PULMONATA

— CHAPTER 17 —

DEFINITION AND GENERAL DESCRIPTION

The Pulmonata is one of the three subclasses into which the class Gastropoda has been subdivided: the other two are the Prosobranchia and the Opisthobranchia. Pulmonates are molluscs that use a lung as the respiratory surface. The name Pulmonata is used here to describe this group of gastropods without necessarily retaining the taxonomic meaning of the grouping. Pulmonates were the subject of a two volume treatise some years ago, well introduced by Fretter (1975). The group can be divided into three major subunits, the orders Systellommatophora, Basommatophora and Eupulmonata (Fig. 17.1); the last consists mainly of the suborder Stylommatophora plus a few minor groups. The Pulmonata is now considered to be a polyphyletic grouping (Solem 1978a; Haszprunar & Huber 1990; Bieler 1992).

Pulmonates are essentially land and freshwater molluscs, but representatives of a few genera, recognised as amongst the most primitive, live intertidally. Land and freshwater groups also occur among some prosobranch groups (some neritopsines and caenogastropods), however, there are no terrestrial opisthobranchs and only one or two opisthobranch species might be termed freshwater taxa. The characters differentiating pulmonates from other gastropods are largely associated with the change from marine to non-marine habitats. The comparatively benign marine environment provides an osmotically stable medium for reproduction, respiration, feeding and body support, in contrast to freshwater and terrestrial habitats. Rather than invoking a serial aquatic route for terrestrial invasion from salt to freshwater, then to land, it is now thought that most pulmonates were derived from marine taxa via salt marsh to terrestrial forms. The present day freshwater fauna thus represents a secondary invasion of the aquatic environment. This better explains similarities in the general organisation of the Basommatophora and Stylommatophora, as well as their mutual differences from other gastropods.

Pulmonates have the general gastropod body form of head, foot and visceral mass. The basic arrangement of the mantle cavity and the digestive and reproductive systems is shown in Figure 17.2. A spirally coiled shell is usually present though it may be limpet-shaped, reduced, wholly enveloped in the mantle, or lost totally. An operculum is lacking in adults except in the Amphibolidae and Glacidorbidae. The mantle cavity lacks a ctenidium, but secondary gills or pseudobranchs may be developed in some marine and freshwater forms. The opening to the mantle cavity is reduced, by fusion of the mantle border with the neck, to a narrow, contractile opening forming a respiratory pore or pneumostome on the right side of the animal. The internal dorsal wall of the mantle cavity is highly vascularised, permitting respiratory exchange. This arrangement is often referred to as a 'lung' or the pulmonary cavity. The kidney opens into the pulmonary cavity via a simple papilla in primitive forms whereas in more advanced forms it voids via a ureter terminating near the pneumostome. Ordinarily the anus is also situated near the pneumostome.

