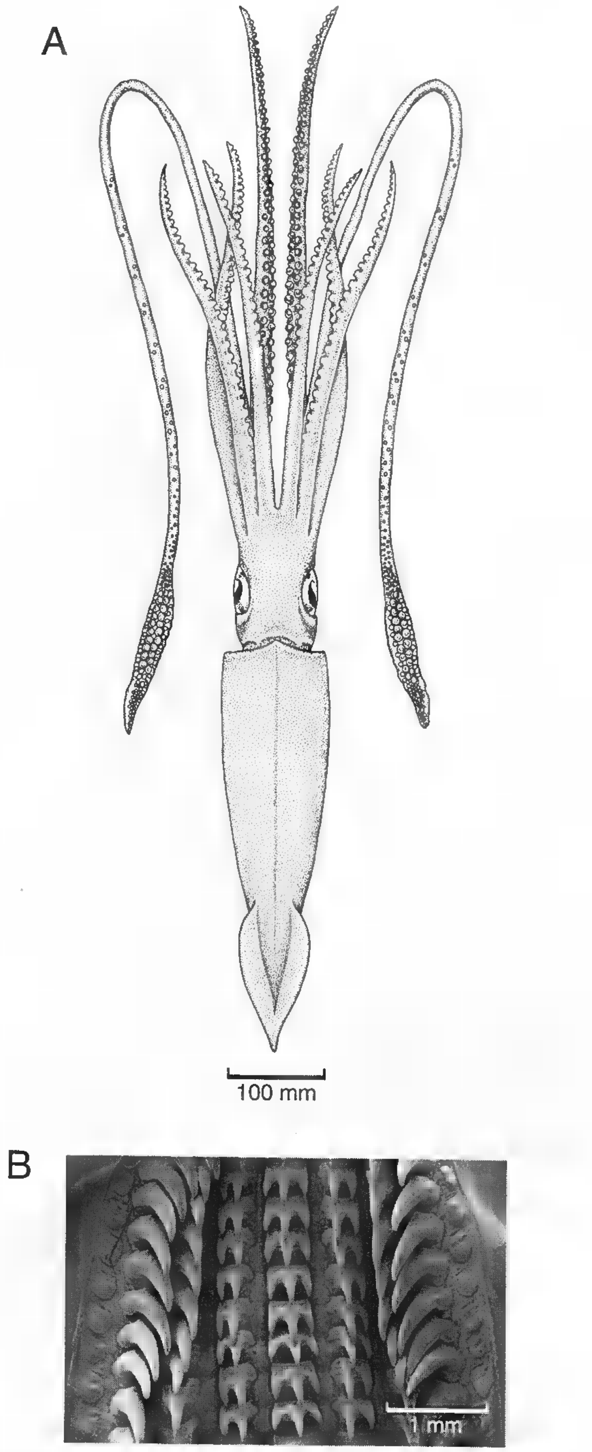


Figure 13.17 Family Architeuthidae. **A**, *Architeuthis* sp. from southern Australia, dorsal view. **B**, portion of radula of *Architeuthis* sp. showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

Size at maturity of male *Architeuthis* appears to be variable and may reflect specific differences. Specimens from 180 mm to more than 1 m mantle length elsewhere have been found with apparently viable spermatophores (Toll & Hess 1981). The size at which females first reach maturity is uncertain. Female *Architeuthis* do not have spermathecae. A recently captured female specimen with a mantle length of 2.4 m was found to be mated. Spermatophores were found embedded in the skin on both ventral arms. On one arm, the remains of several spermatophores up to 80 mm in length radiated under the skin from a single small entry point (*ca* 10 mm in diameter). They did not penetrate the arm musculature. It is unclear how the spermatophores are inserted; the male may inject the spermatophores with the large muscular penis or use his beak to make the entry wound through which they are injected (Norman & Lu in manuscript). If either technique is correct, the status of the hectocotylus needs re-evaluation. Mature *Architeuthis* eggs reach diameters of 1.2–1.8 mm (Roeleveld & Lipinski 1991). Boyle (1986) estimated that the potential fecundity of a female at over 10 million eggs.

Because of its relative rarity, studies of the life history of *Architeuthis* have not been undertaken in Australian waters or elsewhere. The genus is recorded in the diets of lancetfishes, swordfishes, albacore tunas and sperm whales elsewhere (Clarke 1966; Roper & Young 1972; Toll & Hess 1981), from sperm whales and mako sharks in Australian waters (Clarke 1980; Dunning *et al.* 1993), and from sleeper sharks taken off Macquarie Island (Lu unpublished data). Fishes and cephalopods (including ommastrephids and histioteuthids) have been found among the stomach contents of the few specimens of *Architeuthis* examined elsewhere (Pérez-Gándaras & Guerra 1978; Toll & Hess 1981; Roper & Boss 1982; Lu unpublished data). The radular arrangement in an *Architeuthis* species is illustrated in Figure 13.17B.

On the basis of the numbers of *Architeuthis* remains in individual sperm whale stomachs Clarke (1980) suggested that they may be solitary animals. Recent examination of the blood chemistry of *Architeuthis* and the lack of strong musculature in the funnel and fins suggest that these animals are also relatively poor swimmers and passive, sluggish predators (Roper & Boss 1982; Brix 1983). Though the vertical distribution of adults is uncertain, they may live on or near the sea floor in depths of 500–1000 m or more (Clarke 1980; Roper & Boss 1982; Lu unpublished data). Perhaps the capture of a larva in near surface waters off eastern Australia is an indication of ontogenetic descent (Lu 1986). The growth rings on the statolith of *Architeuthis* were similar in appearance to daily growth rings found in other oegopsid and myopsid squids; the statolith of a juvenile female, 422 mm mantle length, had 153 rings (Jackson, Lu & Dunning 1991).

Although *Architeuthis* reaches a considerable size, it has little fisheries potential because ammonium ions present in the muscle tissue render it inedible (Roper & Boss 1982).

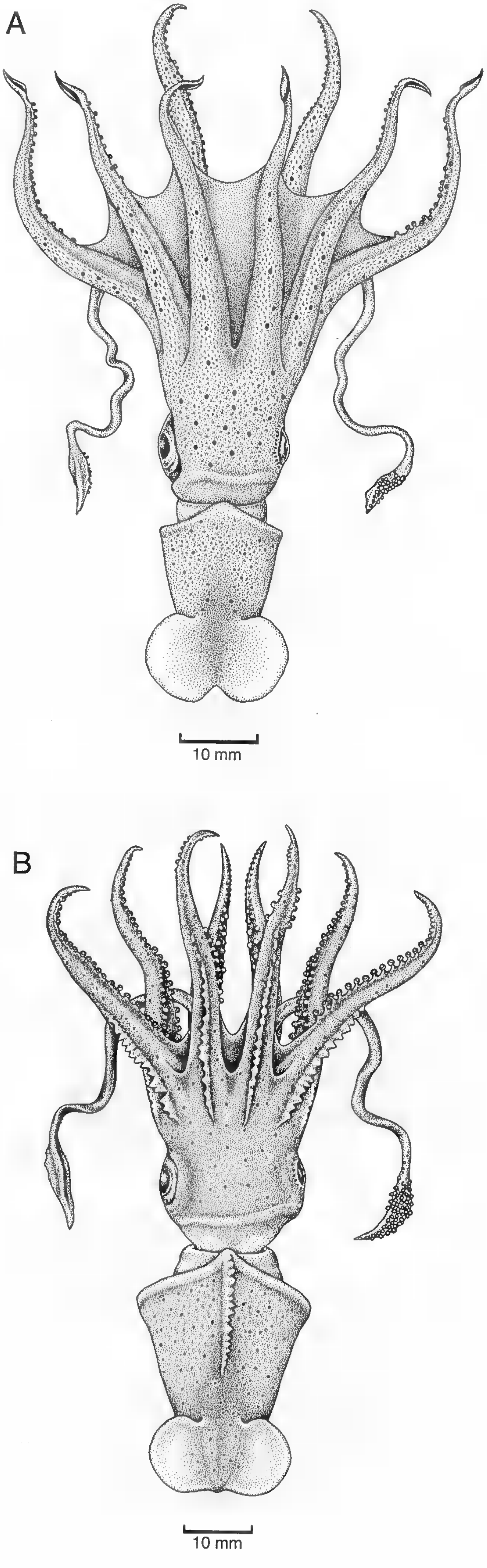
The distribution of *Architeuthis* in Australian waters is not clear, although all records are from south of 32°S.

Family Histioteuthidae

The monotypic family Histioteuthidae comprises medium-sized to large squids, less than 350 mm mantle length, characterised by a simple, straight funnel locking apparatus, unmodified toothed suckers arranged biserially on the arms, and in four and eight rows on the tentacular clubs. The family is readily distinguished by many large, anteriorly directed light organs over the surface of the mantle, head and arms (Fig. 13.18), more concentrated on the ventral surface. Buccal connectives attach to the dorsal border of the ventral arms and both the dorsal arms are usually hectocotylised in males. Adult histioteuthids have a large head, and the left eye is considerably larger than the right (Voss, N.A. 1969).

Berry (1918) described the first histioteuthid from Australian waters, *Histioteuthis miranda*, from a single adult specimen trawled off Gabo Island, Victoria. Larvae of this species were later reported from the New South Wales coast by Allan (1945) and additional species were recognised from the Tasman Sea by N.A. Voss (1969). At least eight histioteuthid species were identified from the stomach contents of sperm whales from south-western Australia and the Tasman Sea (Clarke 1980; Clarke & MacLeod 1982). In their checklist, Lu & Phillips (1985) listed ten Australian species.

R.E. Young (1975b) reviewed the function and peculiar modification of the asymmetrical eyes (Fig. 13.18), unique amongst oegopsid squids. The left eye is tubular, and in some specimens, may be twice the size of its smaller, hemispherical partner. It is thought to detect down-welling light during the day, primarily at depth. The mantle of most species of *Histioteuthis* is



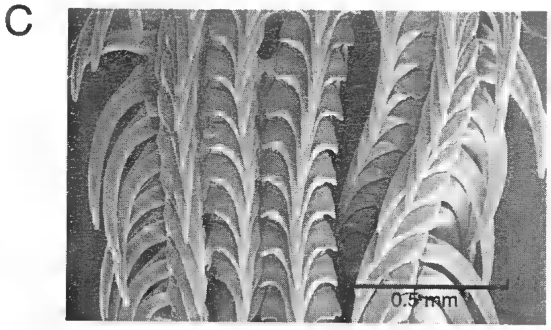


Figure 13.18 Family Histioteuthidae. Numerous photophores on the surface of mantle, head and arms are characteristic of these diverse and abundant squids. **A**, *Histioteuthis bonnellii corpuscula*, dorsal view. **B**, *Histioteuthis miranda*, dorsal view. **C**, portion of radula of *Histioteuthis macrohista*, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

relatively short, broad and conical and, like the rest of the body, is typically somewhat gelatinous. Some histioteuthids are known to be neutrally buoyant (Young, R.E. 1975b; Clarke, Denton & Gilpin-Brown 1979). The terminal fins consist of separate oval lobes, free anteriorly but united posteriorly with a distinct median notch on the posterior border. The convex posterior margin of the fins may extend posteriorly beyond the mantle.

The photophore pattern on the mantle, head and arms and the presence of enlarged terminal photophores on the arms are specific characters and may function in ventral countershading (Young, R.E. 1975b). No internal light organs are present. Interspecific variation in the development of a web connecting the inner margins of the arms shows a gradation. In *Histioteuthis macrohista* and *H. bonnellii* (Fig. 13.18A), the webbing extends over more than 50% of the arm length. R.E. Young (1983) has suggested that the web may conceal the luminescence of struggling prey. A row of small tubercles is present below the epithelium of the midline of the anterior mantle and the basal half of the first three arms in *H. meleagroteuthis* and *H. miranda* (Fig. 13.17B), becoming less apparent with growth. Okutani, Satake, Oshumi & Kawakami (1976) illustrated histioteuthid spermathecae. Spermatophores were found embedded in the inner surface of the funnel of a female *H. atlantica* recovered from a sperm whale caught off Albany, Western Australia (Clarke 1980). Mature eggs of *H. miranda* have a maximum diameter of 0.8 mm.

No comprehensive life history studies of any histioteuthid have been conducted. Clarke (1980) found mature female *H. miranda* among the stomach contents of sperm whales caught off Albany, Western Australia, in November and December, but concluded from size frequency data that spawning was likely to occur throughout the year. Maturity is reached at mantle lengths of approximately 200–250 mm in this species off the eastern Australian coast. Clarke (1980) concluded that *H. meleagroteuthis* elsewhere probably has a life span of less than two years and, from the degenerate condition of the bodies of some specimens, that death occurs soon after spawning.

Beaks in sperm whale stomachs led Clarke (1980) to conclude that histioteuthid species school. Although the family is considered to be primarily mesopelagic (Voss, N.A. 1969), *H. celetaria pacifica* (Voss, G.L. 1962) and *H. miranda* have been caught frequently in deep-water lobster trawls at depths of 300–600 m off the North West Shelf and Great Barrier Reef, suggesting that they are associated with the sea floor during part of their life cycle.

Histioteuthids are important in the diets of sperm whales (Clarke 1983) and are also components of the diets of yellowfin and albacore tunas, scabbard fish, lancetfishes, spotted dolphins (Rancurel 1970; Wolff 1982; Roper *et al.* 1984) and perhaps albatrosses elsewhere (Clarke 1983); they are components of the diets of several pelagic shark species off eastern Australia (Dunning *et al.* 1993). Fishes predominate in the diet of adult histioteuthids (Voss, N.A. 1969; Clarke 1980). The radular arrangement in *Histioteuthis macrohista* is illustrated in Figure 13.18C.

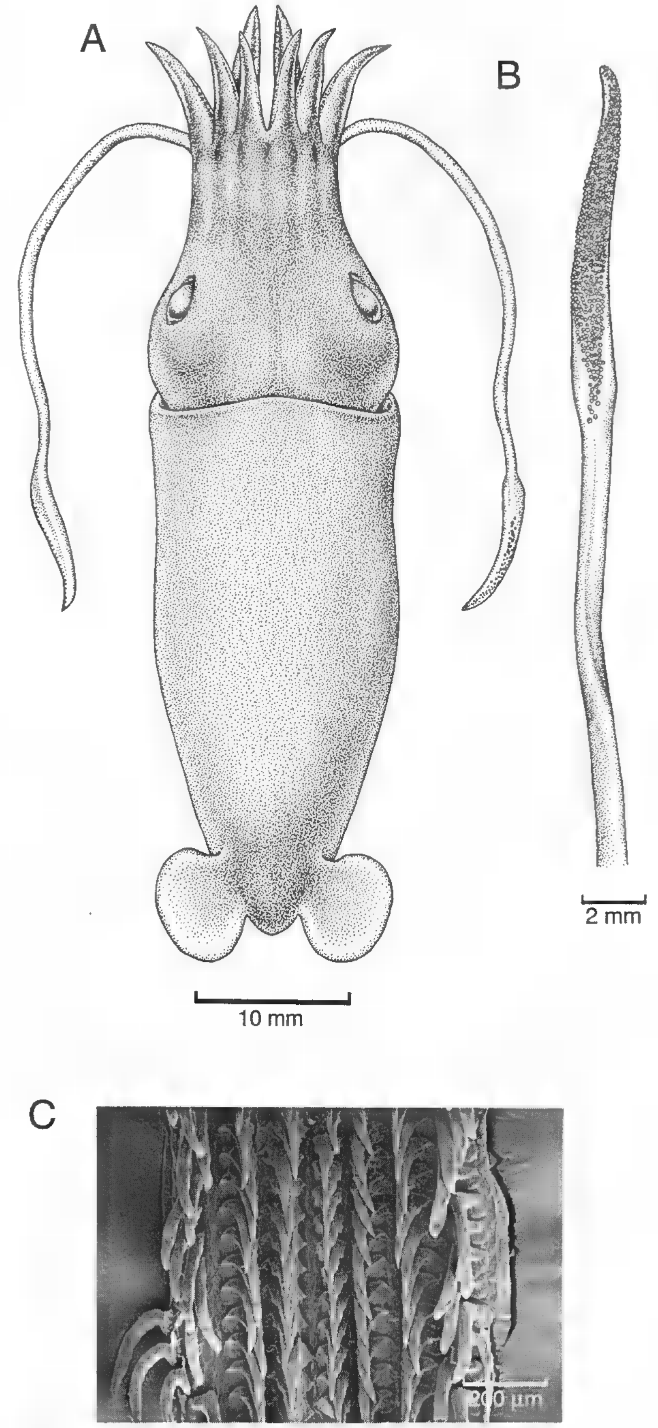


Figure 13.19 Family Bathyteuthidae. *Bathyteuthis abyssicola* is a cosmopolitan bathypelagic species, found even in the Antarctic: **A**, dorsal view; **B**, tentacular club; **C**, portion of radula, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

Off Hawaii, *Histioteuthis dofleini* shows both diel vertical migration and ontogenetic descent. Small squids occur at depths of 200–300 m during the night and descend to 400–700 m during the day. Larger adults have been caught at depths of up to 800 m and only occasionally deeper (Young, R.E. 1975b). Other species are more common in waters of 2000 m and are captured only rarely in the upper 200 m (Voss, N.A. 1969).

Nesis (1979a) considered the five histioteuthid species collected in the Australian region to be primarily tropical and subtropical/notalian species. Of the tropical species, *H. celetaria pacifica* was considered to be restricted to waters north of 30°S, *H. meleagroteuthis* to be more eurythermal occurring southwards to 38°S and *H. dofleini* even more so, occurring as far south as 44°. The subtropical/notalian *H. atlantica* and *H. macrohista* reportedly occur between 35°S and 50°S, and are most abundant from 40° to 45°S. Off South Africa, *H. miranda* (Fig. 13.18B) was most abundant in water depths of less than 1000 m, *H. atlantica* in waters of between 1000 and 2500 m deep, and *H. bonnellii corpuscula* (Fig. 13.18A) at depths of more than 2000 m, as indicated by their abundance in the diet of sperm whales (Clarke 1980).

This family is not presently of commercial interest. Although some histioteuthid species attain in excess of 200 mm mantle length and are frequently, if not abundantly, encountered in Australian waters, the gelatinous nature of their bodies would detract from their market acceptance. For the same reason, they are readily damaged during capture, and therefore are unsuitable for laboratory study.

Family Bathyteuthidae

Squids of the monotypic family Bathyteuthidae are rarely caught except in Antarctic waters. Bathyteuthids (Fig. 13.19A) are small, less than 100 mm mantle length, with round or paddle-like subterminal fins, a simple, straight funnel locking cartilage, and arms suckers in irregular rows. The tentacular club is small with numerous rows of minute suckers (Fig. 13.19B) and the buccal connectives attach dorsally to the ventral arms. A single light organ is embedded at the base of each of the dorsal, dorso-lateral and lateral arms (Roper *et al.* 1969).

Bathyteuthis was first recorded from eastern Australian waters by Lu & Phillips (1985). Because so few specimens have been collected so far, no studies of life span or growth of this *Bathyteuthis* species in Australian waters or elsewhere have been undertaken and its diet and predators are not known. A portion of the radula of *Bathyteuthis abyssicola* is illustrated in Figure 13.19C.

Bathyteuthids are not vertical migrators in other parts of the world and most specimens have been caught between 1000 and 2500 m (Roper & Young 1975). Their small adult size and rarity precludes this family from commercial fisheries interest.

Family Ctenopterygidae

Ctenopteryx, the sole genus in this family, is easily recognised by its long ribbed fins, which extend the length of the mantle in adults (Fig. 13.20). Ctenopterygids are small to medium-sized squids, less than 100 mm mantle length; they have four to six rows of suckers on the distal half of all but the ventral arms, which have very few small suckers in a zig-zag pattern. The tentacular clubs bear eight to 14 rows of small suckers. The funnel locking cartilage is simple and straight and the buccal connectives attach to the ventral border of the ventral arms. Photophores are present on the ink sac and posteriorly within the mantle in some species. Hectocotylisation is unknown (Roper *et al.* 1969).

Allan's (1945) record of this genus from eastern Australian waters was the first from beyond the North Atlantic and Mediterranean regions. Subsequently, it was reported from tropical waters of the central and south-western Pacific by Rancurel (1970), from the north-eastern Indian Ocean by Fujita & Hattori (1976) and from off New South Wales by Brandt (1983). Lu & Phillips (1985) recorded it from the Coral and Tasman Seas.