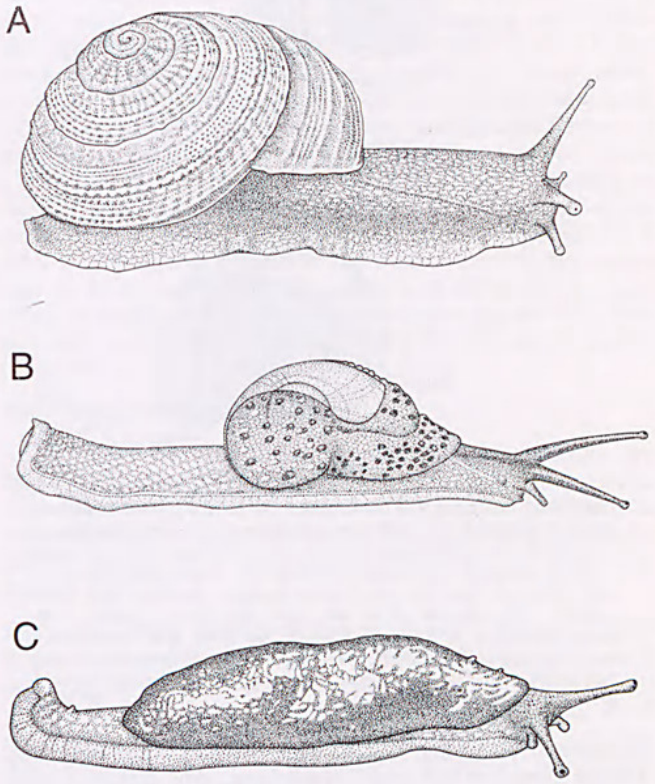

Figure 17.1 Representative eupulmonatan pulmonates. **A**, *Angolypta launcestonensis* (Caryodidae), found in the litter of wet forests in north-eastern Tasmania. **B**, *Fastosarion aquila* (Helicarionidae), a semi-slug from the wet forests of coastal northern New South Wales and south-eastern Queensland: note the mantle lobes over the shell. **C**, *Cystopelta* sp., from Mt Superbus in south-eastern Queensland, one of a small number of slugs of the endemic family Cystopeltidae. **mal**, mantle lobe; **sh**, shell. (A, after photograph by R.C. Kershaw; B, C, after photographs by Queensland Museum) [C. Eadie]

The buccal mass bears a single, dorsal jaw consisting of fine rods or platelets, except in some carnivorous forms in which the jaw has been lost. The radula is usually oblong, typically with straight rows of many small teeth, although this varies greatly, particularly in carnivorous forms. The nervous system is usually euthyneurous, and shows a shortening of the visceral portions and the formation of a circumoesophageal ring composed of five ganglia. The structure of the nervous system and its significance in elucidating the phylogeny of the pulmonates are discussed by Van Mol (1967), Haszprunar (1988), Tillier (1989) and Haszprunar & Huber (1990).

Pulmonates are usually simultaneous hermaphrodites with various levels of fusion of the male and female ducts. Fertilisation is internal and for this a variety of ancillary copulatory structures have developed. Specialised glandular structures are also present to form the egg and facilitate the passage, transfer and receipt of sperm, which are often contained in a spermatophore. Most groups are oviparous and have complex egg formation, including

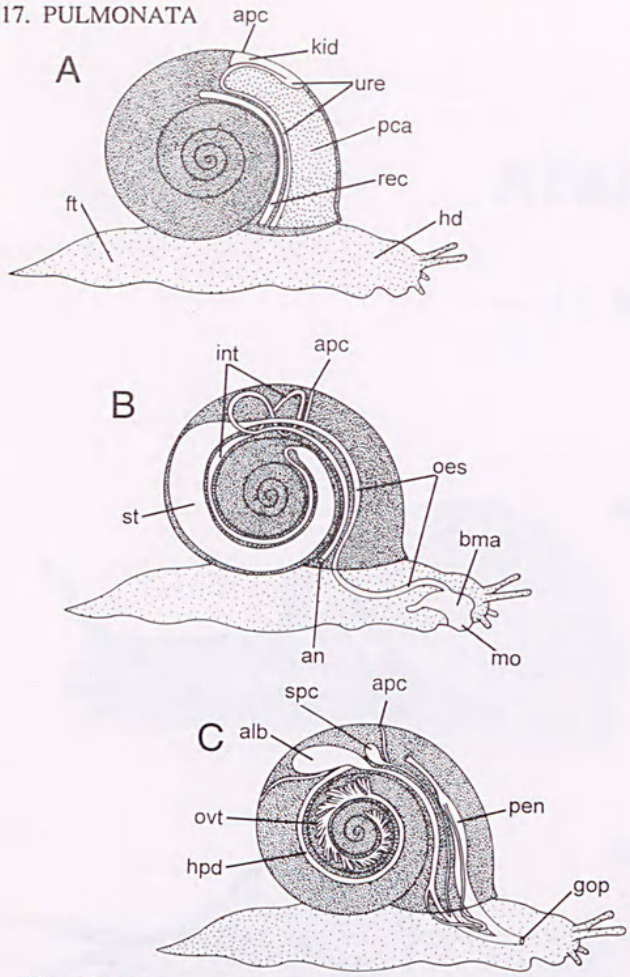

Figure 17.2 Arrangement of basic pulmonate organ systems. **A**, location and extent of the pallial cavity and associated organs. **B**, location of the digestive tract; the digestive gland which occupies most of the area above the stomach has been omitted. **C**, location of the genital tract. Organs above the apex of the pallial cavity (**apc**) are termed 'apical genitalia', those below are 'pallial genitalia'. **alb**, albumen gland; **an**, anus; **apc**, apex of pallial cavity; **bma**, buccal mass; **ft**, foot; **gop**, gonopore; **hd**, head; **hpd**, hermaphroditic duct; **int**, intestine; **kid**, kidney; **mo**, mouth; **oes**, oesophagus; **ovt**, ovotestis; **pca**, pallial cavity; **pen**, penis; **rec**, rectum; **spc**, spermatheca; **st**, stomach; **ure**, ureter. (After Solem 1974) [C. Eadie]

impervious, calcareous shelled eggs in many terrestrial forms. Several groups exhibit ovoviviparity and some members of the Glacidorbidae have been described as viviparous.

The Australian pulmonate fauna consists of 44 families containing about 750 described native and over 40 introduced species (Smith 1992). Thirteen families are represented in the Australian fauna only by recently introduced species, many of which are serious pests. Many of these were well established before 1850. It is thought that only 50% of the total fauna has so far been described; the remainder, awaiting description, is mainly from northern and eastern Australia (Stanisic 1994b). A great many groups are in need of modern revisions and large areas of the continent have never been examined systematically for pulmonates. Though the research collections in the various State museums are large and are expanding, for many species preserved animals are unavailable for anatomical studies.

HISTORY OF DISCOVERY

Between 1770 and 1990 more than 1500 species names were erected for Australian pulmonates (including Lord Howe and Norfolk Islands). Many of these have now been relegated to synonymy by later revisions. The number of pulmonate species with their type locality in Australia (including Lord Howe and Norfolk Islands) described between 1770 and 1990 provides an insight into the pattern of discovery of the Australian pulmonates (1770–1799, 1; 1800–1849, 88; 1850–1899, 726; 1900–1949, 613; 1950–1990, 145).

These periods reflect the four main phases into which the discovery and description of Australia's pulmonate fauna can be subdivided, although these phases are not really chronological and there is a great deal of overlap in time. These are: voyages of exploration; collection for European specialists; studies by early Australian workers; research in State museums and by State specialists, and the work of the American researcher, Alan Solem.

Almost all the species described before 1850 were collected on voyages of discovery and exploration. Consequently, they were collected near or on the coastal fringe, usually near a good anchorage in a bay or inlet and were usually either large, spectacular and/or very abundant, as the collectors were not trained malacologists. With a few exceptions they were also only seen by the describers as dead shells with no information on the animal or habitat. In fact in many instances even the locality given was only a general one (Kershaw 1987a).

Cook's voyages to Australia appear to have yielded no pulmonate specimens that were described, although some may have been collected and described later and their source not recorded. In sharp contrast to this, on several of the early French voyages of exploration, many specimens were collected and transported promptly to Paris for description either by the collectors or by the leading natural historians of the day, such as Lamarck, Férussac and others. The naturalists who collected material on these voyages included Péron and Lesueur (*Le Géographé*, 1800–1802), Quoy and Gaimard (*Uranie*, 1817; *l'Astrolabe*, 1826–1829), Lesson (*La Coquille*, 1822) and Hombron and Jacquinot (*l'Astrolabe* and *Le Zelée*, 1837–1840). These voyages yielded over 50 new Australian pulmonate species, mainly from southern Australia. By comparison, in terms of the pulmonates collected, the only British voyage of importance was that of the HMS *Rattlesnake* (1847–1848), on which MacGillivray collected material from northern Australia. More details of these voyages are given by Dance (1986). Hardly any of the early inland explorers collected snails.