During growth, the arms, tentacles and head all become longer relative to the body, which scarcely changes shape. The fins become relatively longer. They are terminal at mantle lengths of less than 5 mm and extend the whole length of the mantle when it reaches 30 mm (Clarke 1966). The structure of the fins suggests that ctenopterygids are not capable of sustained rapid movement. Undulating movements of the fins, much as in sepiid cuttlefishes, may provide the primary propulsive force. With sexual maturity, male *Ctenopteryx* develop a large photophore within the posterior

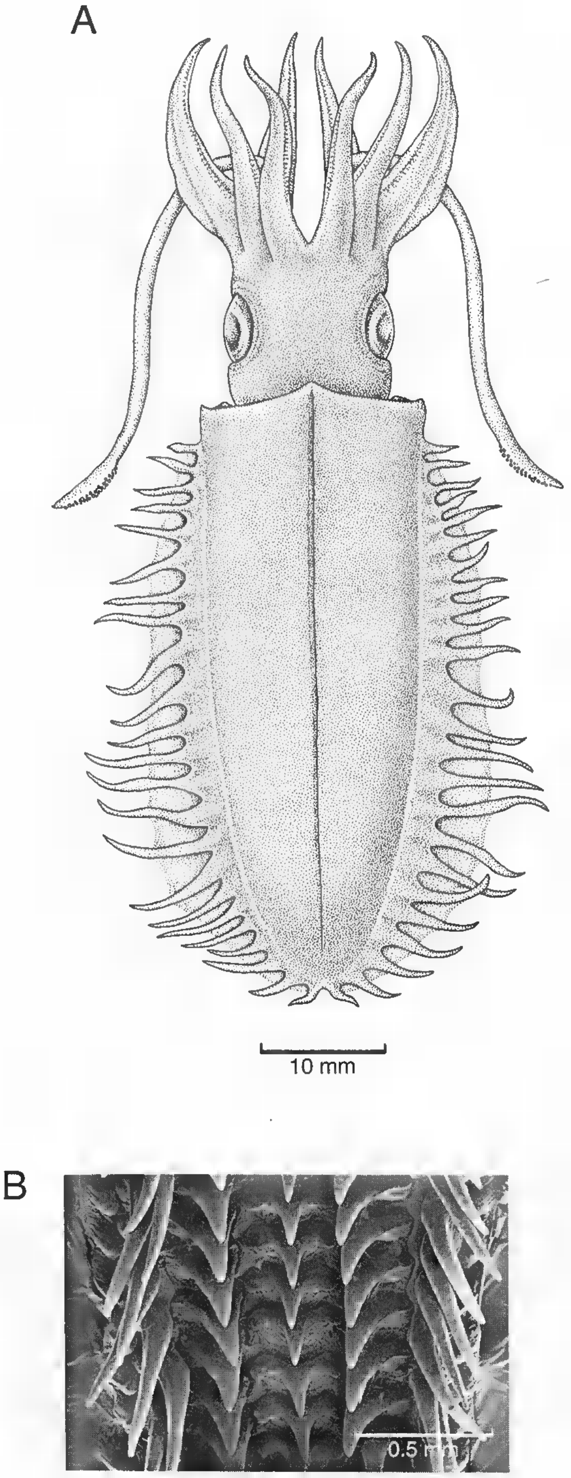


Figure 13.20 Family Ctenopterygidae. *Ctenopteryx sicula*: **A**, dorsal view, showing the characteristic ribbed fins; **B**, portion of radula, showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

region of the body. R.E. Young (1983) concluded that the light produced, which is of a wavelength poorly detected by many potential predators, may be used to attract a mate.

No detailed information is available on the life history of ctenopterygids is available. Larvae have been common, though not abundant in collections made off the New South Wales coast during both summer and winter, suggesting that the spawning season is broad. Elsewhere, ctenopterygids are preyed upon by lancetfishes (*Alepisaurus*), albacore, dolphins and mesopelagic viper-fishes (*Chauliodus*) (Clarke 1966; Rancurel 1970; Fujita & Hattori 1976). The diet of ctenopterygids is unknown. A portion of the radula of *Ctenopteryx sicula* is illustrated in Figure 13.20B.

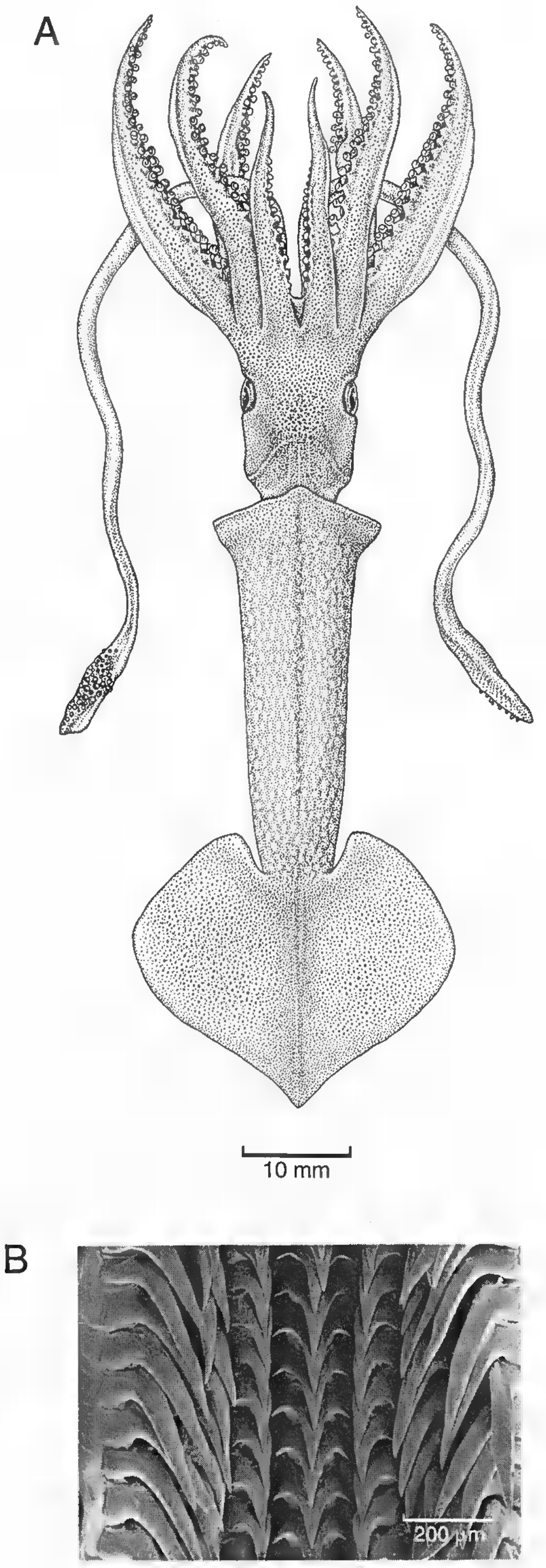


Figure 13.21 Family Brachioteuthidae. **A**, *Brachioteuthis* cf. *picta*, a small squid found on the continental slope of south-eastern Tasmania, dorsal view. **B**, portion of radula of *Brachioteuthis* sp., showing several trnasverse tooth rows. [A, K. Hollis; B, C.C. Lu]

Little is known regarding the vertical distribution of ctenopterygids. Most specimens from Australian waters and elsewhere have been caught in the upper 150 m, although day captures at more than 350 m have been made in the Atlantic. Roper & Young (1975) suggest that this genus inhabits near-surface waters at night. Ctenopterygids are regularly encountered off the east coast in tropical oceanic surface waters and in the East Australian Current system. They do not reach a suitable size or abundance to be of any commercial fisheries interest in Australia.

Family Brachioteuthidae

The taxonomy the monotypic family Brachioteuthidae is based mainly on larval characters, as adults are rarely caught. Brachioteuthids are small to medium-sized squids, less than 100 mm mantle length, with a slender muscular mantle, sometimes produced as a short tail. The terminal fins are rhombic, generally less than 50% of the mantle length (Fig. 13.21). Brachioteuthids have a simple, straight funnel locking cartilage and biserial suckers occur on the arms. Lateral arms have swimming keels in adults. The tentacular club is expanded, and numerous small suckers in the carpal region extend proximally along the club. The buccal connectives attach ventrally to the ventral arms. Light organs are absent.

Brachioteuthis riisei was recorded first from Australian waters by Allan (1945). It has since been taken in midwater trawls in an eddy of the East Australian Current (Brandt 1983). Lu & Phillips (1985) list only *B. riisei* from Australian waters although Nesis (1979a) assigned specimens in his net collections to *B. behni* and Clarke (1966) reported *B. picta* from the southern Indian Ocean and around New Zealand.

The unusually long neck of *Brachioteuthis* larvae distinguish them from all other larvae except those of chiroteuthids. The neck appears to be a single muscular, fluid-filled tube continuous with a large fluid-filled reservoir within the mantle. The neck in the *Doratopsis* 'larva' of chiroteuthids is elongate also, but is supported by many separate chambers. Larval *Brachioteuthis* are believed to orientate in a head down position generally, resembling a drifting bell with hanging tentacles ready to capture prey (Young, R.E., Harman & Mangold 1986).

The eggs of a species of *Brachioteuthis* have been taken occasionally in plankton nets in Hawaiian waters and R.E. Young *et al.* (1986) suggested that females spawn single eggs (as in the Enoploteuthinae). Unlike the enoploteuthids however, adult females do have nidamental glands. No studies of age and growth of brachioteuthids have been undertaken. The occurrence of larvae suggests that in eastern Australian waters *Brachioteuthis riisei* spawns throughout the year (Allan 1945); the diet is not known. The radular arrangement in a *Brachioteuthis* species is illustrated in Figure 13.21B. *Brachioteuthis* species are a dietary component of sperm whales caught off Iceland after recent migration northwards from the tropics (Martin & Clarke 1986).

Larval *Brachioteuthis* are diel vertical migrators off Hawaii, where they occur in the upper 50 m at night and descend to 100–150 m during the day (Young, R.E. *et al.* 1986). The distribution of adults is unknown, although they have been caught in midwater trawls in subtropical oceanic waters off central New South Wales.

The studies of Nesis (1979a) and Brandt (1983) indicate that *Brachioteuthis riisei* is primarily a tropical species, carried southwards by the East Australian Current off the Australian east coast.

Their small adult size and rarity precludes brachioteuthids from commercial fisheries interest. Eggs collected in plankton nets have been successfully hatched in onboard aquaria off Hawaii (Young, R.E. *et al.* 1986). In the East Australian Current north of 32°S, eggs ready to hatch and early hatchlings have been caught in abundance during the summer months, and may lend themselves to laboratory studies of early growth and development.

Family Ommastrephidae

Ommastrephids are medium-sized to large oegopsids, more than 500 mm mantle length, with a strong, muscular, torpedo-shaped mantle (Fig. 13.22A–F). They are characterised by an inverted, T-shaped funnel locking cartilage and biserial suckers on the arms (Fig. 13.22M–R). The tentacular clubs in all Australian representatives have tetraserial suckers. The buccal connectives attach to the dorsal border of the ventral arms and light organs are present in some genera. One or both ventral arms in males are hectocotylised (Fig. 13.22G–L). Three subfamilies, Illicinae, Todarodinae and Ommastrephinae, are recognised on the basis of the presence and structure of the foveola and side pockets in the funnel groove (Fig. 13.22M, S–U). All are represented in Australian waters (Wormuth 1976; Lu & Dunning 1982).

In 1888, McCoy described the first ommastrephid from Australian waters, *Ommastrephes gouldi*. Two additional species, *Ommastrephes gigas* and *Ommastrephes oualaniensis*, were recorded by Brazier (1892) in the first comprehensive list of Australian cephalopods. The first of these two is a mis-identification, and *Dosidicus gigas* occurs only in the eastern Pacific. Nesis (1979b) provided records of additional species from the Australian region. Dunning (1988a, 1988b, 1988c, 1993) reported two ommastrephid species, in addition to those listed by Lu & Phillips (1985).

Sharp, strongly developed conical teeth are present on the chitinous sucker rings of the arms and tentacles. The large muscular fins are generally rhomboidal, except in *Ornithoteuthis* in which the fins and mantle are strongly attenuated posteriorly (Fig. 13.22C). The lateral arms are strongly keeled, particularly in oceanic species (Lu & Dunning 1982). The family has a distinct larval form, the rhynchoteuthion, characterised by fusion of the tentacles which separate over a size of 5–10 mm mantle length.

Nototodarus, *Todaropsis* and *Todarodes* species typically display a dark, narrow mid-dorsal stripe on the mantle (Fig. 13.22D–F), which is replaced in oceanic species by a general darkening of the dorsal surface. Large light organs are present in *Sthenoteuthis*, *Eucleoteuthis* and *Hyaloteuthis*. These are oval or form stripes ventrally or dorsally on the mantle and/or ventrally on the head and bases of the ventral arms. Juveniles of these genera have oval light organs ventrally on the eyes and between the ink sac and intestine (Dunning 1985). Adult *Ornithoteuthis* have an additional midventral, luminous stripe along the viscera. Small subcutaneous light organs are distributed ventrally on the mantle and head of *Ommastrephes* species (Lu & Dunning 1982).

All ommastrephids are active predators; they use the arms and tentacles for grasping food and the heavily chitinised beak for dividing prey. The reproductive organs are typically oegopsid. All species in Australian waters have buccal seminal receptacles for storage of sperm bulbs during copulation. The presence of sperm bulbs in the spermathecae of immature females of several species suggests that copulation may precede spawning by some time in this group.

No direct studies of age and growth of ommastrephids in Australian waters have been undertaken. From examination of population size structure, it appears probable that most species reproduce for a single season only and die after reaching reproductive maturity at less than two years of age. In some species, males mature at considerably smaller sizes than females. Spawning locations remain unknown although larvae have not been found away from continental shelf and slope waters.

Ommastrephids occupy all major marine habitats, including the tropical and temperate continental shelf and slope, and oceanic waters. They feed on a broad range of crustaceans, fishes, squids and other pelagic molluscs, and are at least partially cannibalistic (O'Sullivan & Cullen 1983). The radular arrangement in *Ommastrephes bartrami* is illustrated in Figure 13.22V. Known predators include seabirds, teleosts and sharks, whales, dolphins and seals (Dunning & Brandt 1985; Okutani & Tsukada 1988; Dunning *et al.* 1993). Ommastrephids form schools, which decrease in size as the animals grow. Evidence from commercial fishing operations suggests that neritic species congregate close to the bottom during the day, and move up through the water column at night. Oceanic species have been seen feeding at the surface at night, where large individuals of *Ommastrephes* species have been observed hunting for prey. Juveniles of several species are able to glide like exocoetid flying fishes to escape predators, for distances in excess of 10 m. There is evidence for long distance migration associated with spawning by *Ommastrephes* elsewhere (Dunning & Brandt 1985), and perhaps on a smaller scale by *Nototodarus* in southern Australian (Smith, H.K. 1983) and New Zealand waters (Sato 1985).

Ommastrephid squids occur in all oceans, with the exception of polar waters. Of the 11 recognised genera, nine occur in Australian waters and one subspecies appears to be endemic. Significant distributional overlap occurs for many species, particularly in East Australian Current waters where juveniles of up to five genera have been taken in the same trawl catch (Dunning & Brandt 1985). *Todarodes pacificus pucillus* (Fig. 13.22D) occurs in continental shelf waters north of 27°S. The genus *Nototodarus* is represented in northern slope waters by *N. hawaiiensis* and in shelf waters south of 25°S by *N. gouldi*. The distribution of the former species overlaps with that of the less abundant *Todaropsis eblanae* (Fig. 13.22F). Between 18° and 35°S, *Ornithoteuthis volatilis* (Fig. 13.22C) is common in trawl catches from slope waters. The Subantarctic shelf species, *Martialia hyadesi*, has occasionally been found stranded on the beach after storms at Macquarie Island, sometimes in large numbers.

Hyaloteuthis pelagica and *Eucleoteuthis luminosa* occur in tropical and subtropical oceanic waters off the east coast respectively. *Ommastrephes bartrami* (Fig. 13.22B) is the dominant ommastrephid in the south-eastern Indian Ocean and Tasman Sea north of 40°S, replaced to the south by *Todarodes filippovae* and *T. angolensis* (Dunning 1993). This species is also caught in continental slope waters around the southern Australian coast. Fossil statoliths of late Pliocene *Sthenoteuthis* have been found in California (Clarke & Fitch 1979), although none has yet been discovered in Australia.

Nototodarus gouldi (Fig. 13.22E; Pl. 18.11) is caught incidentally for human consumption in trawling operations around the southern Australian coast (Dunning 1979), and more than 200 tonnes are sold on the domestic market annually. Since 1978, this species has been the target also of a directed jig fishery in Bass Strait by Japanese, Taiwanese and Korean vessels. The highest catch taken during the summer months of 1979/1980 exceeded 8000 tonnes (Dunning 1982). Several species are intermediate hosts for ascaridoid nematodes. Ommastrephids are a source of anisakiasis in man in Japan, where squid is often eaten raw (Hochberg 1983); these parasites pose no public health risk after cooking. Because of their abundance, large adult size and consequently the maximum diameter of their giant nerve axons, this family is of interest to neurophysiologists (Hixon, Ramirez & Villoch 1981).

Collection and laboratory maintenance of these large highly mobile molluscs present major difficulties. Large scale commercial fishing gear is necessary to catch the larger adults and some information has been gained from examination of the stomach contents of squid predators. Larvae have been collected successfully in large plankton nets designed for larval tunas (Dunning 1985). Future laboratory maintenance in large aquarium facilities, such as those used to maintain the ommastrephid *Illex illecebrosus* in Canada (O'Dor, Durward & Balch 1977), may lead to better understanding of the life cycles of Australian species.

Family Thysanoteuthidae

Of the two genera included in this family, only the monotypic genus *Thysanoteuthis* is well known. *Cirrobrachium* is known from larval forms and fragments of adults from the Atlantic only and its taxonomic status is not clear. *Thysanoteuthis rhombus* has a muscular mantle and rhombic fins which extend the length of the mantle in adults (Fig. 13.23A). The funnel locking cartilage has a long narrow longitudinal groove and a short broad transverse groove (Fig. 13.23B). Toothed suckers are present in two rows on the arms and four rows on the tentacular clubs. The lateral arms are strongly keeled in large specimens. Long, cirrate trabeculae on the arms support a well-developed web, and buccal connectives attach to the ventral borders of the ventral arms. The left ventral arm in males is hectocotylised (Pfeffer 1912). No photophores are present (Roper *et al.* 1969).

Rancurel (1970) and Fujita & Hattori (1976) recorded *T. rhombus* in the stomach of lancetfishes from the south-western Pacific and north-eastern Indian Ocean. Net-caught specimens are known from the Australian region (Nesis 1979a), including nearshore waters (Dunning 1982).

Adults may grow to more than 800 mm mantle length. Females spawn gelatinous, sausage-shaped egg masses, 150–200 mm in diameter and up to 1 m long, which have been found near the surface. A spiral, double row of eggs of up to 2 mm diameter is contained in the external layers. Around Japan, spawning occurs during summer. The smallest larvae hatch at 1.1 mm mantle length (Misaki & Okutani 1976; Suzuki, Misaki & Okutani 1979). No studies of age and growth of this species have been undertaken. Lancetfishes (*Alepisaurus*), yellowfin tunas, spotted dolphins and blue marlin prey on *T. rhombus* elsewhere (Clarke 1966; Rancurel 1970; Fujita & Hattori 1976; Rancurel 1976; Wolff 1982). The radular arrangement in *Thysanoteuthis rhombus* is illustrated in Figure 13.23C.

Thysanoteuthis rhombus is an oceanic species, generally caught in the upper 50 m of the water column. Juveniles are apparently capable of leaping out of the water but do not glide in the same manner as ommastrephids and onychoteuthids. Adults are slow swimmers (Nishimura 1966). In Australian waters, *T. rhombus* has been observed singly or in pairs, although groups of up to 20 have been observed elsewhere (Clarke 1966; Dunning 1988c).

This species occurs circumglobally in tropical surface waters and in the East Australian Current system as far south as north-eastern Tasmania. Juveniles have been recorded also from tropical waters off the North West Shelf.

Although not fished in Australian waters, *T. rhombus* is caught using drifting jigs and set nets in the Sea of Japan and is renowned for its tender flesh which is sometimes eaten as sashimi (Okutani 1977).

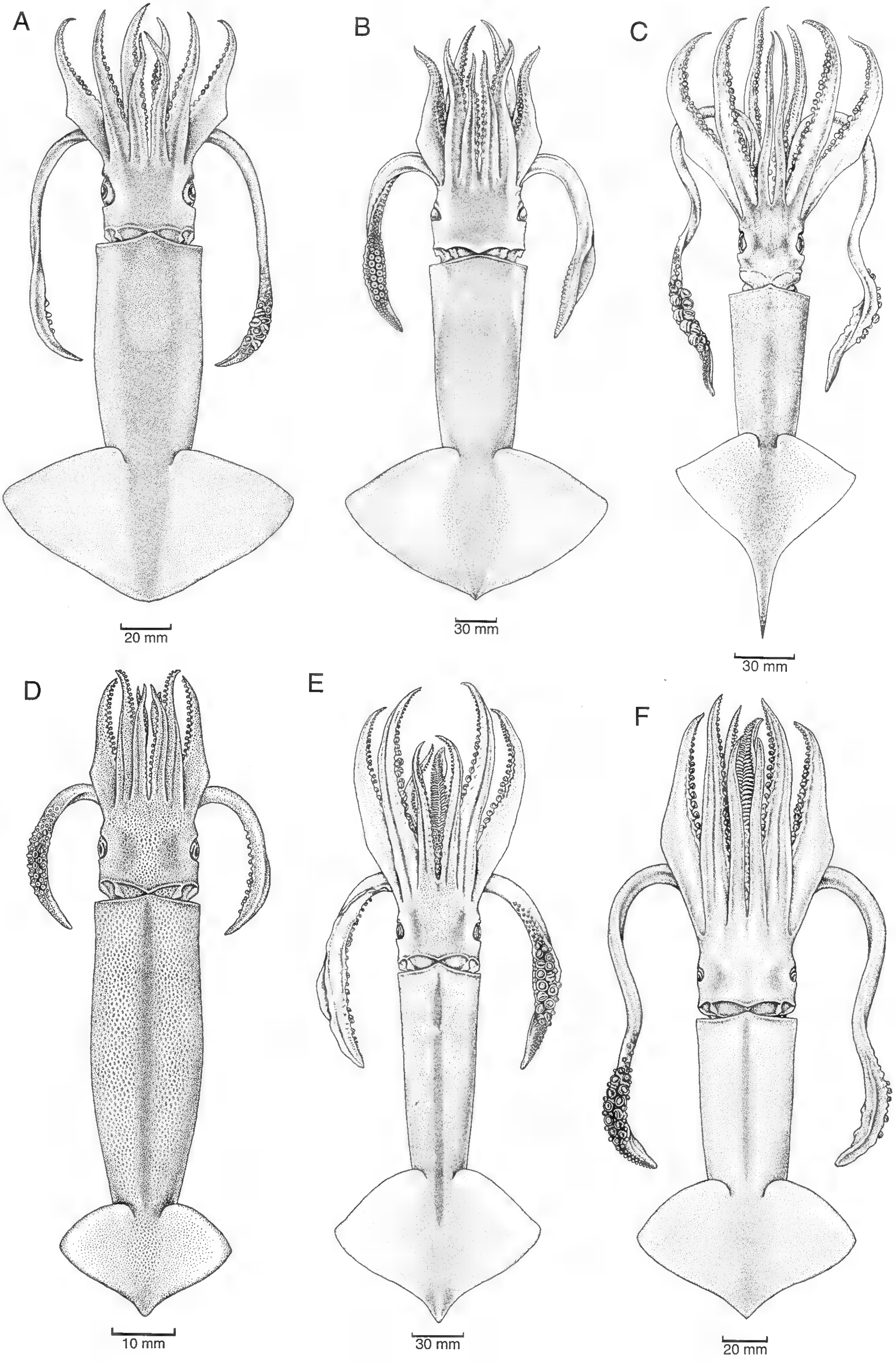
As with other large mobile cephalopods, laboratory maintenance of *T. rhombus* could present major difficulties. However, these squids are regularly encountered on the surface at night and smaller individuals can sometimes be caught in hand-held scoop nets. They may represent suitable subjects for the study of locomotion and social behaviour in oceanic squids when large aquarium facilities become available.