As the continent became better known and more settled, some of the early pioneers were either interested enough to collect snails for their own sake, for example, George French Angas, or were employed to collect specimens by dealers based in Europe. Perhaps the best known of all the dealers was Hugh Cuming who employed several snail collectors in Australia including Cunningham, Strange and MacGillivray. Specimens thus collected were sent back to Europe where they were made available to various experts for description; many were figured in the large illustrated monographs produced at the time.

Several of the more prominent workers who described many Australian pulmonates in the mid-nineteenth Century were H. Pfeiffer, A. Adams, and L.A. Reeve, and several of the Sowerby family. Placement of type specimens of the newly described species in European museums was characteristic of this period, even though, with the discovery of gold, many of the well-established, richer colonies had their own natural history museums, quite capable of being safe repositories for the primary reference material of this 'new' fauna.

The era of collectors soon gave way to, and overlapped with, the era of the early Australian pulmonate researchers. These resident malacologists started publishing their findings, and lodged their reference material in Australia. The founder and dominant personality of this era was undoubtedly Dr J.C. Cox, who first published a catalogue of Australian land shells (Cox 1864) and then his illustrated *Monograph of Australian Land Shells* (Cox 1868). A complete description of Cox's contribution is given by Richardson (1970). Cox encouraged people like Legrand to continue to document the fauna, and influenced regional workers like Petterd, besides establishing a foundation for the era of the professional malacologists such as Brazier, Hedley, Iredale and Cotton.

Very soon after the various State museums were established, regional studies of the pulmonate fauna were initiated. From about 1870 to the 1930s, many parts of Australia were covered by regional reports and local lists by such workers as Petterd, Johnston, Tate and Gabriel. These culminated in the publication of basic lists of the land and freshwater Mollusca of Australia by Iredale (1937a, 1937b, 1938, 1943a). These lists formed a watershed in pulmonate taxonomic studies in Australia and provided a springboard for the modern studies by Kershaw, Smith, Solem, Stanisic, and others.

MORPHOLOGY AND PHYSIOLOGY

External Features

The external features of pulmonates are of primary importance in their identification and reflect their way of life as well as the relationships of the species. External features can be categorised under two main headings: those concerned with the shell and those to do with the soft anatomy of the body of the animal.

Shell

Possession of a helicoid coiled shell is probably the primitive condition of both basommatophoran and stylommatophoran pulmonates. This shell would have had a large last whorl into which the animal could withdraw its whole body. In common with other groups of molluscs, the shell consists of an outer layer or periostracum made of the complex organic material 'conchin' (similar to arthropod chitin) and several layers of crystalline calcareous material. The periostracum may contribute much of the shell sculpture and colour patterning.

Modifications to the basic shell form occur across groups of pulmonates. Ten of the 44 pulmonate families that occur in Australia, have some or all members with the shell absent, or so reduced that the animal can no longer withdraw into it, or internal and reduced to a fragile remnant or a few calcareous fragments. Animals in which the shell is either lost or remains internal are called slugs. Those in which the shell is greatly reduced are considered to represent a trend towards the slug-like form and have been called 'semi-slugs' by Solem (1974).

Three distinct characteristics of pulmonate shells have significance in the identification of families, genera and species within the group. These are shape and form; sculpture of both the protoconch and teleoconch; and colour pattern.