Family Chiroteuthidae

Chiroteuthids are small to medium-sized squids, less than 400 mm mantle length, with somewhat gelatinous bodies (Fig. 13.24A). They are characterised by an oval funnel locking apparatus with one or two knobs projecting towards the centre of the cavity (Fig. 13.24B). The arms, including the greatly enlarged ventral pair, bear biserial, toothed suckers. All Australian representatives have very elongate tentacles (up to five times the mantle length) and distinctive clubs with tetraserial suckers on long stalks. Buccal connectives attach to the ventral borders of the ventral arms. Abundant photophores are present along the tentacle stalks and the ventral arms. Large light organs are also present ventrally on the eyes, at the tips of the tentacular clubs and embedded in the ink sac on both sides of the intestine.

A *Chiroteuthis* species was reported among the stomach contents of lancetfishes from the south-western Pacific and north-eastern Indian Ocean (Rancurel 1970; Fujita & Hattori 1976; Okutani & Tsukada 1988). Nesis (1979a) recorded *Chiroteuthis picteti* from the Australian region and Brandt (1983) caught a *Chiroteuthis* species inside an East Australian Current warm-core eddy. Lu & Phillips (1985) listed *C. imperator* and another *Chiroteuthis* species from the Tasman Sea and off north-western Australia.

The distinctive larval form of this family, termed a *Doratopsis*, attains an unusually large size, up to 60 mm mantle length in some species. It has an elongate spindle-shaped mantle, almost circular fins and the gladius projects posteriorly as a narrow rod. The head is attached to an extraordinarily long, transparent neck. The neck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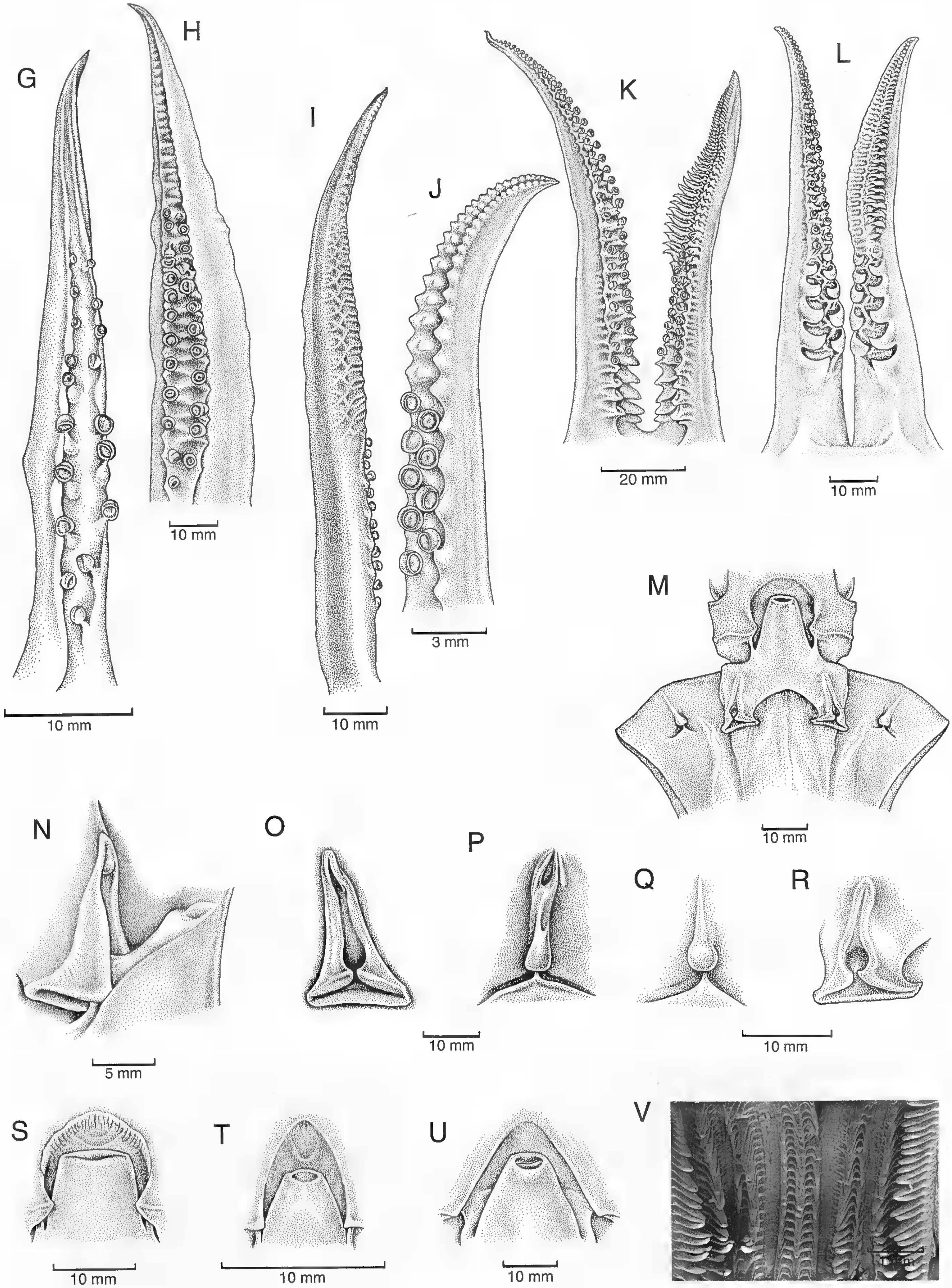


Figure 13.22 Family Ommastrephidae. Members of this diverse family live in surface, mid and bottom waters of the continental shelf and slope, and in the open ocean. A–F, external appearance, dorsal view. G–L, hectocotylised arm. M–R, funnel-mantle locking apparatus. S–U, funnel groove in the three subfamilies. A, G, N, *Sthenoteuthis oualaniensis.* B, H, Q, R, V, *Ommastrephes bartrami.* C, I, M, O, P, *Ornithoteuthis volatilis.* D, J, *Todarodes pacificus pusillus.* E, K, *Nototodarus gouldi.* F, L, *Todaropsis eblanae.* S, Ommastrephinae. T, Todarodinae. U, Illicinae. V, portion of radula showing several transverse tooth rows.
[A–U, K. Hollis; V, C.C. Lu]

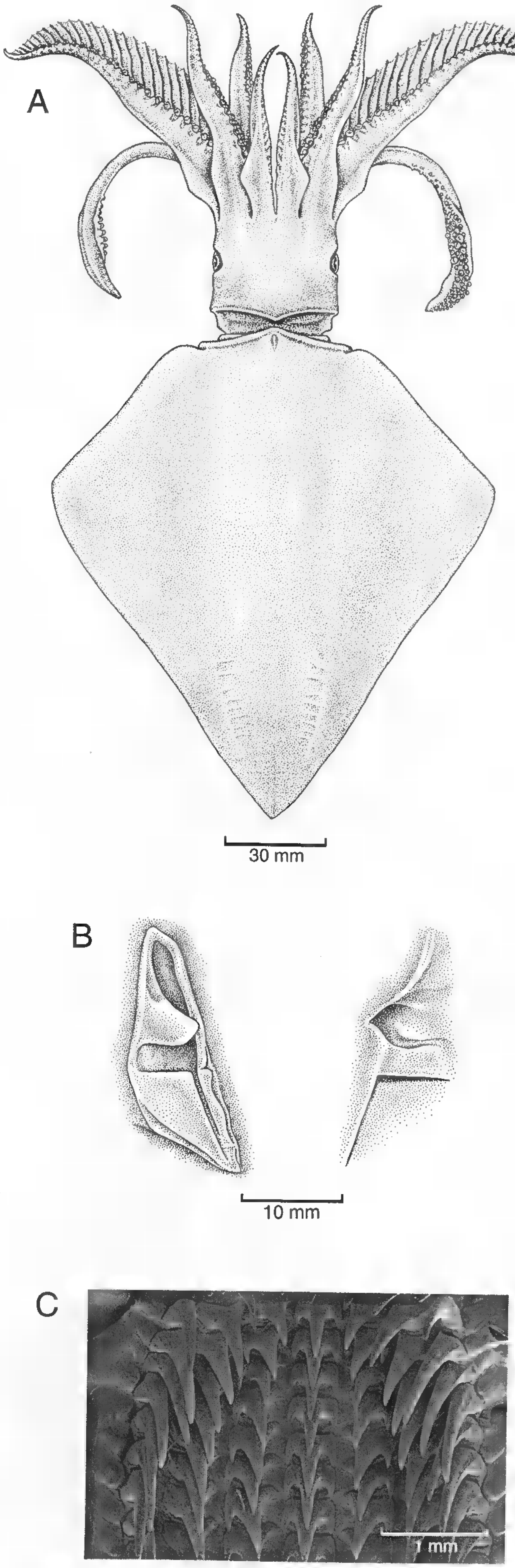


Figure 13.23 Family Thysanoteuthidae. *Thysanoteuthis rhombus*, a large oceanic squid of the tropical and subtropical waters worldwide: **A**, dorsal view; **B**, funnel-mantle locking apparatus; **C**, portion of radula, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

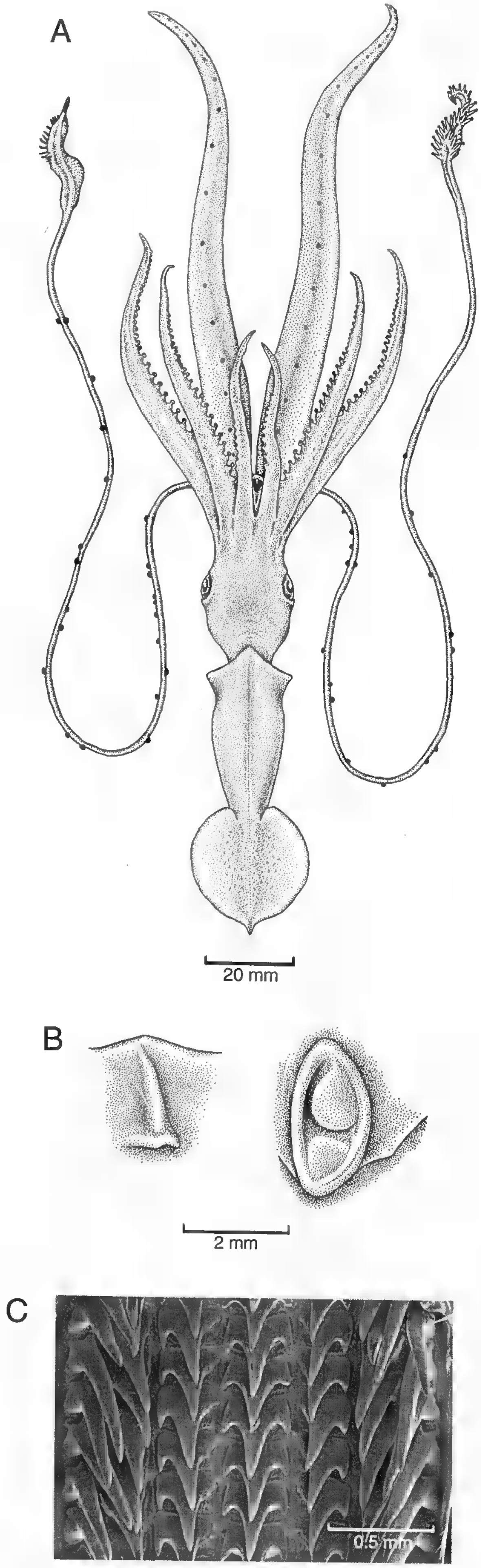


Figure 13.24 Family Chiroteuthidae. **A**, **B**, *Chiroteuthis calyx*, a species found regularly off south-eastern Tasmania: **A**, dorsal view; **B**, funnel-mantle locking apparatus. **C**, portion of radula of *Chiroteuthis imperator*, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

has many membranous partitions, unlike that of *Brachioteuthis* larvae. Clarke *et al.* (1979) concluded that the neck region provides buoyancy for the whole animal. In smaller specimens, the long tentacles and the ventral arms may be up to 60% of the mantle length, and approximately equal in length. The remaining arms are poorly developed. Light organs are not readily apparent in the larval stages.

In post-larval stages, the head is shortened through loss of the post-orbital neck, and the mantle and fins broaden. The advanced development of the ventral arms seen even in larval stages is maintained with growth, and these structures contribute most to the buoyancy of adult chiroteuthids. It is likely that adults float with these uppermost (Clarke *et al.* 1979). Some species lose the tail, and in others a cylindrical gelatinous projection is retained.

No comprehensive life history studies of chiroteuthids have been undertaken. The broad size distribution of specimens examined by Kubota, Koshiga & Okutani (1981) may indicate an extended spawning season for *C. imperator* in Japanese waters. No information on the life span or growth rate of any chiroteuthid species is currently available. Chiroteuthids form part of the diet of sperm whales off south-western Australia and in the Tasman Sea (Clarke 1980; Clarke & MacLeod 1982) and of lancetfishes and yellowfin tunas in the Coral Sea and north-eastern Indian Ocean (Rancurel 1970; Fujita & Hattori 1976; Rancurel 1976). Off Japan, *C. imperator* feeds on micronektonic crustaceans, molluscs and fishes (Kubota *et al.* 1981). The radular arrangement in *Chiroteuthis imperator* species is illustrated in Figure 13.24C.

From its abundance among sperm whale stomach contents, Clarke (1980) concluded that *Chiroteuthis joubini* forms schools off southern Africa, but it is unknown whether this behaviour is characteristic of other members of the family. *Chiroteuthis* displays ontogenetic descent. The smallest larvae are abundant in the upper 100 m and those metamorphosing to the subadult stage predominate at depths of 500–700 m. Adults apparently occur below 500 m during the day but are distributed throughout the water column during the night. Diel vertical migration of larvae and adults is also evident in some species (Roper & Young 1975).

A *Chiroteuthis* species was taken recently in bottom trawls in continental slope waters at depths of 300–600 m off the North West Shelf, although considered to be predominantly oceanic. It has been trawled also in nearshore waters off Japan (Kubota *et al.* 1981).

The distribution of this family in Australian waters is poorly known; *Chiroteuthis picteti* is considered to be restricted to oceanic waters north of 30°S (Nesis 1979a).

Chiroteuthids have soft gelatinous bodies and have no commercial fisheries potential. They are readily damaged during capture in sampling nets, because of the nature of their bodies and the protruding tail in larvae of many species, and therefore are poor subjects for laboratory study.

Family Mastigoteuthidae

Mastigoteuthids are medium-sized to large squids (Fig. 13.25A), attaining 0.5–1.0 m mantle length, with a gelatinous body consistency. The funnel locking cartilage is oval, with inward projecting knobs (Fig. 13.25B). Unlike those of chiroteuthids, the posterior knob generally and the medial knob occasionally are poorly developed. The arms bear biserial, toothed suckers and the ventral arms are greatly enlarged, like those of chiroteuthids. The long, whip-like tentacles, bearing many hundreds of minute suckers, are characteristic of the family. The buccal connectives attach to the ventral borders of the ventral arms. The fins are large. Many species have photophores on the surface of the mantle, and the ventral surfaces of the head, the ventral arms and on the eyeball.

Seventeen species belonging to two genera, *Mastigoteuthis* and *Echinoteuthis*, have been described. The taxonomy of the family, on a worldwide basis, is badly in need of revision. Allan (1945) recorded the first *Mastigoteuthis* species from Australian waters. Four nominal species were listed by Lu & Phillips (1985).

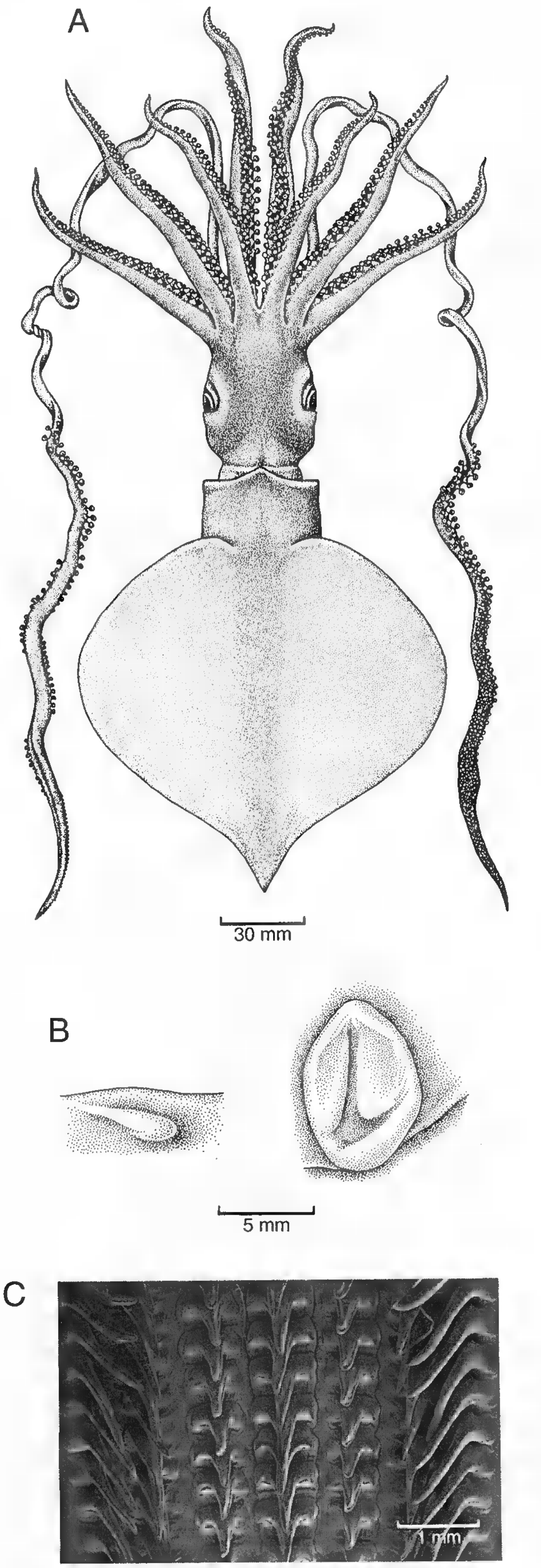


Figure 13.25 Family Mastigoteuthidae. Members of this family are named whip squids, for their long, slender tentacles which bear numerous minute suckers. *Mastigoteuthis cordiformis*, a large species commonly found on the continental slope of north-western Western Australia: **A**, dorsal view; **B**, funnel-mantle locking apparatus; **C**, portion of radula, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

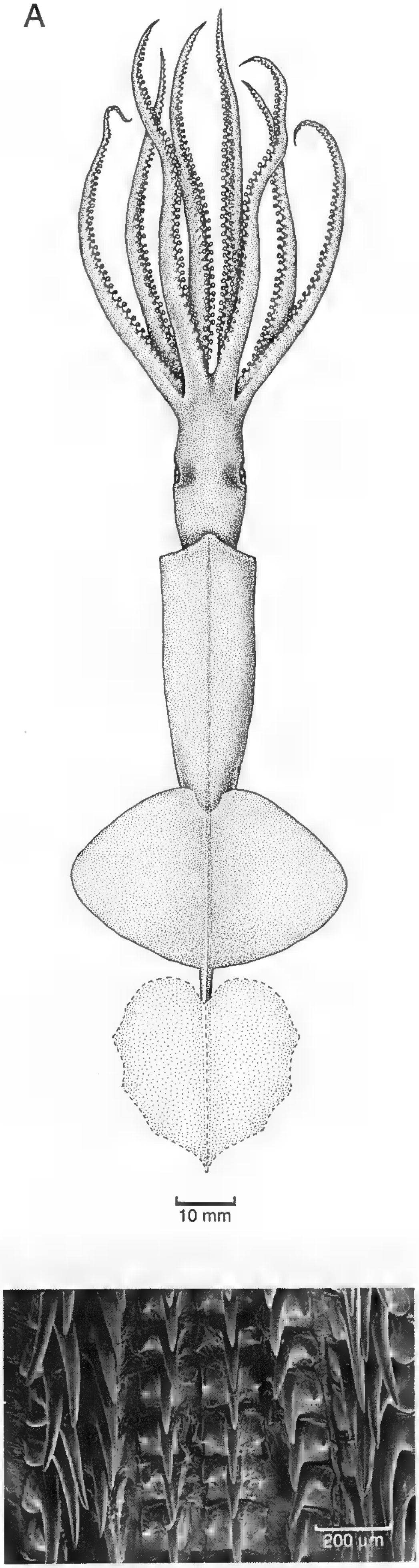


Figure 13.26 Family Grimalditeuthidae. *Grimalditeuthis bomplandii*, a rare squid, is one of the two species with an accessory fin: A, dorsal view; B, portion of radula, showing several transverse tooth rows.
[A, K. Hollis; B, C.C. Lu]

The body in *Mastigoteuthis* species is often pink or brick red in colour. Some species have minute dermal tubercles covering the body surface. These structures consist of elastic cartilage or fibro-cartilage in *Mastigoteuthis cordiformis* and *M. hjorti*, and may aid in the reduction of drag, at least in *M. cordiformis* (Roper & Lu 1990).

The tissues at the front of the head, and in the arms, mantle, fins and cartilage of *Mastigoteuthis* are highly vacuolated (Dilly, Nixon & Young 1977). On the other hand, the tentacles have a dense musculature. The vacuolated tissues containing ammonium-rich fluid provide buoyancy (Clarke *et al.* 1979). Based on the distribution of vacuolated tissue, Dilly *et al.* (1977) suggested that a stationary mastigoteuthid lies vertically in the sea with arms held upwards, and tentacles hanging downwards.

No comprehensive information on the biology of mastigoteuthids is available. Verrill (1882) and Rancurel (1971) found crustacean remains among the stomach contents of *Mastigoteuthis agassizii* and *M. grimaldi*. The radular arrangement in *Mastigoteuthis codiformis* is illustrated in Figure 13.25C. Although various species of *Mastigoteuthis* have been captured frequently in mid-water trawl tows, they are rarely found among the stomach contents of predators (Clarke 1986). The known predators of various species of *Mastigoteuthis* include *Alepisaurus ferox*, *Globicephala melas*, *Hyperoodon planifrons*, *Mesoplodon carlhubbsi* and *Physeter catodon* (Rees & Maul 1956; Clarke 1986).

Male mastigoteuthids do not have a hectocotylised arm. There is no distinctive larval stage.

Mastigoteuthids are deep living squids occurring from the tropical waters to the polar regions. Closing net data indicate that all species live at depths of 500–1000 m in daytime and may ascend to shallower water at night, even to as shallow as 50–100 m (Clarke & Lu 1975; Lu & Clarke 1975b; Roper & Young 1975). With increased fishing effort using bottom trawls on the continental slopes of Australia in recent years mastigoteuthids have been captured, the largest of which was a specimen of *M. cordiformis* of 0.7 m mantle length (Roper & Lu 1990).

Several mastigoteuthid species (at least four) have been recorded from Australian waters but their detailed distributions are unknown. None of the species is endemic in Australian waters, and some may have cosmopolitan distribution (Nesis 1982).

Members of this family have no commercial fisheries potential because of their gelatinous body consistency and the ammonium content of the mantle and arms. No specimen has ever reached the deck of a research vessel alive from the great depths at which these animals live. They are easily damaged during trawling operations also, particularly the long tentacles, and consequently they are not good subjects for laboratory study.

Family Grimalditeuthidae

This rare, monotypic family of medium-sized oceanic squids, less than 250 mm mantle length, is recognised easily by the fused funnel locking cartilages and free dorsal nuchal locking apparatus. The body and mantle are soft, delicate and semitranslucent. The long slender tail bears a delicate accessory fin, which may be lost during capture (Fig. 13.26A). The presence of an accessory fin is unique among cephalopods and whether it functions in concert with the primary fin remains to be clarified.

Biserial suckers, some with attenuate teeth, are present on the long slender arms, which lack protective and swimming membranes and trabeculae. Tentacles are lacking; stubs which may have a sensory function are generally present. Buccal connectives attach to the ventral border of the ventral arms and photophores may be present at the tips of the arms. Little pigmentation is evident on the body (Roper *et al.* 1969; Young, R.E. 1972a).

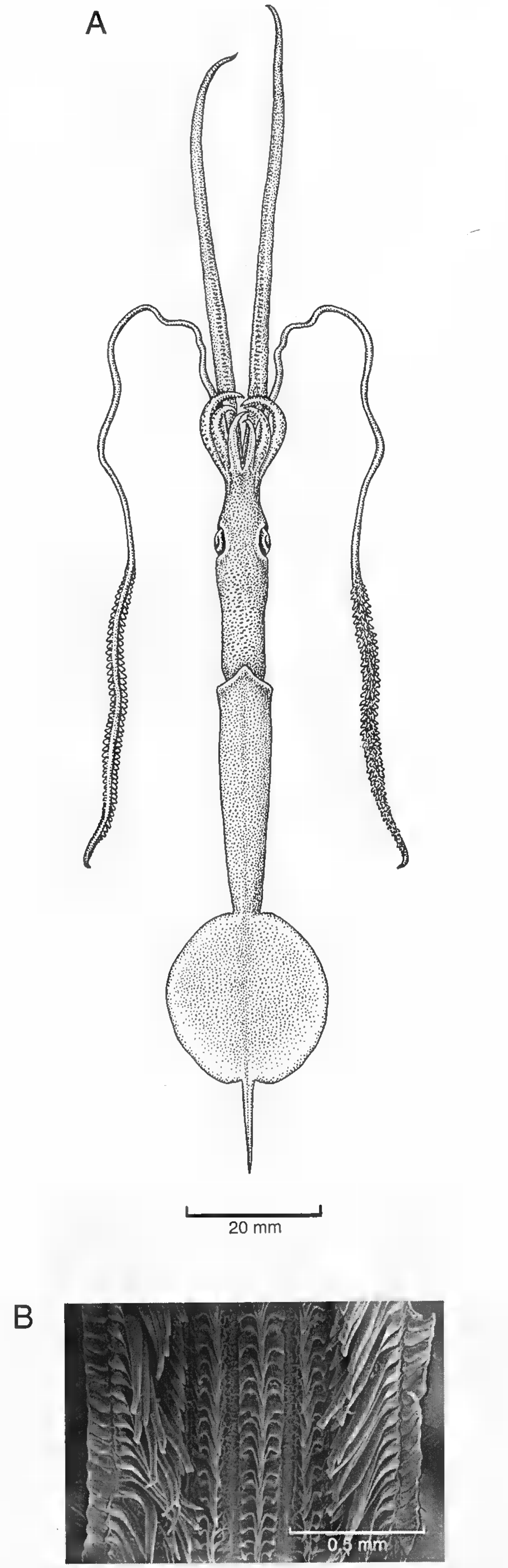


Figure 13.27 Family Joubiniteuthidae. *Joubiniteuthis portieri*, characterised by the elongate tail: A, dorsal view; B, portion of radula, showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

The only species in this family, *Grimalditeuthis bomplandii*, was recorded recently from continental slope waters off southern New South Wales (Lu & Phillips 1985). Because of their rarity in existing collections, no information regarding the life history of *G. bomplandii* is available. The radular arrangement is illustrated in Figure 13.26B. Like many other oceanic squids, this species forms part of the diet of lancetfishes (Clarke 1966; Okutani & Tsukada 1988).

Grimalditeuthis bomplandii has been caught at the surface elsewhere (Clarke 1966) but the vertical distribution of this species remains unknown. Clarification of the distribution of *Grimalditeuthis* in Australian waters awaits the collection of further specimens.

The soft gelatinous body and low capture rate of *Grimalditeuthis* removes all potential for laboratory study or as a fisheries resource.

Family Joubiniteuthidae

The sole species in this monotypic family, *Joubiniteuthis portieri*, is easily recognised by its slender tail, projecting beyond the mantle by slightly more than its own mantle length, and the small, oval, subterminal fins (Fig. 13.27A). The slender arms are more than twice the mantle length, and bear six rows of suckers on each of the dorsal, lateral and dorso-lateral arms. There are four rows on the ventral arms. The tentacles are long and thread-like, and each laterally compressed club carries up to 12 rows of small, smooth-ringed suckers. The distal tip of the club is bordered by a distinct protective membrane with no apparent supports. The funnel locking cartilage is small and oval and the buccal connectives attach to the ventral border of the ventral arms. Photophores are absent and males show no apparent hectocotylisation (Young, R.E. & Roper 1969b).

Joubiniteuthis portieri was recorded recently from eastern Australian waters by Lu & Phillips (1985). Collection of further specimens from Australian waters is necessary to clarify its distribution. Less than 20 specimens are known worldwide (Young, R.E. & Roper 1969b).

Males reach maturity at less than 105 mm mantle length (Young, R.E. & Roper 1969b); an 85 mm mantle length female collected off Japan was immature. The female reproductive system is typically oegopsid with paired nidamental glands (Okutani & Kubota 1972). No information regarding the life history of this rare species is available. The radular arrangement in *Joubiniteuthis portieri* is illustrated in Figure 13.27B.

Because of its rarity, the vertical distribution of this species is poorly known. Atlantic specimens examined by R.E. Young & Roper (1969b) were caught at depths of between 330 and 2500 m. Okutani & Kubota (1972) concluded that the specimen recovered from the stomach of a lancetfish stranded in Japan was captured in the upper 150 m, suggesting that adult *J. portieri* may occupy a broad depth range.

This species has a soft gelatinous body, and is rarely caught. Consequently, it has no potential for laboratory study or as a fisheries resource.

Family Cranchiidae

Members of the ubiquitous and abundant family Cranchiidae range in size from small to very large oceanic squids more than 1 m mantle length, which display great morphological diversity (Fig. 13.28). The mantle of all cranchiids is fused to the head in the nuchal region and to the funnel at its two posterior lateral corners. Generally, the arms bear biserial, sharp-toothed suckers, and the armature of the tentacular clubs has four rows of suckers, hooks or hook-like suckers. Buccal connectives attach to the ventral borders of the ventral arms, and photophores are present on the eyes and on the arm tips in some species (Roper *et al.* 1969). Several rows of the radula of *Cranchia scabra* are shown in Figure 13.29.

The 13 cranchiid genera currently recognised are divided into the subfamilies Cranchiinae (Fig. 13.28A–E) and Taoniinae (Fig. 13.28F–L). The Cranchiinae are characterised by one or two cartilaginous strips which extend posteriorly from the anterior apex of the funnel-mantle fusions and the fusion of the funnel to the head laterally (Fig. 13.28B, D). The eyes bear four or more small, round or oval photophores. The right or left ventral arms are hectocotylised in mature males.

In the Taoniinae, no cartilaginous strips are present and the funnel is free from the head laterally. One to three crescent-shaped light organs, dissimilar in size, are present on the eyes. Hectocotylisation does not occur.

Secondary sexual modification of the ends of the arms in mature males and development of brachial end-organs on the arms of mature females may occur in both subfamilies. The recent generic revision (Voss, N.A. 1980) and detailed studies of individual genera (Voss, N.A. 1985) provide a more comprehensive treatment of this complex group.

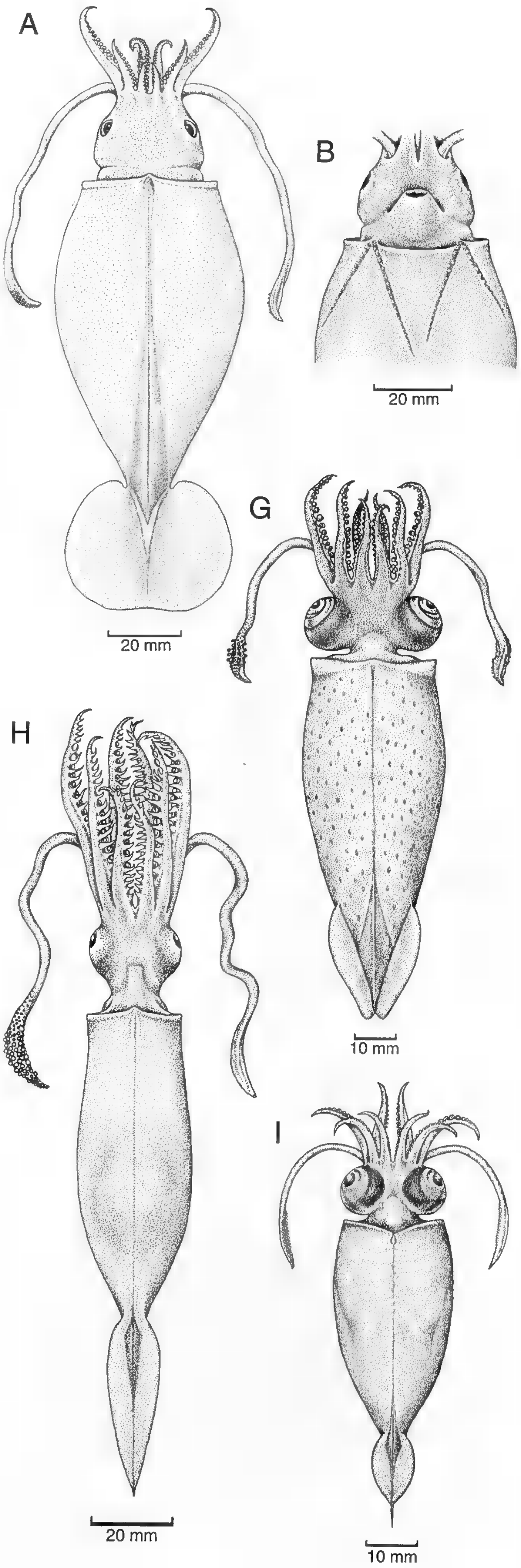
Cranchiids were first recorded from eastern Australian waters by Allan (1940, 1945), with '*Pyrgopsis pacificus*' (probably *Leachia* sp.) being the most numerous cephalopod in her plankton collections. Brandt (1983) recorded at least five cranchiid species from both subfamilies in a warm-core eddy of the East Australian Current. Recently, Lu & Phillips (1985) listed some 13 species and species groups from off the east coast.

The taxonomic confusion surrounding this family remained until the recent work of N.A. Voss (1980, 1985) was partially the result of the major morphological changes which accompany growth in many cranchiids. The different early larval characters, such as stalked eyes and paddle-shaped fins, are lost or modified at varying stages during growth (Clarke 1966; Voss, N.A. 1980, 1985; Rodhouse & Clarke 1986).

Cranchiid reproductive systems show typical oegopsid characteristics, with the exception of the four nidamental glands in a female *Ascocranchia joubini* from the North Atlantic (Voss, G.A. 1962). Female cranchiids have no spermathecae. In *Teuthowenia pellucida* (Fig. 13.28G), a species abundant in eastern Australian waters, spermatophores are embedded externally on the anterior half of the mantle, either dorsally or ventrally. The sperm reservoirs penetrate the inner wall and release sperm into the mantle cavity, where fertilisation of mature eggs leaving the oviducal glands apparently occurs. The large, swollen nidamental glands seen in mature females suggest that the eggs are deposited in one or more gelatinous egg masses. An estimated 6000–8000 eggs of 3.0 mm maximum length were carried by two mature female *T. pellucida* of 177 and 187 mm mantle length (Voss, N.A. 1985).

No comprehensive life history studies of cranchiids from Australian waters have been undertaken. Nixon (1983) reviewed available information on the life cycle of North Atlantic *T. megalops*. N.A. Voss (1985) concluded that female *T. pellucida* probably shed all their eggs over a short period and do not survive beyond one spawning period. Males may mate more than once, but like the females, do not survive past one limited mating season. No information on the life span and growth rates of any cranchiid species is available. The radular arrangement in *Cranchia scabra* is illustrated in Figure 13.29. Cranchiids form a minor part of the diet of sperm whales off south-western Australia and in the Tasman Sea (Clarke 1980; Clarke & MacLeod 1982). They are included also in the diets of lancetfishes and yellowfin tunas from the Coral Sea and north-eastern Indian Ocean (Rancurel 1970, 1976; Fujita & Hattori 1976; Okutani & Tsukada 1988), and elsewhere they are eaten by seabirds (Imber 1978), blue sharks (Clarke & Stevens 1974), albacore tunas and dolphins (Clarke 1966).

Some cranchiids show ontogenetic descent. The smallest larvae of *T. pellucida* are more abundant in the upper 600 m, and those metamorphosing to the subadult stage predominate at depths of 700–800 m. Adults generally occur below 500 m and as deep as 2400 m. Mature *T. pellucida* have only been caught in water depths of more than 3800 m (Voss, N.A. 1985). *Leachia pacifica*



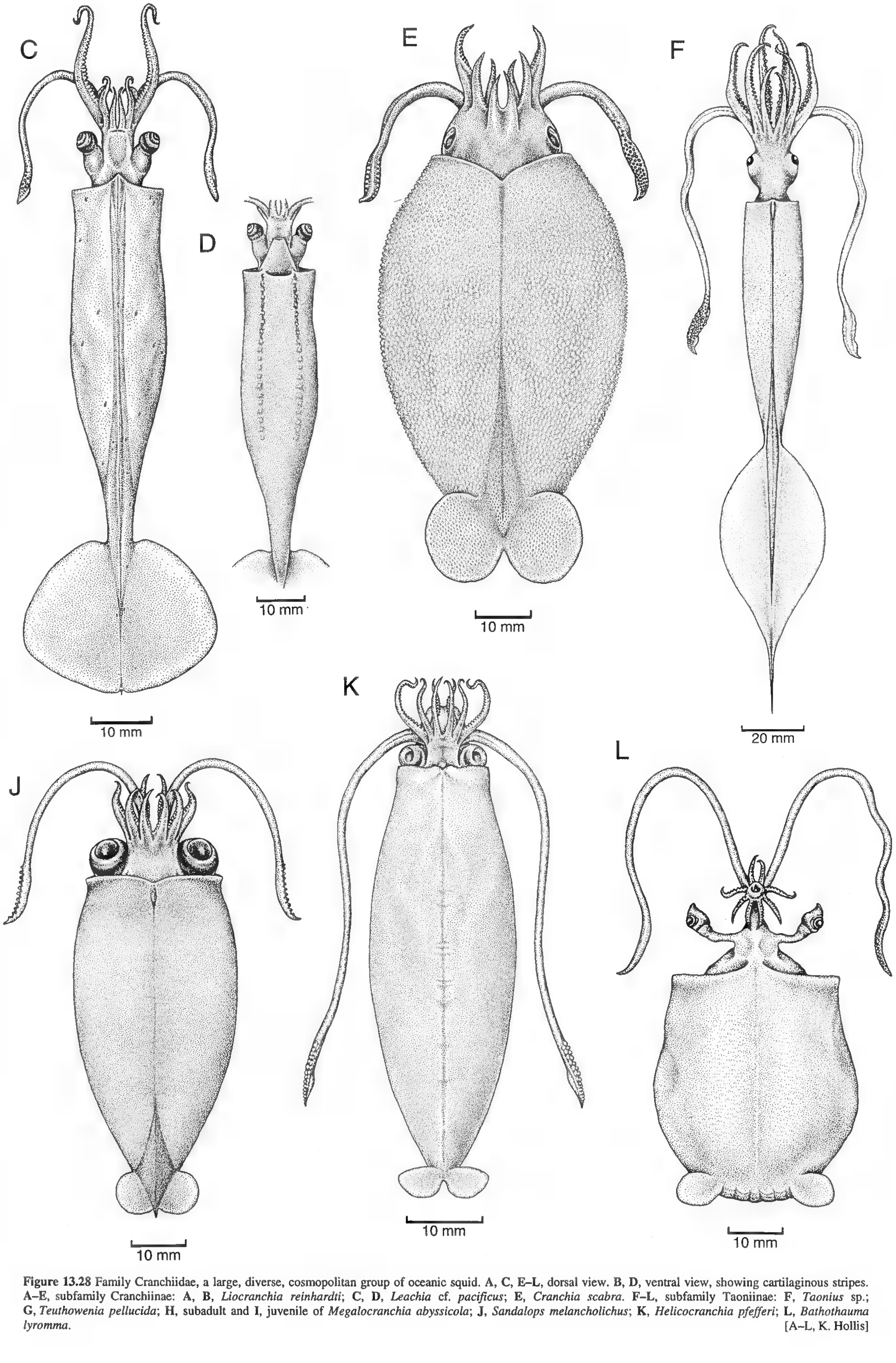


Figure 13.28 Family Cranchiidae, a large, diverse, cosmopolitan group of oceanic squid. A, C, E–L, dorsal view. B, D, ventral view, showing cartilaginous stripes. A–E, subfamily Cranchiinae: A, B, *Liocranchia reinhardti*; C, D, *Leachia* cf. *pacificus*; E, *Cranchia scabra*. F–L, subfamily Taoniinae: F, *Taonius* sp.; G, *Teuthowenia pellucida*; H, subadult and I, juvenile of *Megalocranchia abyssicola*; J, *Sandalops melancholichus*; K, *Helicocranchia pfefferi*; L, *Bathothauma lyromma*. [A–L, K. Hollis]

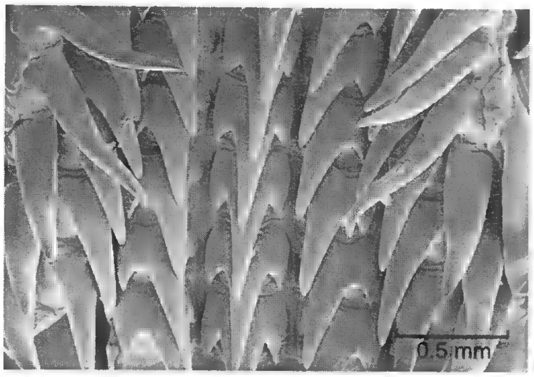


Figure 13.29 Family Cranchiidae. Portion of the radula of *Cranchia scabra*, showing several transverse tooth rows. [C.C. Lu]

(Fig. 13.28C) off Hawaii lives in near-surface waters until it reaches about 80% of its maximum length. Both males and females then descend to depths of up to 2300 m where they mature, mate and then apparently spawn (Young, R.E. 1975a). Diel vertical migration of larval or adult cranchiids has not been demonstrated conclusively elsewhere (Roper & Young 1975; Young, R.E. 1975a). The recent capture in a demersal trawl of a *Taonius* species (Fig. 13.28F) off north-western Australia perhaps suggests that this species is associated with the sea floor in continental slope waters during at least part of the day.