Pulmonate shells can vary in shape from high-spired to globose to planispiral. In one planorbid genus, *Ancylastrum*, the spire is reduced to a vestigial spiral on a large limpet-like shell, whereas three families, the Siphonariidae, Trimusculidae and Ancylidae, have virtually lost all trace of coiling to become entirely limpet-shaped. The presence or absence of an umbilicus in helicoid shells and its diameter compared to the diameter of the shell are important taxonomic features, as are the size of the last whorl compared to the rest of the shell, the size and shape of the aperture and whether the aperture is protected by 'teeth', lamellae or other barriers. Several families are characterised by the type of apertural 'teeth' they possess and their precise location around the aperture. Finally the thickness of the shell can give an indication of the environmental variation experienced by the animal. Most freshwater groups have comparatively thin shells with few calcareous elements, perhaps reflecting availability of calcium. Carnivorous species, of Rhytididae and Zonitidae, also show a reduction in calcareous shell elements giving a much lighter more flexible shell, possibly related to the carnivorous habit. On the other hand many groups have thick, solid shells which provide effective protection from many forms of predation and desiccation. The Amphibolidae and Glacidorbidae are the only pulmonate families with a horny operculum. This is an unusual feature in pulmonate snails, but is typically seen in other shelled gastropods.

All species of shelled pulmonates show lines on their shells corresponding to discontinuities in shell growth throughout their lives. Some of the many forms of shell sculpture are shown in Figure 17.3. Also many species have thickened ridges, mainly in the periostracum, giving the shell a regular sculpture. This can take the form of simple radial or spiral ridges or lines or can be a complex mixture of primary ribs with secondary riblets or a reticulate pattern of fine lines (Fig. 17.3). Sculpture can also take the form of an irregular rugose pattern or even granulations and a mat of fine hairs or spines. The sculpture found on the embryonic shell (protoconch) can be totally different from that found on the adult shell (teleoconch) and this too can be an indicator of relationships among species, or useful in distinguishing taxa.

The colours, and the nature and intensity of the colour pattern are of major importance in identification. These are largely features of the periostracum. Shells can have a variety of background colours, mainly white, cream, yellow and shades of brown in Australia, although the shells of some tropical pulmonates can be bright green or red. Superimposed on this background colour is a variety of regular bands, either a darker or lighter variant of the ground colour, a contrasting colour or a series of blotches or flames. In some forms, the colour and patterning are constant and constitute a species-specific character, whereas in others, the patterning is variable and sometimes may be related to specific habitat preferences of morphs. The patterning can be so variable that a shell with a normally cream background colour can be almost black in appearance due to the broadening of dark brown bands to cover the entire shell. Also, within pulmonate species, shell size and shape often exhibit extreme variation, with some recurrent environmental correlations (Goodfriend 1986).

Body of the Animal

After the shell, the external features of the body of the animal are the next most accessible characters for the family and generic placement of any pulmonate specimen. External characters can be considered under four main headings. These are: shape, form and colour; mantle and pneumostome; features of the head; and features of the tail.

The general shape of the body can be important. Members of the Rhytididae are adapted for carnivory. The shell is carried far back on the animal almost over the tail (Fig. 17.51A). The anterior part of the body is greatly elongated to accommodate the much enlarged buccal mass (Fig. 17.8B; Solem 1974), more normally short as in Figure 17.8A. In the native slug family Cystopeltidae, unlike any other slug family, the visceral mass is separated from the foot posteriorly, and is carried more like the visceral mass of a snail (Fig. 17.1C). Body colour and pattern are also important, particularly in slugs, many of which show cryptic colouration. In contrast, two colour forms of a species in the Athoracophoridae have a bright orange or red body colour. The possibility that this is a warning colour needs experimental verification.

The shape and position of the mantle are very important taxonomic characters, particularly in slugs, as are the position of the pneumostome and the presence of mantle appendages. The mantle covers and encloses the mantle cavity (pulmonary cavity), which in most pulmonates is the principal site of respiration. It is usually at the front of the visceral hump and creates a space into which the animal can withdraw its head-foot complex. The pneumostome usually opens on the right mantle margin. The mantle is reduced to a small triangular area in the mid-dorsal region in the Athoracophoridae, from which short trachea-like tubes carry air to the major organs; in the Testacellidae, it is situated at the posterior end of the body, under the vestigial shell. The mantle and mantle cavity are absent in the slugs belonging to the Onchidiidae, Rathouisidae and Veronicellidae. Several families have characteristic mantle appendages. The Physidae, a group of sinistral freshwater snails introduced into Australia, is characterised by digitate mantle processes (Fig. 17.35B). Large mantle lappets are present in some helicarionids. These fleshy lobes extend over the reduced shell of some species and provide protection and camouflage (Fig. 17.1B).