Often abundant, most representatives of this family in Australian waters are small and have thin-walled mantles, sometimes filled with highly ammoniacal body fluids (Pl. 18.10), and hence they have no commercial fisheries potential.

Cranchiids are among the most speciose and abundant oegopsid squids and occur in all oceans from the surface to depths of in excess of 3500 m. Of the 13 genera recognised by N.A. Voss (1980), eight are known from Australian waters, none of which is endemic. The distribution of most species in Australian waters is poorly known. N.A. Voss (1985) concluded that *T. pellucida* is distributed circumglobally in the mixed waters of the Subtropical Convergence, its local occurrence being affected by surface winds, currents and water depth.

The abundance of cranchiids in near surface waters off the Australian coast and the resilient nature of the body of some species suit cranchiids to shipboard laboratory studies of flotation physiology, luminescence, functional morphology and behaviour as have been conducted elsewhere (Clarke 1962; Young, R.E. 1975c; Voss, N.A. 1980).

Order VAMPYROMORPHA

These deep-water (bathypelagic) animals have four pairs of arms. A pair of special additional appendages is located on the outer side of the web between the first and second arms. These long, thread-like filaments are retractable into pockets, and lack suckers. The arms are connected by a moderately deep web. The arm suckers align in one row, between two rows of cirri which lie parallel to the sucker row. The suckers lack chitinous rings, and are absent from the proximal parts of the arms. One elongate, paddle-like fin is situated on each side of the mantle (Fig. 13.30A). The larvae may have two pairs, one of which disappears by the end of the larval stage. The mantle is always fused with the head in the occipital area but not with the funnel. Numerous, small simple photophores of composite structure are present. The gladius is a wide, very thin plate.

Family Vampyroteuthidae

This monotypic family is characterised by the presence of a single pair of fins (Fig. 13.30A), and a pair of retractile, sensory filaments in addition to the eight sessile arms. The suckers are arranged in a single row and alternate with lateral cirri along most of the arm. The mantle is fused to the head and the mantle opening is wide. Photophores are present.

The sole member of the family, *Vampyroteuthis infernalis* was described from a specimen from the Guinea Basin, South Atlantic (Chun 1903), and was originally regarded as an octopod. Subsequently the species has been taken in the Pacific Ocean and the Indian Ocean (Young, R.E. 1972a) and elsewhere in the Atlantic Ocean. The family was erected by Thiele in 1915. Transferred to a new order of its own, Vampyromorpha, the species was studied extensively by Pickford (1939a, 1939b, 1940, 1946, 1949a, 1950, 1952, 1959). Her reports on the natural history and distribution (Pickford 1946) and external anatomy (Pickford 1949a) remain the most extensive studies on the species.

The first Australian records of *Vampyroteuthis infernalis* were from the *Dana* Expedition in 1929 in the western Tasman Sea (Pickford 1946). The species was reported off south-eastern Tasmania by Lu & Phillips (1985).

Externally *Vampyroteuthis infernalis* is jet black in colour. The body is gelatinous in consistency. The mantle is broad and short, and fused with the head on its dorsal side. The large, paddle-like fins are located laterally and subterminally towards the posterior end of the mantle. In adults, a pair of small pockets, representing the degenerated larval fins, is present behind the fins.

The head is broad and the eyes are very large (Fig. 13.30A). Each of the eight arms bears a single row of suckers that lack chitinous rings. The arms are connected by a deep web that extends to about two thirds of arm length. Paired cirri alternate with the suckers along most of the oral surface of the arms. About four to 10 pairs of primary cirri occur proximal to the first sucker. Between the dorsal and dorso-lateral arms, a slender filament extends from a pocket on the dorsal surface of the web. The filament is retractile and often is completely retracted within the pocket. These filaments were considered to be homologous with arms (Pickford 1940). R.E. Young (1967) studied their nerve innervation and concluded that they are not homologous with the arms. However, J.Z. Young (1977) believed that the filaments are indeed the modified second pair of arms of a decapod. Thus presently, the true origin of the filaments remains unclear.

Vampyroteuthids have a shell-sac which runs from the neck backwards to the apex of the body where it bends towards the ventral surface. The following description of the shell is based on Pickford's (1949a) thorough studies. The shell, located within the shell sac is a thin, plate-like, transparent, non-calcified structure. There is a little cup-shaped conus, but no trace of a chambered phragmocone. There are no significant differences between sexes in the shape and structure of the shell. The shell of larvae is more slender than that of adults. The posterior three-quarters of the shell consists of the united lateral plates and conus vanes and is arched so that it appears boat-shaped when viewed from below. The anterior quarter is formed largely of the broad middle plate of the pro-ostracum. The thin middle plate is separated from the lateral plates in the posterior region by the inner asymptotic zone. The lateral plate is separated from the conus vane by the outer asymptotic zone. The function of the shell is unknown.

Many photophores are scattered over the surface of the head, mantle, fins and arms, particularly on their ventral surfaces. Posterior to each fin is a single large photophore. An oval patch of thickly packed, small photophores is located on the dorso-lateral surface of the mantle (Fig. 13.30A) at the level of the mantle opening. Photophores are absent on the web area and the oral surface of the arms.

The mantle musculature of *V. infernalis*, particularly the circular muscle, is poorly developed, and bundles of radial muscle fibres are interspersed with gelatinous material. According to R.E. Young (in Roper & Brundage 1972), *V. infernalis* swims at a moderate speed with the arms pointed forward to the direction of motion and the fins provide propulsion. Rapid swimming is produced by a medusoid action of the arms and web. Slow swimming is achieved by water ejection through the funnel, with the fins spread as stabilisers. R.E. Young also stated that the first is the primary method. The second method is rarely used and the third method needs verification (Young, R.E. in Roper & Brundage 1972). The propulsion provided by the fins in the first method is produced by a well-developed muscular band in the anterior margin of the fins, which is attached to the pen (Clarke 1988).

The mantle cavity of *V. infernalis* is simple, and lacks the median and lateral mantle adductor muscles. The visceral mass is fused dorsally to the mantle, and there is no antero-dorsal communication between the right and left sides above the viscera.

According to J.Z. Young (1977), the muscles of the buccal mass of *V. infernalis* contain many vacuoles suggesting that they are not strong. A beak and radula (Fig. 13.30B) are present. The presence of very large anterior salivary glands and subradular glands suggest the production of a mass of secretion for entangling small prey. J.Z. Young (1977) reported the presence of plankton, including diatoms and copepods in the crop of a specimen of *V. infernalis* and suggested that the species feeds by collecting small organisms.

The nervous system of *V. infernalis* shows features of both decapods and octopods. As in decapods, the brain of *V. infernalis* has a ventral magnocellular lobe believed to be concerned with escape reactions. There are no giant fibres. The magnocellular lobe is missing in octopods, and J.Z. Young (1977) believed that *V. infernalis* may represent an intermediate stage between decapods and octopods.

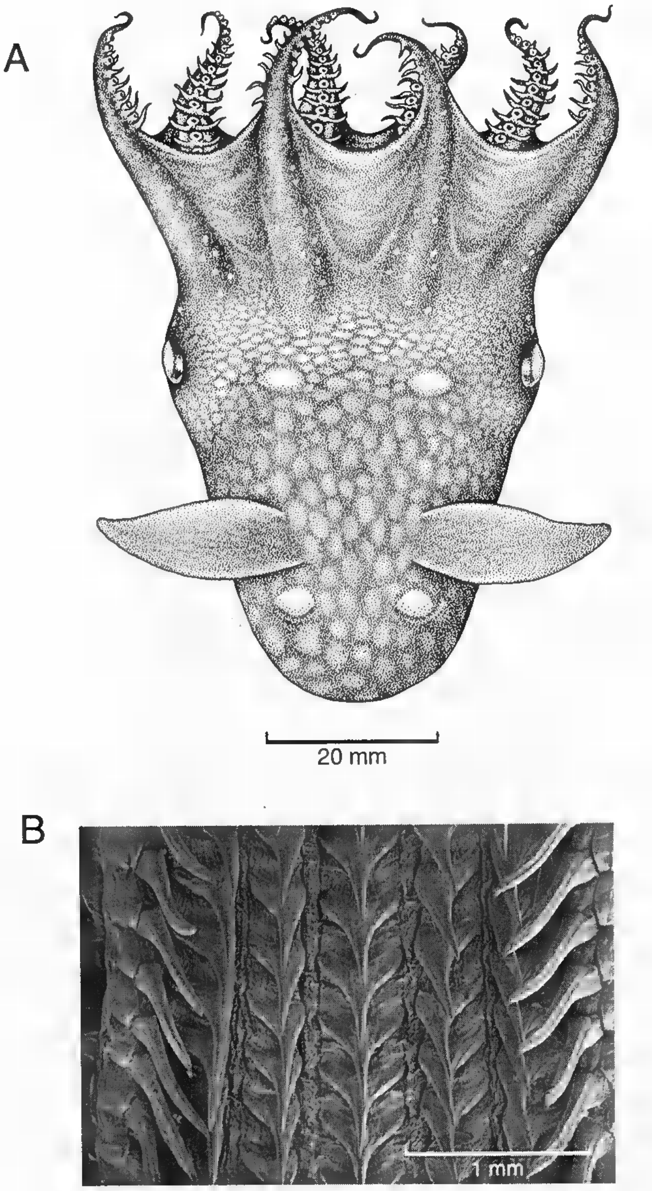


Figure 13.30 Family Vampyroteuthidae. *Vampyroteuthis infernalis* lives at depths of 500–1500 m; morphologically, it is considered to represent an intermediate stage between decapods and octopods: **A**, external view; **B**, portion of radula, showing several transverse tooth rows.
[A, K. Hollis; B, C.C. Lu]

Further evidence supporting the intermediate nature of the brain of *V. infernalis* is found in the inferior frontal system, which is concerned with the processing of tactile information. The inferior frontal system is better developed in *V. infernalis* than in any decapod but not as highly differentiated as in *Octopus*. The superior buccal lobe is attached to the rest of the brain but separated by long connections from the inferior buccal lobes below the buccal mass, a condition found in all octopods but not in any decapods. The median and lateral superior frontal lobes are not sharply differentiated, but abundant transverse bundles exist. The anterior basal lobe is large and in two parts. The median basal lobe is moderate sized but the lateral basal lobe (the chromatophore centre) is absent.

The large eyes of *V. infernalis* are of the oegopsid type. There is no sinus.

Pickford (1946, 1949a, 1949b, 1959) and Healy (1989) have provided much of the limited information on the reproductive biology of *V. infernalis*. Females are larger than males. Males lack a hectocotylus. The single penis lies on the left side of the visceral mass and projects freely into the mantle cavity. In adult males, the penis lies inside the funnel, with which *V. infernalis* probably transfers spermatophores into the seminal receptacles of the females. The spermatophores are about 20 mm long. The females lack nidamental glands, but a well-developed oviducal gland is present at the end of each oviduct. There is a pouch-like seminal receptacle in front of each eye. The spherical eggs are devoid of any jelly, about 3.5 mm in diameter and are pelagic. Nothing is known about the embryonic development of *V. infernalis*.

Pickford (1946, 1959) reported that larvae of *V. infernalis* were captured at all seasons of the year and the sexually mature adults were taken in various months from August to January in different oceans. The gonad contains a wide range of egg sizes, suggesting that there probably is no reproductive seasonality (Young, R.E. in Arnold & Williams-Arnold 1977).

The most notable metamorphosis of the larva involves the progression from one pair of larval fins only, to a four-finned stage as the pair of adult fins develops, and the regression of the larval fins to mere rudiments (Pickford 1946).

Vampyroteuthids are stenothermic and stenohaline. The majority of specimens studied by Pickford (1946) were taken in waters from 2.0° to 5.9°C and salinity of 34.70–34.99‰. Furthermore, they prefer the water relatively poor in oxygen (below oxygen minimum). Pickford (1946) reported also that density is a common factor delimiting the water layers inhabited by *V. infernalis*. The majority of specimens have been taken in layers between sigma-T values of 27.4 and 27.8.

Vampyroteuthids have been reported in the stomach contents of the pygmy sperm whale, *Kogia breviceps* and the dwarf sperm whale, *K. simus*, from South African waters and the northern bottlenose whale *Hyperoodon ampullatus* off Denmark (Clarke 1986).

The species has no commercial fishery value due to its rarity and gelatinous body consistency.

Vampyroteuthis infernalis is a cosmopolitan species, distributed in all three major oceans, from tropical to temperate latitudes. It is absent from the Mediterranean Sea. It inhabits the lower mesopelagic to bathypelagic zones from 500–1500 m, with the peak of distribution at depths of 800–900 m in the North Atlantic (Lu & Clarke 1975b). Off California, the centre of vertical distribution ranges from 500–1200 m, with the peak at 700–800 m (Roper & Young 1975). There is no diel migration in the adults (Lu & Clarke 1975b), although young less than 20 mm mantle length generally live in water deeper than 900 metres while the adults and subadults primarily live at depths less than 900 metres. The young undergo ontogenetic ascent when the larval fins are resorbed (Roper & Young 1975).

Key to suborders and families of order Octopoda

1 (a) One pair of paddle-shaped fins. Row of cirri adjacent to arm suckers. Radula generally absent. Suborder Cirrata 2

(b) Fins absent. No cirri adjacent to arm suckers. Radula always present. Suborder Incirrata 4

2 (a) Web single without secondary web (Fig. 13.31; Pl. 19.1). Funnel short. Gill filaments almost parallel to gill axis ('half-orange' shape). Cirri short .... Opisthoteuthidae

(b) Web attached to arms by means of a secondary web. Gill filaments diverge markedly from axis ('sepioid' type). Cirri long and conspicuous. Radula absent 3

3 (a) Mantle aperture small and funnel long. Shell thick and saddle-shaped. All but tip of arms enclosed in web .... Cirroteuthidae

(b) Mantle aperture tube-like and closed around small funnel. Shell a thick, open, V-shaped rod. About 20% of arms project beyond web, and lack cirri on this part of arms .... Stauroteuthidae

4 (a) Body gelatinous, semi-gelatinous or transparent. Arm suckers in one row, or one row within web and two rows distally 5

(b) Body muscular, firm or soft to the touch but neither gelatinous nor transparent. Suckers in one or two rows over the entire arm length except in *Aphrodoctopus* 9

5 (a) Mantle aperture wide. Funnel not fused with mantle 6

(b) Mantle aperture reduced to two slits on sides of head. Very long funnel fused with mantle 8

6 (a) Arm suckers in one row. Eye diameter not exceeding 25% of mantle length. Head width usually less than 60% of mantle length. Multicuspid rhachidian tooth 7

(b) Arm suckers in one row within umbrella and on tip of each arm, two rows between. Eyes enormous, diameter 33 to 40% of mantle length. Head width equals or exceeds mantle length. Rhachidian tooth tricuspid .... Alloposidae

7 (a) Arms not longer than the mantle (Fig. 13.32A). Diameter of suckers 3 to 7% of mantle length. Eyes round or oval. Liver oval, positioned anterior to stomach. Radula comb-like (Fig. 13.32B) .... Bolitaenidae

(b) Arms of adults two to three times longer than mantle (Fig. 13.34A). Proximal suckers small and set widely apart. Distal suckers very large, close set, diameter 10 to 17% of mantle length in adults. Eyes narrow, almost rectangular. Liver long, thin and acuminate, positioned posterior to the stomach. Radula not comb-like; first and second lateral radular teeth unicuspid (Fig. 13.34B) .... Vitreledonellidae

8 (a) Eyes telescopic, set close together on the 'head crown' and directed upwards (Fig. 13.33A). Web well developed. Funnel not fused ventrally with head. Body transparent, almost colourless. Gelatinous covering present .... Amphitretidae

(b) Eyes normal. Web short, thin. Funnel ventrally fused with head, only anterior funnel end free. Body semitransparent but with numerous chromatophores. Gelatinous covering absent .... Idioctopodidae*

9 (a) Mantle-funnel locking apparatus absent. Suckers in one or two rows. Benthic animals (Fig. 13.35A–D; Pls 19.2–20.6 .... Octopodidae

(b) Mantle–funnel locking apparatus present. Suckers in two rows. Epipelagic (very rarely mesopelagic) animals 10

10 (a) Web very weakly developed (Fig. 13.38A, B; Pl. 21.3). No cephalic water pores. Ventro-lateral arms shorter than other arms in females; left ventro-lateral arm in male hectocotylised, other arms are of subequal length .... Argonautidae

(b) Dorsal and dorso-lateral arms connected by a wide web (Fig. 13.36A–C). Two pairs of cephalic water pores at the base of dorsal and ventral arms. Dorsal and dorso-lateral arms much longer than ventro-lateral and ventral arms (tips of dorsal arms may be autotomised in females); right ventro-lateral arm of male hectocotylised .... Tremoctopodidae

(c) Web absent (Fig. 13.37A–C). One pair of cephalic water pores at the base of ventral arms. Dorsal and ventral arms much longer than dorso-lateral and ventro-lateral arms; right ventro-lateral arm of male hectocotylised .... Ocythoidae

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*Hochberg, Nixon & Toll 1992 and Hochberg *et al.* (1992) suggested that *Idioctopus gracilipes* Taki, 1962, the only species in the family Idioctopodidae is synonymous with *Amphitretus pelagicus* Hoyle, 1885, the type species of Amphitretidae. Consequently Idioctopodidae may be a junior synonym of Amphitretidae.

In Australian waters, the majority of captures have been from the waters off the east coast from Cape York to south-east of Tasmania with one specimen taken from the Great Australian Bight (Pickford 1946; Lu unpublished data). The lack of specimens from the west coast of Australia may reflect the paucity of sampling.

Order OCTOPODA

In the order Octopoda, suckers on the four pairs of arms form one to two rows. The suckers are sessile, rarely stalked, and lack chitinous rings. The arms are commonly connected by a moderate to deep web. There is one pair of fins, if present. The mantle is always fused with the head in the occipital area but generally not with the funnel. The mantle cavity is generally connected with the exterior by one opening at ventral side of body. The mantle and funnel cartilages, if present, are simple, in the form of a tubercle and pit. External photophores of composite structure are lacking, and only a few species have simple photophores. The gladius is represented by a cartilaginous fin support, reduced to small cartilaginous rods, or absent. The above key to the suborders and families of the Octopoda is after Nesis (1982) and G.L. Voss (1988a).

Suborder CIRRATA

In suborder Cirrata, there is one pair of paddle-shaped fins, each supported by a U-, V-, or saddle-like cartilage. A single row of arm suckers is flanked on each side by a row of cirri. The mantle opening is reduced to a very narrow slit around the funnel base, and is sometimes obliterated. The web is usually very deep, and may reach the tips of the arms. No ink sac or radula is present. Only the left oviduct develops. All are deep-water, benthic, or rarely, pelagic animals.

Family Opisthoteuthidae

The body of these small to medium-sized animals has a semi-gelatinous consistency, and is often flattened but can be bell-shaped, depending on the state of contraction during preservation (Fig. 13.31A). The mantle opening is reduced to a narrow slit. The funnel is small. The arms are connected by deep, thick webs reaching almost to the arm tips (Pl. 19.1). There is no secondary web. The two small fins are attached subterminally to the posterior end of the mantle. The eyes are large. Each arm bears a single row of suckers, with paired, short cirri alternating with the suckers. The paired posterior fins are short. The shell is V- or U-shaped.

This family was erected by Verrill in 1896 for his species *Opisthoteuthis agassizii*, captured during the Blake Expedition off the West Indies, and published in 1883. The genus *Opisthoteuthis* was placed in the family Cirroteuthidae by Chun (1915), Berry (1918), and Sasaki (1929). Robson (1932) accepted Verrill's original designation and this was followed by Thiele (1929–1935), G.L. Voss (1977, 1988a, 1988b) and Nesis (1982).

The first Australian records of this family were Berry's (1918) description of *Opisthoteuthis pluto* from the Great Australian Bight and *O. persephone* (Fig. 13.31) from the Great Australian Bight and off Genoa Peak, Victoria. Lu & Phillips (1985) extended the distribution of *O. persephone* to New South Wales and Tasmania.

The cartilaginous shell of the Australian opisthoteuthids, *Opisthoteuthis pluto* and *O. persephone*, is broadly U-shaped. G.L. Voss (1988a) reported that when the animal is in a discoidal state, the shell is nearly flat. However, when the animal assumes a horizontal swimming position, and is bell-shaped, the shell is strongly curved.

The semi-gelatinous mantle of *Opisthoteuthis* species has reduced muscle fibres and a thick watery cellular matrix. Aldred, Nixon & Young (1983) suggested the semi-gelatinous body of the cirrate octopods may provide buoyancy through storage of ammonium ions. Simple tests by heating pieces of mantle tissue of *O. pluto* with KOH solution failed to detect ammonia odour (Lu unpublished data).

Roper & Brundage (1972) concluded from studies of a large series of deep sea photographs that three styles of locomotion are employed either singly or concurrently. They are jet propulsion, typical of other octopods; pulsation produced by opening and closing the web and arms; and a drogue-like or umbrella phase utilising outstretched web and arms. The pulsating type of locomotion was observed directly by Pereyra (1965) on *Opisthoteuthis californiana* in a shipboard aquarium.

The radula is absent in the family, and the genus *Opisthoteuthis* lacks salivary glands. Scott (1910) found many crustacean species in the stomach of ■ species of *Grimpoteuthis* and fragments of polychaetes were found in the stomach of *G. glacialis*. Meyer (1906) reported small crustaceans and small fishes, some swallowed whole, in the stomachs of *O. depressa*. Nothing is known about the diets of Australian opisthoteuthids.

The mature male opisthoteuthids have enlarged suckers near the base or near the tip of all arms (Sasaki 1929; Nesis 1982). The eggs of opisthoteuthids are large. The maximum size of eggs in *O. californiana* was reported to be 9 x 5 mm (Berry 1952) and 11 x 6 mm for the eggs in oviducts (Pereyra 1965). Ripe ovarian eggs of *O. vossi* are 9.9 mm in diameter (Sanchez & Guerra 1989).

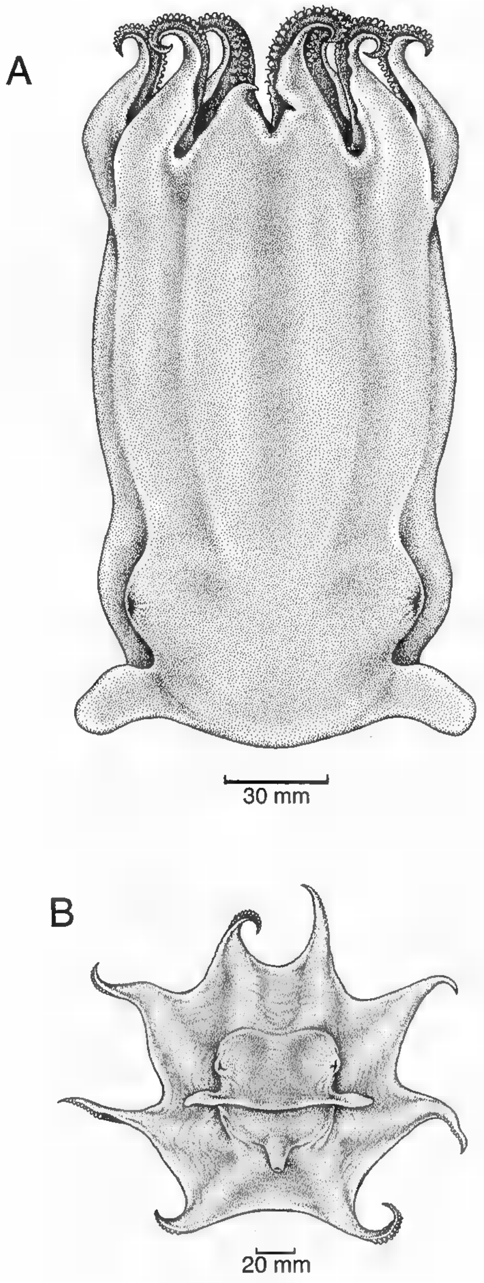

Figure 13.31 Family Opisthoteuthidae. *Opisthoteuthis persephone*: **A**, dorsal view; **B**, posterior view. [K. Hollis]

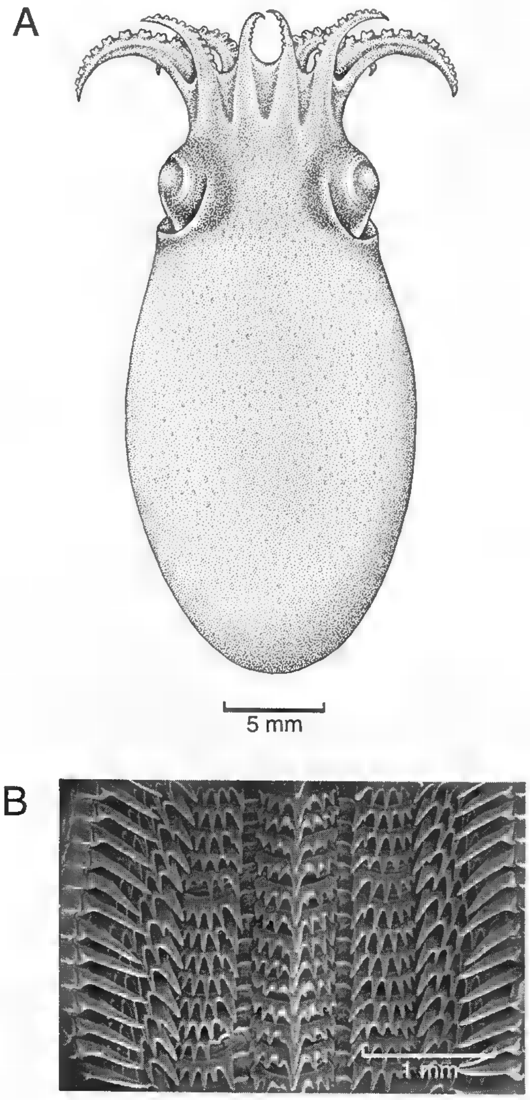

Figure 13.32 Family Bolitaenidae. *Japetella diaphana* is a gelatinous-bodied pelagic octopod common in warm oceans; young animals live at shallower depths than adults and subadults: **A**, dorsal view; **B**, portion of radula, showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

Adult opisthoteuthids are benthic, at depths of 100–2250 m, and concentrate at 100–1000 m. The known depth ranges are 350–1254 m for *O. pluto* and 396–660 m for *O. persephone.* Young opisthoteuthids are probably planktonic. The smallest planktonic juvenile recorded is a specimen of 15 mm mantle length (Berry 1912). The specimen only has suckers on the arms, and the cirri had yet to develop.

Opisthoteuthids are not fished commercially, because of their rarity in catches and their semi-gelatinous body consistency.

The family occurs in tropical and temperate seas, from 50°N to 48°S (Voss, G.L. 1988b; Lu unpublished data). G.L. Voss (1988b) summarised the distributional data of all known species. Recent collections have extended the ranges of the two Australian endemic species. *Opisthoteuthis pluto* is known from continental slope waters from the Great Barrier Reef to Tasmania and the South Tasman Rise, and along the southern and western coasts of Australia to the north-western slope of Western Australia. *Opisthoteuthis persephone* occurs in the slope waters from New South Wales to Tasmania, and to the Great Australian Bight.

Suborder INCIRRATA

There are no cirri on the arms, fins are lacking, and the gladius is reduced or absent. The arms bear one to two rows of suckers. The mantle opening is usually medium-sized or broad, sometimes reduced to two slits on the sides of the head. The web usually does not extend to the tips of the arms. The radula is always present. The ink sac may be present or absent, and both oviducts are developed.

Family Bolitaenidae

Members of this pelagic octopod family have a gelatinous body, with arms shorter than the mantle. The arms bear a single row of suckers and are connected by a web of moderate depth. The mantle is oval-shaped with a wide mantle aperture (Fig. 13.32A). There is no hectocotylus in males.

The family Bolitaenidae was erected by Chun (1911) to include the genera *Eledonella* and *Bolitaena*. Robson (1932) re-established *Japetella* as a valid genus. Thore (1949) provided the first and only comprehensive taxonomic study of the family. Allan's (1945) record of *Eledonella sheardi* off the coast of New South Wales was the first reported occurrence of the family in Australia, and Brandt (1983) reported on *Japetella* species from the same region. The distribution of the latter is now known to include the Coral Sea (Lu & Phillips 1985).

Almost nothing is known about the biology of members of this family. The radular arrangement in *Japetella diaphana* species is illustrated in Figure 13.32B. Bolitaenids have been reported from the diets of *Alepisaurus ferox* captured in the south-western Pacific (Rancurel 1970). R.E. Young (1972b) reported capturing a mature female *Bolitaena microcotyla* brooding 12 larvae in a large chamber formed by the arms and web. R.E. Young believed the finding supported the likelihood that brooding is universal in pelagic incirrate octopods.

In the North Atlantic, *J. diaphana* was reported to exhibit ontogenetic descent: young smaller than 25 mm occurred at 100–330 m depth, and adults and subadults were found at depths of 600–3000 or 4000 m (Lu & Clarke 1975b; Roper & Young 1975; Hochberg *et al.* 1992). Animals of this family have no economic value, because of their rarity in catches, and the gelatinous nature of their bodies.

Members of this family occur in all major oceans in tropical to temperate waters. In Australian waters they have only been captured in the Coral Sea and Tasman Sea (Lu unpublished data). The absence of records from the coast of Western Australia probably reflects the paucity of sampling.

Family Amphitretidae

The sole member of the family, *Amphitretus pelagicus*, has a gelatinous body enveloped in a layer of thick gelatinous tissue. The long arms are connected by a deep web. The suckers lie in a single row. The mantle aperture is reduced to two small openings lateral to the funnel, which is fused to the mantle (Fig. 13.33A). The third right arm is hectocotylised with a long, narrow ligula and short calamus. The tubular eyes are directed dorsally. There is no shell vestige.

The family was erected by Hoyle (1886) for a specimen captured in the central Pacific Ocean off the Kermadec Islands. Thore (1949) reported and described specimens captured in the Pacific and Indian Oceans during the *Dana* Expedition. Allan (1945) reported the first Australian specimen captured off Tasmania, and Lu & Phillips (1985) extended the distributional range to include the Coral Sea and south-western Tasmania.

Almost nothing is known about the biology of *A. pelagicus*; the radular arrangement is illustrated in Figure 13.33B. Thore (1949) reported that mature ovarian eggs measure about 5 x 2 mm, and that young about 7 mm in total length had the same morphological characteristics as adults. Allan's (1945) specimen had a mantle length of 4 mm and total length of 12 mm. The species has been found in the diet of *Alepisaurus ferox* captured in the south-western Pacific (Rancurel 1970). *Amphitretus pelagicus* has no value for fisheries because of its gelatinous body and its rarity.

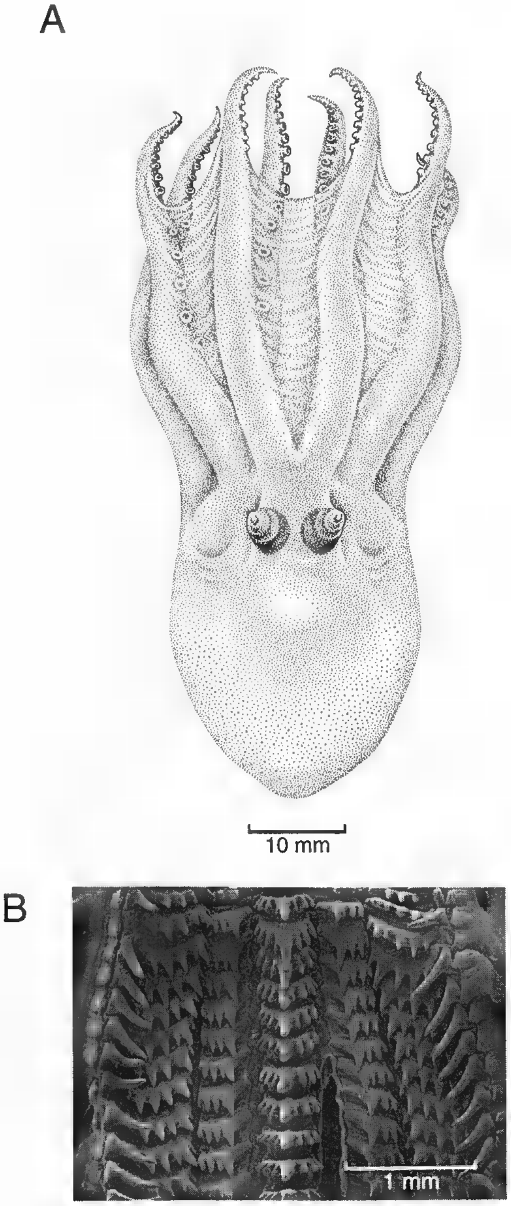

Figure 13.33 Family Amphitretidae. *Amphitretus pelagicus*, the pelagic octopod, has a gelatinous body and tubular, dorsally directed eyes: **A**, dorsal view; **B**, portion of radula, showing several transverse tooth rows.
[A, K. Hollis; B, C.C. Lu]

The species is widespread in tropical and temperate waters of all oceans. There is some evidence for ontogenetic descent, as juveniles smaller than 30 mm total length live in surface waters at depths less 150 m, and adults and subadults occur in the mesopelagic to bathypelagic zones from 150–2000 m (Hochberg *et al*. 1992).

Family Vitreledonellidae

The pelagic octopods of this monotypic family have a gelatinous sac-like body. The arms are of moderate length, about two to three times the body length in adults and are connected by webs extending to about half the arm length (Fig. 13.34A). The arm suckers are in a single row, widely spaced within the web and closely set outside the web. The mantle opening is single and wide. The tip of the third left arm is hectocotylised with a short ligula. The digestive gland is long and slender, and almost cigar-shaped. The gills consist of only the outer demibranchs, and the inner demibranchs are absent. The eyes are small, rectangular and directed laterally. The radular arrangement in *Vitreledonella richardi* is illustrated in Figure 13.34B.

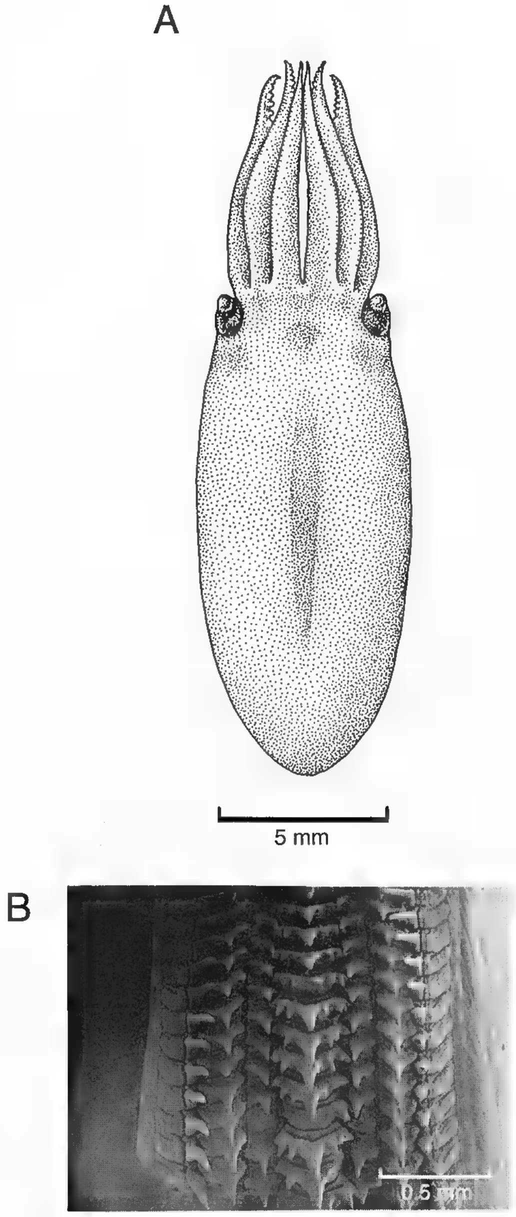

Figure 13.34 Family Vitreledonellidae. *Vitreledonella richardi* is recognised readily by its gelatinous body and the cigar-shaped digestive gland within: **A**, dorsal view; **B**, portion of radula, showing several transverse tooth rows.
[A, K. Hollis; B, C.C. Lu]

The sole member of this family, *Vitreledonella richardi*, was first described by Joubin in 1918 from specimens captured in the North Atlantic. Joubin (1918) also provided detailed anatomical studies of the animal. Subsequent reports on taxonomy, anatomy and distributions were provided by Robson (1930, 1932) and Thore (1949). Lu & Phillips (1985) first reported the occurrence of the species in Australian waters.

Very little is known of the biology of *V. richardi* and nothing has been published on the specimens from Australian waters. The species is eaten by lancetfishes *Alepisaurus ferox* in the south-western Pacific (Rancurel 1970). The mature eggs are unknown, and possibly the species is viviparous, as large number of larvae were taken with an adult female (Joubin 1937; Thore 1949). North Atlantic records suggest that this octopod extends its bathymetric limits as it grows (Lu & Clarke 1975b). No captures have been made by opening-closing nets in Australian waters.

The species has no commercial value because of its gelatinous body and its rarity in catches. It is found in tropical and subtropical waters of all oceans. Australian specimens were captured from the Coral Sea, the Tasman Sea off Sydney, and the Great Australian Bight (Lu unpublished data).

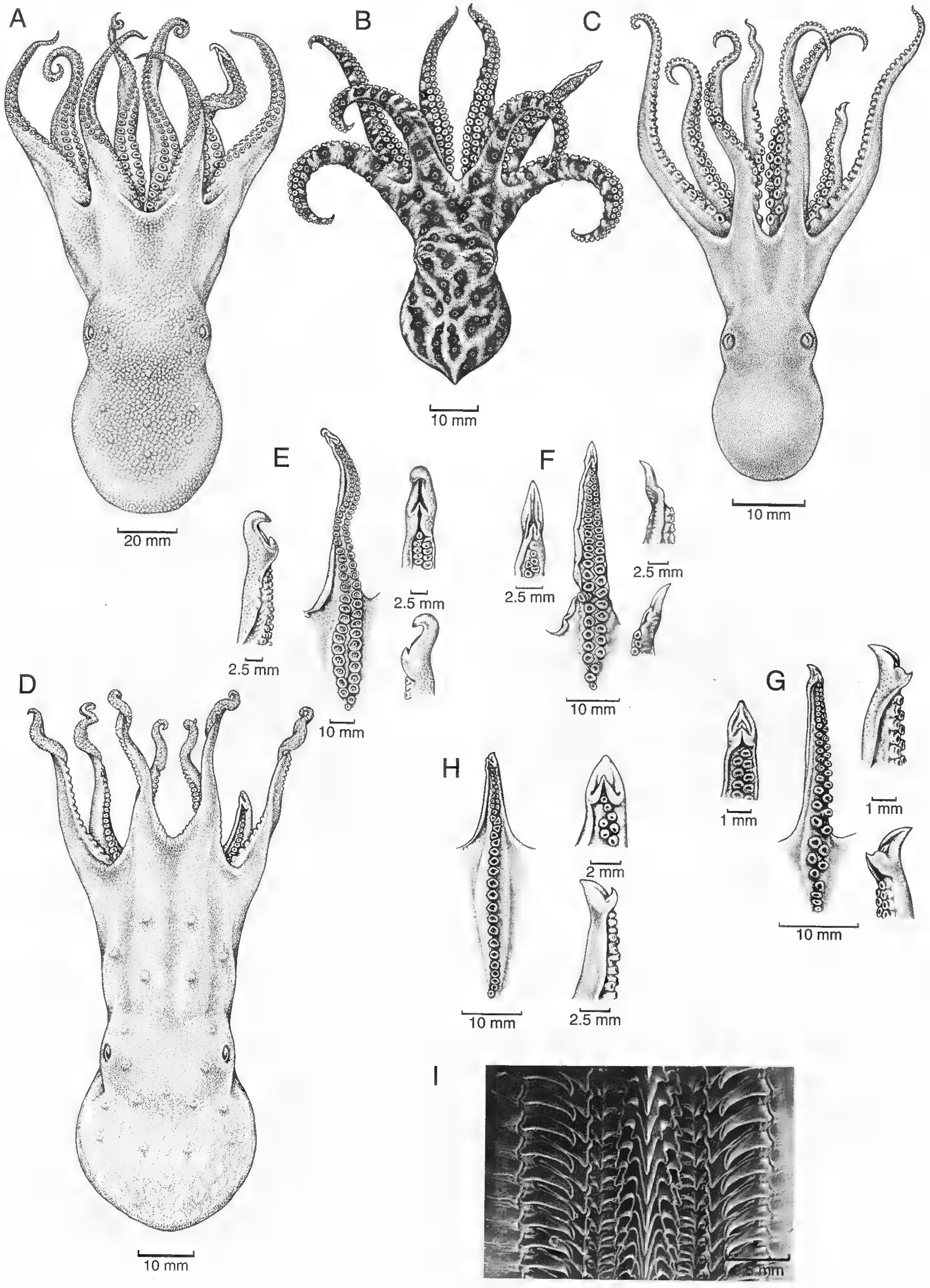

Figure 13.35 Family Octopodidae. **A–D**, external appearance, dorsal view. **E–H**, hectocotylised arms. **A**, **E**, *Octopus pallidus*. **B**, **F**, *Hapalochlaena maculosa*, the common blue-ringed octopus of southern Australia. **C**, **G**, *Grimpella thaumastocheir*, an uncommon species, endemic to South Australia. **D**, **H**, *Eledone palari*, a deep water species found on the continental slope around Australia. **I**, portion of radula of *Octopus ornatus*, showing several transverse tooth rows. [A–H, K. Hollis; I, C.C. Lu]

Family Octopodidae

The Octopodidae are a diverse group of benthic eight-armed cephalopods, including the inshore octopuses. The body consistency is predominantly muscular (Fig. 13.35A–D; Pls 19.2–20.6, 21.1). The arms are equipped with one or two rows of suckers, which lack chitinous rings, and the webs connecting the arms are shallow to moderately deep. The mantle aperture is not reduced and the mantle funnel locking apparatus is absent. Internally, the digestive gland is located anterior to the stomach and caecum. The crop may be present or absent and the ink sac may be present, vestigial or absent. Octopodids completely lack a shell or have degenerated shell vestiges, represented by a pair of cartilage-like stylets embedded in the mantle. This family is divided into the four subfamilies, Octopodinae, Eledoninae, Bathypolypodinae and Graneledoninae, and is distributed from the Arctic to the Antarctic and from the littoral to the abyssal zone.

Studies on the octopuses of the Mediterranean date from Aristotle's time. However, more critical work only began in the 18th century. Lamarck (1798) erected the genus *Octopus.* Blainville (1826) made the first attempt to treat the group comprehensively, and Orbigny (in Férussac & Orbigny 1835–1848) provided the first critical work on the group. Subsequently, many other workers added to our knowledge of the groups, as noted by Robson (1929), whose monograph on Octopodinae laid the foundation for future comparisons. The most recent comprehensive study is that of Hochberg *et al.* (1992), who provided an extensive identification guide to larval octopods and literature on the order Octopoda.