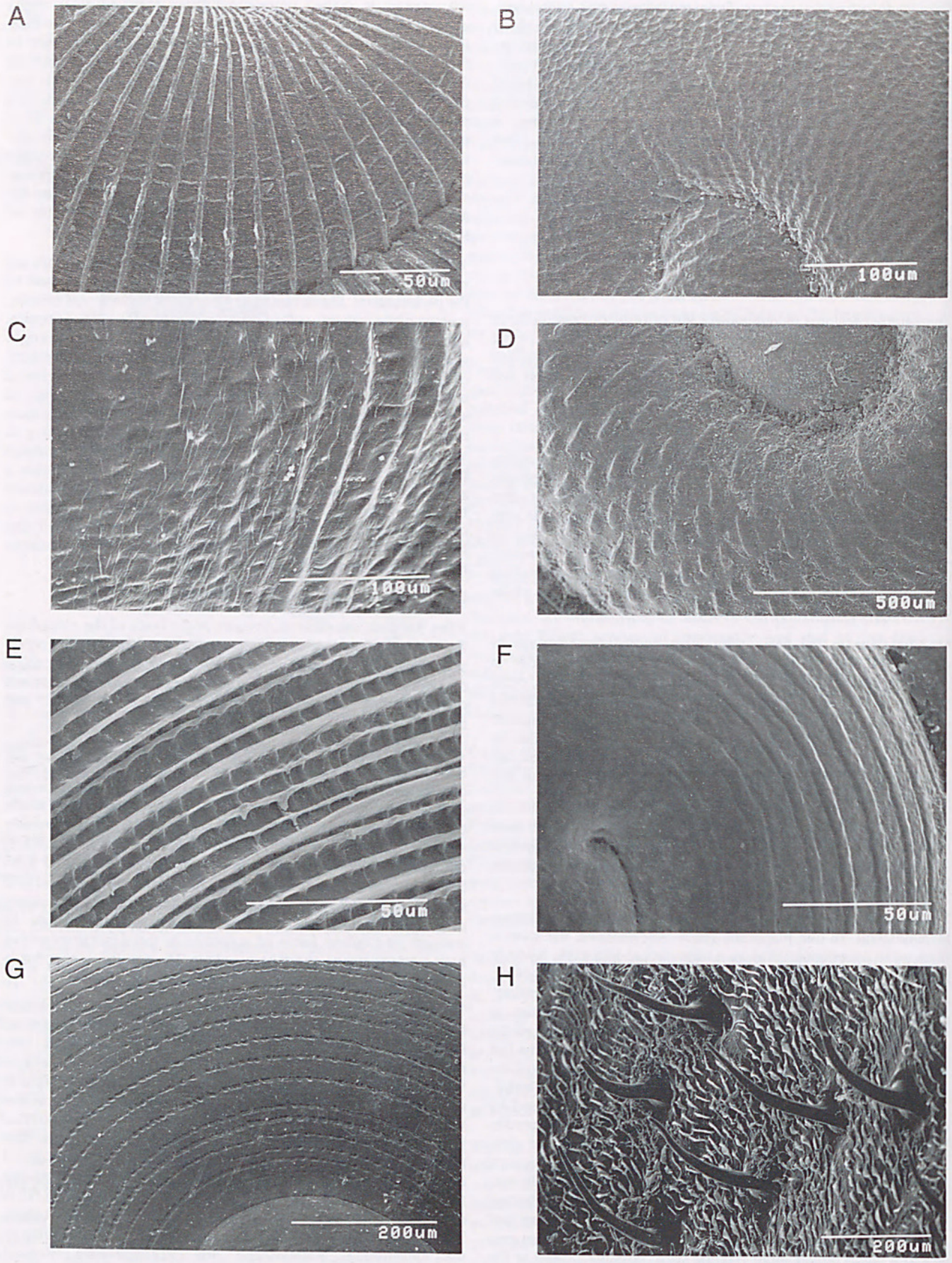

Figure 17.3 Pulmonate shell sculpture. **A**, prominent radial ribs and weak spiral cordlets on the protoconch of *Discocharopa aperta* (Charopidae). **B**, minute punctations on the protoconch of *Pupisoma circumlitum* (Pupillidae). **C**, malleate sculpture on the body whorl of *Cylindrovertilla hedleyi* (Pupillidae). **D**, elongate pustules on the protoconch of *Tolgachloritis jacksoni* (Camaenidae). **E**, reticulate sculpture on the body whorl of *Oreomava otwayensis* (Charopidae). **F**, spiral cords on the protoconch of *Iotula microcosmos* (Punctidae). **G**, notched incised spiral grooves on the protoconch of *Nitor medioximus* (Helicarionidae). **H**, periostracal setae on the body whorl of *Austrochloritis porteri* (Camaenidae).
[Queensland Museum]

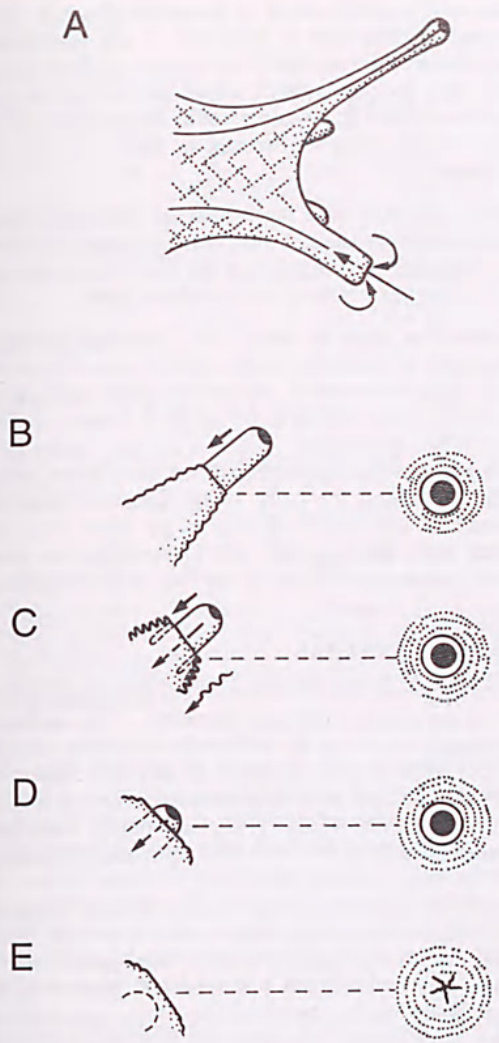

Figure 17.4 Retraction of the optic tentacles in pulmonates. A, stylommatophoran with introversible tentacles. B–E, progressive tentacle retraction in the Athoracophoridae – corresponding lateral and dorsal views. The proximal portion of the tentacle contracts while the distal eyestalk is withdrawn (not introverted) into the snail's anterior body. (After Burch 1968)
[C. Eadie]

Systellommatophorans and basommatophorans usually have one pair of tentacles (absent in species of *Smeagol*) whereas stylommatophorans typically have two pairs (Fig. 1.61C). Eyes are situated at the base of the tentacles in basommatophorans, at the tip of each longer, superior tentacle in stylommatophorans (Fig. 17.4A) and the tip of the only tentacles in the Onchidiidae, Rathouisiidae and Veronicellidae. The family Athoracophoridae is unique amongst pulmonates in that the optic tentacles retract rather than invert (Fig. 17.4B–E; Burch 1968). The other external feature associated with the head is the genital pore which typically opens on the right side of the head about half way between the optic tentacle and the pneumostome.