The first scientific report of Australian *Octopus* was by Lesueur (1821), who recorded two octopodids as *Sepia boscii* and *Sepia peronii.* Lacking descriptions, type material and illustrations, these names were considered *nomina nuda* by Robson (1929). Blainville's (1826) descriptions of *Octopus caerulescens, O. pustulosus* and *O. variolatus* based on Lesueur and Péron's specimens from Dorre Island, Western Australia, were too brief and no type material was mentioned. Therefore the taxa cannot be recognised and must be considered *nomina dubia.* Type material is extant for *O. superciliosus* from Westernport Bay, *O. cyanea* and *O. polyzenia* from northern Australia, and *O. tenebricus* from Queensland, described between 1832 and 1884 (Robson 1929).

Though extensive for the period, the lists of Cox (1882) and Brazier (1892) serve little useful purpose today, because of the poor state of taxonomic knowledge of the time. In 1928, Robson described *Grimpella* (Pl. 21.1), a new genus of Octopoda based on a single male specimen from Port Lincoln, South Australia, and placed it in the subfamily Bathypolypodinae. Little further progress was made for several decades on studies of the Australian octopodid fauna, until Lu & Phillips (1985) compiled a list of octopodids known from Australian waters, emphasising that it must be regarded as tentative, and that the taxonomy of Australian Octopodidae was desperately in need of detailed studies.

Tait (1982), Stranks (1988a, 1988b, 1990), Stranks & Lu (1991) and Stranks & Norman (1992) all contributed to the taxonomy of Octopodidae from southern Australia. In 1991, Lu & Stranks described a new species *Eledone palari* from the continental slope of Australia, which was the first record of the genus outside the Atlantic Ocean. Recently, Norman described many new octopodid taxa from the shallow water of the Great Barrier Reef and examined their classification and biogeography in a series of articles and a dissertation (Norman 1991, 1992a, 1992b, 1993a, 1993b, 1993c). He recognised 16 distinct species of which only two were named prior to his study (Norman 1992b).

Octopodids can move by jet propulsion (Pl. 19.3), although it is an inefficient technique for them because of their globular body-shape and lack of fins. Most frequently, they crawl across the sea floor, in the process using their suckers to anchor the body, a method for which the muscular arms are more suited.

Octopodids feed mainly on molluscs and crustaceans, particularly crabs, as well as polychaetes and fishes. Joll (1977) reported that *O. tetricus* of Western Australia consume about 200 000 pot-caught rock lobsters per year. Most of the Great Barrier Reef octopods prey on crustaceans, particularly brachyuran crabs (Norman 1992b). Some species prefer other prey, such as hermit crabs or bivalves. Several species are cannibalistic, including *Hapalochlaena fasciata* (as *H. maculosa*) (Tranter & Augustine 1973). Mangold (1983) and Boletzky & Hanlon (1983) reviewed the diets of octopods both in nature and in captivity.

Octopodids kill their prey using the secretion produced in the posterior salivary glands. The toxin appears to be able to penetrate a crab without any wound being made in the carapace of the victim (Ghiretti 1959, 1960). The toxin injected by the bite of the blue-ringed octopus (Fig. 13.35B; Pl. 19.2) is known to cause death in bitten victims (Flecker & Cotton 1955; Savage & Howden 1977; Sutherland 1983).

External digestion is involved in the feeding process. According to Bidder (1966) the body contents of crabs are reduced almost to soup by octopus salivary enzymes. The soup is then swallowed, leaving an almost intact exoskeleton.

Octopodids are capable also of boring holes in the shells of molluscs and eating the flesh. A portion of the radula of *Octopus ornatus* is illustrated in Figure 13.35I. Fujita (1916) and Arnold & Arnold (1969) described the hole-boring predation by *O. vulgaris* on pearl oysters and gastropods respectively. The salivary papilla of *Octopus* is covered by a thin cuticle forming very small teeth, and larger teeth are present at the extremity of the salivary duct which can be everted for drilling shells (Nixon 1980).

The right ventro-lateral arm of mature males is hectocotylised (Fig. 13.35E–H), except in *Scaeurgus* in which the hectocotylus is on the left. In some species, a few suckers at the bases of certain arm pairs are enlarged in mature males. Apart from these, there is little external sexual dimorphism in the Octopodidae.

During mating, a female typically submits to the demands of the male which will sit on or beside her, caressing her head and abdomen with his hectocotylised arm. The spermatophores are passed to the female from the hectocotylised arm inserted into her mantle cavity. Copulation may continue for an hour or more (Wells 1978).

Eggs produced by various octopod species fall into two categories. Boletzky (1977, 1978, 1987) proposed that egg size relative to mantle length of adults provides an indication of hatchling behaviour. Small eggs produce planktonic larvae while large eggs produce young which take up the adult benthic mode of life. Species which have small eggs usually produce large numbers of eggs (several thousand to 500 000) while species with large eggs produce few (50–1000). In Australia, species which produce small eggs include *O. tetricus* (Joll 1976), *H. lunulata* (Overath & Boletzky 1974), *O. maorum* and *O. warringa* (Stranks 1988b, 1990), *O. cyanea* (Pl. 19.5), *O. marginatus*, *O. mototi* and *O. ornatus* (Norman 1992b), and an unidentified *Octopus* species recorded as *O. cyanea* (Dew 1959b). The species known to have large eggs include *H. fasciata* (as *H. maculosa*, Dew 1959b), *H. maculosa*, *O. berrima*, *O. pallidus*, *O. superciliosus*, *O. kaurna* and *O. bunurong* from southern Australia (Stranks 1988b, 1990; Stranks & Lu 1991), *O. alpheus*, *O. polyzenia*, *O. dierythraeus*, *O. graptus*, *Ameloctopus litoralis* (Norman 1992b) and *Eledone palari* (Lu & Stranks 1991).

Octopods are semelparous. The animals die after a single reproductive season. Van Heukelem (1973) reported that female *O. cyanea* die after the eggs hatch, while the males may mate several times with several different females but do not outlive females. In Hawaiian waters, this species spawns throughout the year. Van Heukelem (1973) believed the time of spawning is determined by the age of the female.

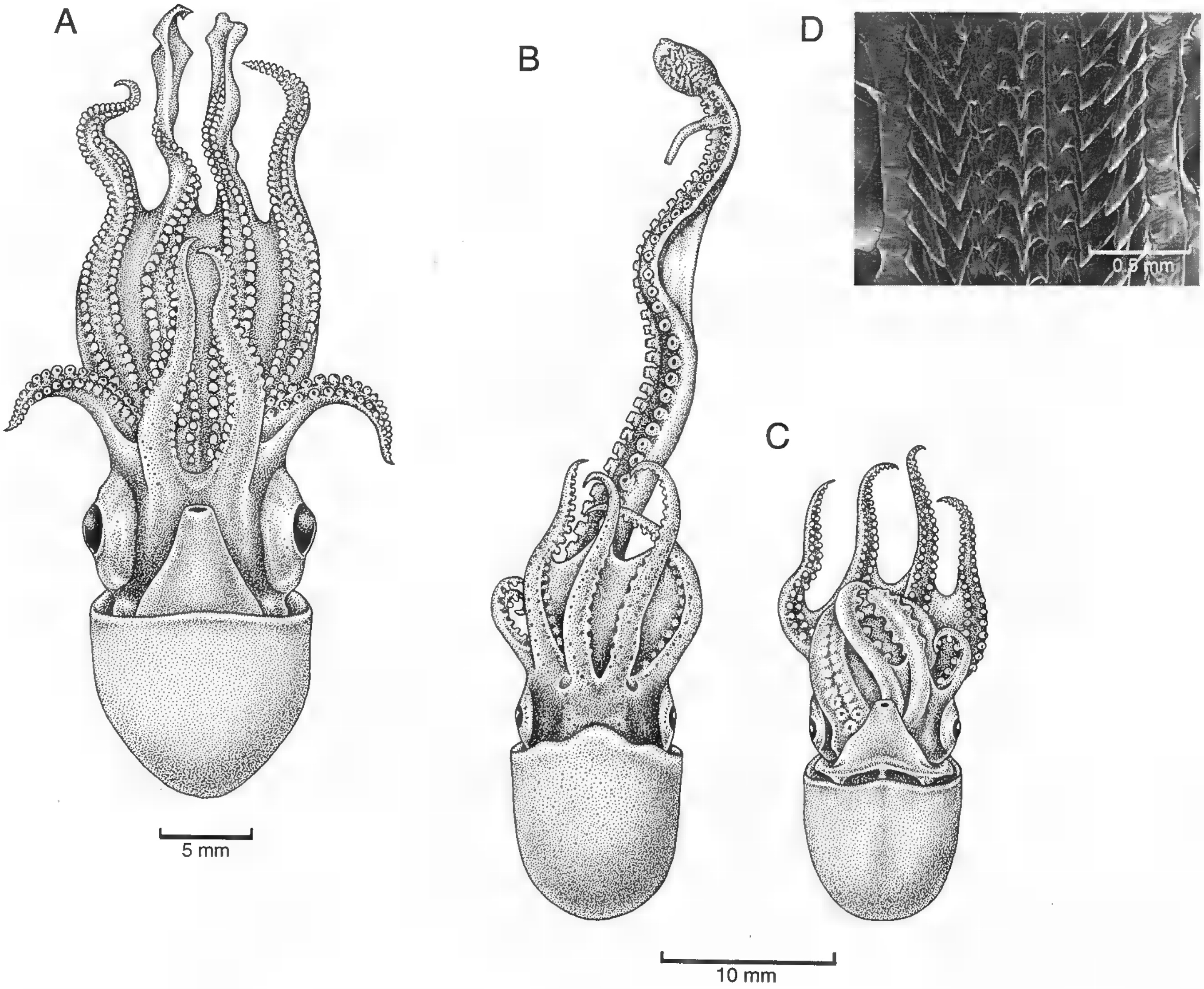

Figure 13.36 Family Tremoctopodidae. *Tremoctopus violaceus* exhibits enormous sexual dimorphism in size, the male grows to about 40 mm total length, whereas the female may attain 2 m in length: **A**, female, ventral view; **B**, **C**, males, in which the hectocotylised arm is extended and retracted, respectively; **D**, portion of radula, showing several transverse tooth rows. [A–C, K. Hollis; D, C.C. Lu]

Octopuses have many predators. Clarke (1986) listed eight cetacean species known to eat octopodids, from information on stomach contents. Gales *et al.* (1992) found *O. maorum* among the stomach contents of pilot whales, and *O. pallidus* and *O. berrima* in the diet of bottlenose dolphins from Tasmania. *Octopus maorum*, *O. berrima*, *O. superciliosus* and *O. pallidus* have been found among the stomach contents of Australian fur seals from Tasmania (Gales *et al.* 1994). Octopodids are also eaten by hammerhead sharks off eastern Australia (Dunning *et al.* 1993).

Octopuses have been exploited for food for well over 2000 years, chiefly in Asia and southern Europe. In 1981 the octopus catch worldwide was 190 000 tonnes, representing 14.6% of the world cephalopod fisheries in that year (Roper *et al.* 1984). Australia has only a small scale fishery. In 1981, the catch of *Octopus* species from New South Wales was about 160 tonnes (Winstanley *et al.* 1983). Joll (1977) estimated that rock lobster fisherman caught about 138–247 tonnes of *O. tetricus* annually. Kimura (1980) estimated that 30 000 tonnes could be caught annually between Fremantle and north of Geraldton. *Octopus tetricus* is responsible for the destruction of over $390 000 worth of rock lobsters per season in Western Australia (Joll 1977).

The Octopodidae have a wide distribution from the Arctic to the Antarctic. As the taxonomy of the family, including that of Australian representatives, is in a poor state, discussion of biogeography is limited.

Stranks (1988b, 1990) and Stranks & Norman (1992) established that nine species of shallow-water octopods occur in southern Australia. Seven of these species (*H. maculosa*, *O. berrima*, *O. pallidus*, *O. superciliosus*, *O. kauma*, *O. bunurong* and *Grimpella thaumastocheir*) are endemic to the region. All have large eggs and benthic young with limited vagility. The remaining two species (*Octopus maorum* and *O. warringa*), known also from New Zealand, have small eggs with planktonic larvae which disperse by ocean currents. The deep water of the Tasman Sea clearly presents an effective barrier for dispersal of the shallow-water animals with benthic hatchlings.

Norman (1992b) divided the inshore octopuses of the Great Barrier Reef into four categories: an Indo-West Pacific element, the northern Australian endemics, the north-eastern Australian endemics, and localised endemics. He believed that distribution is influenced by several biotic and ecological factors, such as egg size and hatchling behaviour, habitat specificity and continuity and currents. Historical factors, such as changes in sea levels, sea temperatures, and the position of thermal boundaries between tropical and temperate waters, may also have contributed to the patterns of distribution.

The studies of Stranks (1988b) and Norman (1992b) indicate that octopodid species diversity is high in Australian waters and that a large number of these species are endemic to Australia.

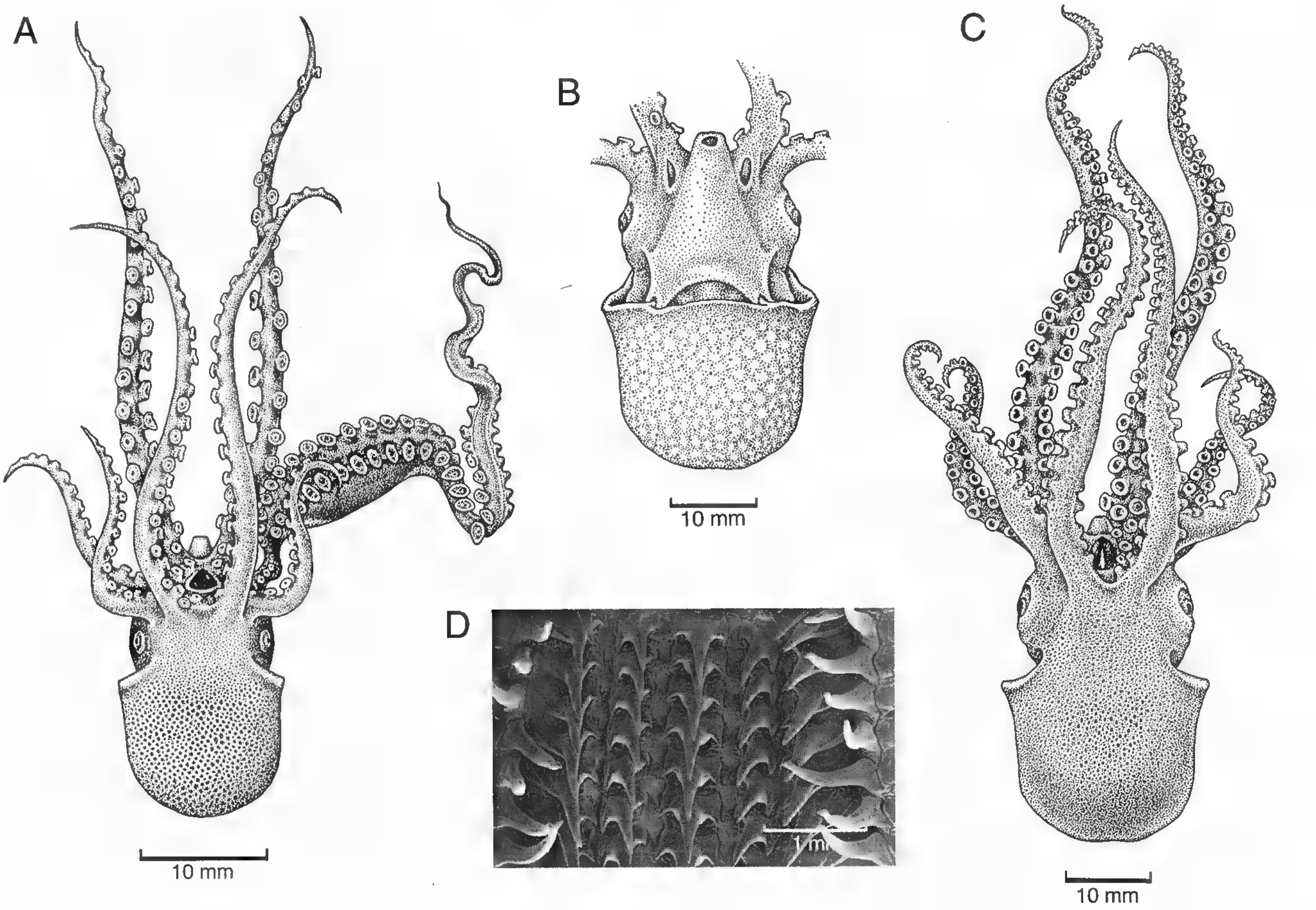

Figure 13.37 Family Ocythoidae. The pelagic octopod *Ocythoe tuberculata*, is strongly sexually dimorphic in size and form: **A**, male, dorsal view, with the hectocotylised arm extended; **B**, mantle of female, ventral view, showing reticulate sculpture of ridges and tubercles, and water pores at the base of the ventral arms; **C**, female, dorsal view; **D**, portion of radula, showing several transverse tooth rows. [A–C, K. Hollis; D, C.C. Lu]

Family Tremoctopodidae

The pelagic octopods of the family Tremoctopodidae exhibit tremendous size and sexual dimorphism (Fig. 13.36A–C). Female size greatly exceeds that of males and may reach 2 m in total length. The body is muscular and firm. The two dorsal pairs of arms are longer than the two ventral pairs. The web is deepest between the dorsal arm pairs, and very shallow to almost absent ventrally. A dorsal and a ventral pair of cephalic water pores are located on the head. The arm suckers form two rows.

The right ventro-lateral arm of mature males is modified extensively by hectocotylisation (Fig. 13.36B). The basal and middle parts of the hectocotylus bear two rows of small suckers, flanked by a border of small cirri-like papillae in the basal part. The distal part of the hectocotylus is modified into a seminal sac, which contains the sole spermatophore and a penial filament. The hectocotylus develops in an enclosed sac.

The family was established by Tryon (1879) based on the genus *Tremoctopus* of Delle Chiaje in 1830. Robson (1932) revised the genus. More recently, Thomas (1977) reviewed the systematics, distribution and biology of *Tremoctopus*. Lu & Phillips (1985) recorded *Tremoctopus violaceus* from the coast of New South Wales, the first Australian record of the family. Subsequent records are from Queensland, South Australia and Western Australia (Zeidler 1989).

Thomas (1977) described the reproductive system of *Tremoctopus violaceus* in detail. There is no penis. Needham's sac is blind and the entire structure with the enclosed spermatophore is transferred to the spermatophore reservoir at the tip of the hectocotylised arm. Only a single spermatophore is produced in the lifetime of the male. The spermatophore reservoir connects with the penial filament by means of a duct that passes into the filament. *Tremoctopus* autotomises its hectocotylised arm during mating. Sexually mature females are frequently found with a detached arm lying in the mantle cavity, with the 'penis' missing and the spermatophore reservoir burst.

The females lay over 100 000 small eggs, cemented together by the egg stalks to form root-like structures. The rods are held by the suckers of the dorsal arms where the eggs are brooded (Naef 1923; Hamabe 1973b). As a defence mechanism, young *Tremoctopus* usually carry pieces of tentacles from Portuguese-Man-of-War, *Physalia* sp., in the dorsal and dorso-lateral arms and the suckers are filled with batteries of *Physalia* nematocysts (Jones 1963).

The food of *Tremoctopus* species is varied. Orbigny (1840, in Férussac & Orbigny 1835–1848) reported finding abundant shells of pteropod molluscs in the guts of young animals, and adult females feed chiefly on small fishes (Thomas 1977). Zeidler (1989) reported fish scales, cephalopod flesh, green algae, brown algae and polychaete jaws in the guts of Australian specimens. The radular arrangement in *Tremoctopus violaceus* species is illustrated in Figure 13.36D.

Tremoctopids are components of the diet of *Alepisaurus ferox* captured in the south-western Pacific (Rancurel 1970) and of the scalloped hammerhead shark, *Sphyraena zygaena* off eastern Australia (Dunning *et al.* 1993).

Tremoctopus live epipelagically (Clarke & Lu 1975; Lu & Clarke 1975b; Roper & Young 1975), in tropical, subtropical and temperate waters. According to Thomas (1977), the family

Tremoctopodidae comprises two species, one of which has two subspecies. *Tremoctopus gelatus* is found from off the eastern coast of Florida, Hawaiian Islands and the Indian Ocean. *T. v. violaceus* occurs in the Atlantic Ocean, the Mediterranean Sea, Gulf of Mexico and the Caribbean Sea. *T. v. gracilis* is found in the Pacific and Indian Oceans.

Family Ocythoidae

The single species in the family Ocythoidae is pelagic and exhibits extreme sexual dimorphism in size (Fig. 13.37A–C). The females attain a size of up to 310 mm in mantle length, while the males are dwarf and probably do not exceed 30 mm mantle length (Roper & Sweeney 1976). All mature males from Australian waters are smaller than 20 mm mantle length (Lu unpublished data). Males often live in the test of pelagic salps.

The body is round or oval. The arms are long, with no web between them, and bear two rows of suckers. The long funnel has a well-developed, complex funnel locking apparatus. One pair of cephalic water pores is located ventrally on the head at the base of the ventral arms. The ventral mantle surface of the adult females is sculpted in a reticulate pattern of ridges and tubercles (Fig. 13.37B). In males, hectocotylisation affects the entire third right arm, develops in a pouch and is detachable.

Ocythoe tuberculata was first described by Rafinesque in 1814 from a specimen captured in the Mediterranean Sea. Gray (1849) established the family Ocythoidae to cover *Ocythoe* and *Argonauta*. Jatta (1896) also placed the genus *Ocythoe* in the family Argonautidae, a usage followed by many workers. Robson (1932) was the first author to reinstate the name Ocythoidae. Roper & Sweeney (1976) reviewed the literature on the species and described the first specimen captured in Australian waters.

The hectocotylus containing the spermatophores is detached during mating and remains in the mantle cavity of the female. *Ocythoe tuberculata* produces a large number of eggs; the large female from South Australia contained about 104 000 eggs (Roper & Sweeney 1976). The species is viviparous, and developing embryos of various stages are found in the expanded oviducts (Jatta 1896; Naef 1923).

Ocythoe tuberculata has been observed living in the chamber of the salps, *Salpa tilesii* and *Tethys vagina* (Jatta 1896; Hardwick 1970). The association is reversible in that the octopod may leave the test and re-enter it.

The species lives in the epipelagic zone from the surface to about 200 m. It is a dietary component of lancetfishes *Alepisaurus borealis* and *A. ferox*, tunas, *Thunnus alalunga*, *T. thunnus* and *Germon germon*, and Risso's dolphins, *Grampus griseus* (Joubin 1900; Bouxin & Legendre 1936; Berry 1955; Rees & Maul 1956; Rancurel 1970; Iverson 1971; Pinkas 1971; Dunning *et al.* 1993). The radular arrangement in *Ocythoe tuberculata* is illustrated in Figure 13.37D, B.

At present, there is no fisheries interest in the species. The species is palatable – Rafinesque reported eating his type specimen (see Roper & Sweeney 1976).

Ocythoe tuberculata is recorded from the subtropical and temperate waters of the Pacific and Atlantic Oceans, but is not known from the Indian Ocean or from tropical waters between 20°N and 20°S (Roper & Sweeney 1976). In Australian waters, the species has been captured from the open waters of New South Wales to southern Tasmania and the Great Australian Bight, Western Australia (Lu & Phillips 1985; Lu unpublished data).

Family Argonautidae

Argonautids exhibit extreme sexual dimorphism in size. The females are large, reaching over 100 mm mantle length, while the males are minute, up to 15 mm mantle length, depending on the species (Fig. 13.38A–D).

The mantle is ovoid in females and round or conical in shape in males. The head of the female is small and the eyes are prominent. In males, the head is proportionally larger and the eyes are large. The long funnel has a knob-like funnel locking cartilage. The mantle surface is smooth.

The web connecting the arms is weakly developed. Water pores are absent. The arms bear two rows of small suckers. The dorsal arms of females are equipped with very broad, glandular membranes which secrete and hold the delicate shell (egg case) (Pl. 21.3). The third left arm of the males is hectocotylised and detachable. The hectocotylus consists of three parts; a basal spermatophoric reservoir, a central section bearing suckers, and distally, a long, lash-like 'penis'.

The shell of *Argonauta* is a is a single-chambered egg case with a flat keel fringed by two tubercles. It is a thin, laterally compressed calcareous structure (Fig. 13.38E–H). The lateral sides of the shell are ribbed with the centre pressed in, or bent outwards into a prominent 'ear' or 'horn'. The shell provides protection and flotation and is a site of attachment for the eggs (Young, J.Z. 1960).

Records and studies of *Argonauta* date back several hundred years. Many names, records and descriptions exist in an extensive bibliography ranging from sale-catalogues of curios to serious zoological literature (see Robson 1932). Dell (1952) studied the shells of four *Argonauta* species from New Zealand waters and described the anatomy of *A. nodosa*. Nesis (1977) reported on the biology of *A. boettgeri* and *A. hians*, based on specimens captured in the western Pacific and the seas of the East Indian Archipelago.

The study of *Argonauta* also had an impact on the whole science of teuthology. In 1827 Stefano delle Chiaje discovered a small body attached to a female argonautid. He concluded that it was a parasitic worm. In 1829 Baron George Cuvier studied more specimens, concluded that they belonged to a new genus of parasites and named the genus *Hectocotylus*, meaning 'the worm of a hundred suckers' because the 'worms' resembled a cephalopod arm, bearing about 100 suckers. In 1845 and 1846, Kölliker pointed out that the skin of the 'worm' contained chromatophores, and the suckers were similar to those on the female argonautid. He found also that the 'worm' had a small cavity in which he found sperm cells similar to those of a cephalopod. He concluded that the 'worm' was the male argonautid which had entered the female to fertilise the eggs. His published description, in 1849, of this 'male argonaut' included the digestive, circulatory and respiratory organs! The true male argonautid was described by Müller in 1853 and Kölliker admitted his error. The name 'hectocotylus' continued to be applied to the specialised, modified arm for transferring spermatophores in many male cephalopods (see Lane 1960 pp. 116–118 for detailed account).

McCoy (1882) described *Argonauta oryzata* and illustrated a specimen found at Brighton, Victoria. McCoy considered *Argonauta nodosa* to be a junior synonym of *A. oryzata*. Brazier (1892) in his catalogue of the Australian Museum collection listed *A. argo*, *A. nodosa*, *A. hians* and *A. boettgeri* from Australian waters. Lu & Phillips (1985) updated the distributional records and confirmed the presence of *A. argo*, *A. nodosa* (Fig. 13.38A, B) and *A. hians* (Fig. 13.38C, D) in Australian waters. The presence of *A. boettgeri* remains to be confirmed.

Observations of live female *A. argo* in an aquarium showed that the web, or membrane on the dorsal arm of the female, besides secreting the shell, acts as a receptor in feeding. When disturbed, red chromatophores of the upper part of the web, arms, eyes, head, funnel and mantle expand, providing a startling colour over a blue and white background (Young, J.Z. 1960). A second colour pattern is produced as a sudden flash of white as the web is withdrawn.

Argonautids feed primarily during the day (Nesis 1977). Okutani (1960) reported that off Japan, female *A. boettgeri* prey on the pteropod, *Cavolinia tridentata*. Nesis (1977) also found that pelagic molluscs, such as heteropods and pteropods are dominant in the prey of western Pacific *A. boettgeri*, and other octopodids

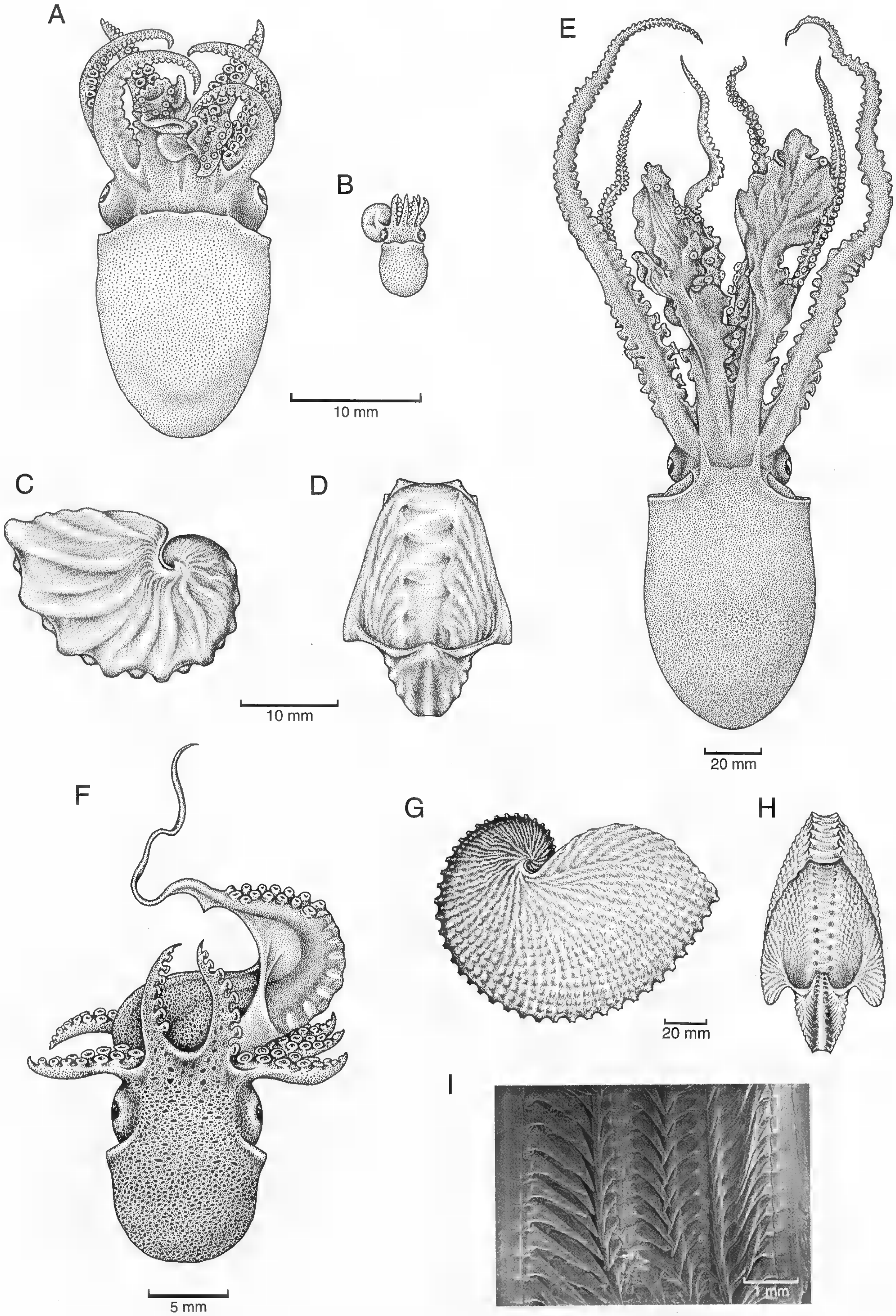

Figure 13.38 Family Argonautidae. Paper nautiluses are common in surface waters of the open ocean; all species show extreme sexual dimorphism. **A–D**, *Argonauta hians*: **A**, female, dorsal view; **B**, male, dorsal view; **C**, egg case, lateral view; **D**, egg case, anterior view. **E–I**, *Argonauta nodosa*: **E**, female, dorsal view, showing expanded dorsal arms; **F**, male, dorsal view; **G**, egg case, lateral view; **H**, egg case, anterior view; **I**, portion of radula, showing several transverse tooth rows.
[A–H, K. Hollis; I, C.C. Lu]

are found less frequently. Remains of heteropods were also found in the stomachs of *A. hians* (Nesis 1977). There are no published accounts on the prey of argonautids from Australian waters. The arrangement of the radula in *Argonauta nodosa* is illustrated in Figure 13.38I.

Argonautids have many predators. Okutani & Suzuki (1975) reported *A. boettgeri* among the stomach contents of a yellowfin tuna from the Indian Ocean. Rancurel (1970) reported finding *A. argo*, *A. hians* and *A. nodosa* in the stomach contents of *Alepisaurus ferox* from the south-western Pacific. *Argonauta nodosa* has been found among stomach contents of Australian fur seals, *Arctocephalus pusillus doriferus* in the Bass Strait and southern Tasmania (Gales *et al.* 1994) and is an important part of the diet of blue sharks, *Prionace glauca*, off eastern Australia (Dunning *et al.* 1993).

Males of *A. boettgeri* and *A. hians* mature at about 7 mm mantle length, presumably the maximum size attained (Nesis 1977). Males of *A. argo* mature at 8 mm mantle length (Naef 1923). No data are available for male *A. nodosa*

Mating occurs shortly before the eggs are laid. Female *A. boettgeri* 11–13 mm mantle length already have hectocotyli in the mantle cavity. Egg laying begins when females reach a size of 14–15 mm mantle length. Female *A. hians*, of 18–20 mm mantle length, have laid eggs. The size at which egg laying commences differs in different regions of the world ocean (Nesis 1977). Female *A. argo* mature at about double the size of *A. boettgeri* and *Argonauta hians* (Naef 1923). No information is available on the maturation of *A. nodosa.*

The eggs are laid in clusters of many small eggs connected by a stalk. They are attached to the apex of the shell, and occupy its posterior part. Clusters of eggs of different developmental stages are found in the shell. The egg clusters of *A. boettgeri* can be separated clearly into three parts, each with a cohort of eggs at the same developmental stage (Nesis 1977). The proximal part lying closest to the aperture of the shell contains eggs at an early stage of development. The central part contains eggs at stages from the appearance of the red eye pigment to the beginning of chromatophore formation. The part most distal to the aperture of the shell contains eggs with embryos that are fully formed and ready to hatch. The chromatophores, ink sac and dark coloured eyes are fully formed. Reid (1989) found similar development in the egg mass in *A. nodosa* from southern Australia (Pls 21.4, 21.5).

Hatching takes place at night; newly hatched larvae can be caught in plankton samples at night. Egg laying probably also occurs at night. Nesis (1977) suggested that three stages of development in the egg clusters represented the products of three successive nights. Egg incubation lasts three days at temperatures of 26–29°C.

Female argonautids begin to reproduce when young, and continue to grow and reproduce for a long time. Shells of a large size range have been collected. Those of recently mature females contain only a small cluster of eggs at the first stage of development. Shells of large females generally contain eggs at all three stages.

The eggs of *A. boettgeri* measured 0.85–0.9 mm, 0.9–1.0 mm, and 1.0–1.1 mm in the first to third stages of development respectively. The hatchlings are 0.85–1.00 mm mantle length and have a total length of 1.0–1.3 mm. A female of 35 mm mantle length had about 40 000 eggs in her shell. The eggs of *A. hians* are of similar sizes (Nesis 1977).

Both *A. hians* and *A. boettgeri* are known to cling to any object floating on the surface of the sea, including other argonautids (Nesis 1977). A chain of argonautids clinging to each other may occur, perhaps involving 20 to 30 animals of similar size, in which the first female usually holds onto some other object while other females in the chain hold onto the preceding one on the ventral part of the shell (Voss, G.L. & Williamson 1971; Nesis 1977).

Argonautids are epipelagic, living predominantly in the upper 100 m (Lu & Clarke 1975b; Roper & Young 1975). According to Nesis (1977), mature animals are not restricted to the surface layer but live at all epipelagic depths. *Argonauta argo* and *A. hians* are cosmopolitan in tropical to subtropical oceans, whereas *A. boettgeri* occurs only in the tropical and subtropical waters of the Indo-West Pacific Ocean. *Argonauta nodosa* is known only from the Southern Hemisphere in the Indian and Pacific Oceans.

In Australia, *A. nodosa* is known from southern Australia from New South Wales to Tasmania and South Australia. *Argonauta argo* is found in warmer waters off Western Australia and north of Gabo Island, Victoria. *Argonauta hians* is known from the North West Shelf of Western Australia.

REFERENCE MATERIAL

Material illustrated in Figs 13.1 to 13.38 is held in the Museum of Victoria (NMV), under the following registration numbers: Fig. 13.1A – F54962; Fig. 13.1B – F54990; Fig. 13.2A,B – F57140; Fig. 13.2C – F30865; Fig. 13.2D – F55045; Fig. 13.2E,F – F71713; Fig. 13.3A – F55045; Fig. 13.3B – F30865; Fig. 13.3C – F57140; Fig. 13.3D – F71713; Fig. 13.3E – F74342; Fig. 13.4A – F71696; Fig. 13.4B – F31565; Fig. 13.4C – F77332; Fig. 13.5 – F31565; Fig. 13.6A – F71716; Fig. 13.6B – F51813; Fig. 13.6C – F71711; Fig. 13.6D – F71714; Fig. 13.6E – F68225; Fig. 13.6F – F68225; Fig. 13.7A,F – F52104; Fig. 13.7B, G – F51813; Fig. 13.7C,H – F71714; Fig. 13.7D,I – F68225; Fig. 13.7E – F71711; Fig. 13.7J – F71706; Fig. 13.7K – F78302; Fig. 13.8 – F51444; Fig. 13.8F – F78302; Fig. 13.9A,B – F31788; Fig. 13.9C–E – F31130; Fig. 13.9F–H – F31555; Fig. 13.9I–K – F30876; Fig. 13.9L – F31611 13.10A – F71726; Fig. 13.10B – F52304; Fig. 13.10C – F30244; Fig. 13.11A – F71700; Fig. 13.11B – F71727; Fig. 13.11C – F50872; Fig. 13.11D – F50771; Fig. 13.11E – F71698; Fig. 13.11F – F71700; Fig. 13.12A – F52397; Fig. 13.12B – F50771; Fig. 13.12C – F77987; Fig. 13.13A – F51082; Fig. 13.13B – F74469; Fig. 13.14A – F71694; Fig. 13.14B – F71690; Fig. 13.14C – F74470; Fig. 13.15A – F71693; Fig. 13.15B – F51039; Fig. 13.16A,B – F51099; Fig. 13.16C,D – F53159; Fig. 13.16E – F74344; Fig. 13.17A – F57913; Fig. 13.17B – F74471; Fig. 13.18A – F51120; Fig. 13.18B – F51111; Fig. 13.18C – F74472; Fig. 13.19A,B – F51179; Fig. 13.19C – F66635; Fig. 13.20A – F71720; Fig. 13.20B – F74473; Fig. 13.21A – F71695; Fig. 13.21B – F52128; Fig. 13.221,G – F71688; Fig. 13.22B,H – F51649; Fig. 13.22C,I – F51657; Fig. 13.22D,J – F50542; Fig. 13.22E,K – F30877; Fig. 13.22F,L – F31125; 13.22V,L – F74343; Fig. 13.23A,B – F71687; Fig. 13.23C – F66206; Fig. 13.24A,B – F71718; Fig. 13.24C – F54826; Fig. 13.25A – F71689; Fig. 13.25C – F74475; Fig. 13.26A – F71725; Fig. 13.26B – F74474; Fig. 13.27A – F71697; Fig. 13.28A,B – F71691; Fig. 13.28C,D – F71723; Fig. 13.28E – F71692; Fig. 13.28F – F53547; Fig. 13.28G – F71703; Fig. 13.28H – F71709; Fig. 13.28I – F71724; Fig. 13.28J – F71710; Fig. 13.28K – F51904; Fig. 13.28L – F71702; Fig. 13.30A – F71704; Fig. 13.30B – F74478; Fig. 13.31 – F30924; Fig. 13.32A,B – F71721; Fig. 13.33A – F52114; Fig. 13.33B – F52351; Fig. 13.34A – F71730; Fig. 13.35A,E – F52090; Fig. 13.35B,F – F71701; Fig. 13.35C,G – F53145; Fig. 13.35D,E – F71715; 13.35I – F57918; Fig. 13.36A – F53415; Fig. 13.36B,C – F30250; Fig. 13.36D – F74479; Fig. 13.37A – F71729; Fig. 13.37B,C – F71728; 13.37D – F74476; Fig. 13.38A – E,F – F58721; Fig. 13.38B – F71699; Fig. 13.38C,D,G,H – F71705; 13.38I – F74477.

Material from other sources: Fig. 13.15C – USNM R/V Walter Herwig, Stn 451-III-71; Fig. 13.27B – USNM P/V Anton Dohrn Stn 234-IV-79.

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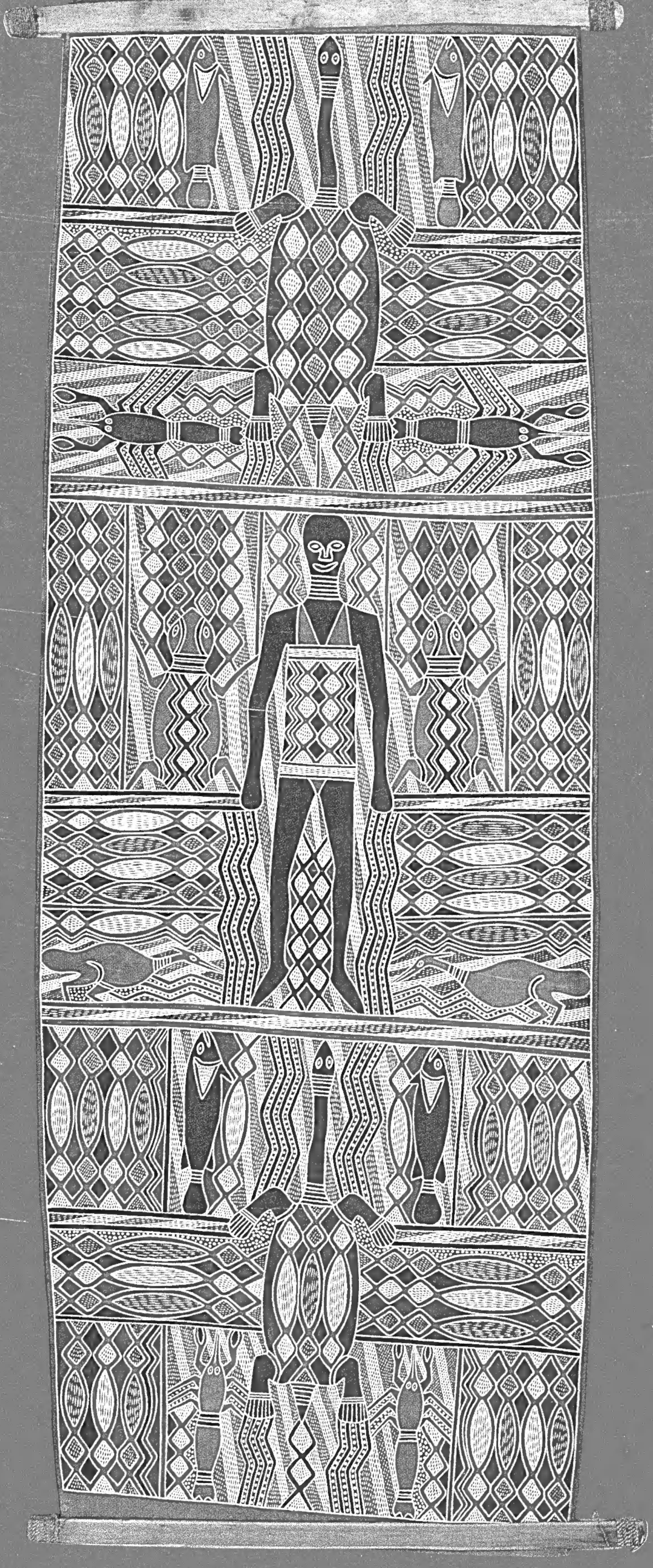

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