The posterior end of the foot varies in shape from hemispherical in section to triangular when the tail bears a mid-dorsal keel. In a few families, particularly the Arionidae, Helicarionidae and Charopidae, a prominent caudal gland on the tip of the tail produces extra mucus associated with locomotion, feeding or reproductive activity.

Musculature and Locomotion

The mechanism and functions of the hydrostatic skeleton found in pulmonates are outlined under Circulation.

The gross anatomy of the musculature of the head-foot region described in outline here is based largely on an account of the musculature of *Helix pomatia* by Trappman (1916). The foot is highly muscular and contains longitudinal, transverse and dorso-ventral fibres, and muscles inclined at various angles to these three directions, as well as circular muscles around the head-foot (Fig. 1.13C). Most of these muscles insert on different parts of the body wall at both ends. The space between the muscle fibres of the foot is filled with blood as part of the haemocoel. The anterior half of the foot is served with bundles of retractor muscles which are convergent with the columellar muscle. The head is also served with retractor muscles which converge with the columellar muscle, including a buccal retractor muscle and four tentacular retractor muscles (Fig. 17.5). The single penial retractor muscle originates on the dorsal body wall. The body wall of the head and foot is highly muscular with longitudinal, circular and oblique muscle fibres. Attached to the body wall near the mouth are several discrete muscles concerned with the operation of the buccal mass. The highly muscular floor of the mantle cavity contributes to breathing and the protrusion of the head-foot from the shell. A slug has very similar musculature to that of *Helix*, except that the retractor muscles insert on the body wall in the vicinity of the vestigial shell. The primary function of the retractor muscle system is the withdrawal of the head-foot complex into the shell, a detailed sequence for which is given by Jones (1975) and Emberton (1989).

Pulmonates are primarily adapted for locomotion over hard substrata. The foot is a muscular organ with a large sole upon which the animal crawls and remains attached to the substratum, using the adhesive properties of mucus. During locomotion a continuous trail of mucus is laid down from the supra-pedal mucous gland at the anterior end, and the sole passes over this using either cilia on the sole or waves of muscular contraction. Most pulmonates move by utilising both the ciliary and muscular functions of the pedal sole. Aquatic species and some small terrestrial species use mainly cilia, and larger terrestrial species use muscular waves.

Two main types of muscular waves are seen in pulmonates. Direct pedal waves which move in the same direction as the animal and retrograde pedal waves which move in the opposite direction to the animal. Both wave types may traverse the foot as a single or monotaxic system of waves or they may pass along the foot as two systems of waves, one each side of the mid-line, a condition termed ditaxic. Ditaxic waves may be alternate or opposite. A third arrangement found occasionally has four separate systems of waves, termed tetrataxic. Almost all pulmonates using muscular pedal waves for locomotion use direct, monotaxic waves.

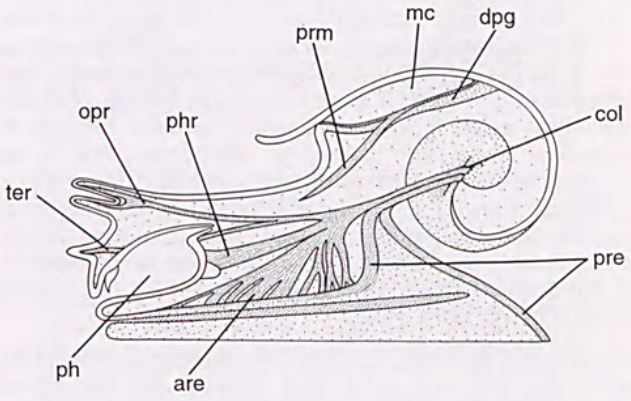

Figure 17.5 The retractor muscle system of a typical snail genus, *Helix*. **are**, anterior retractor muscle; **col**, columella; **dpg**, diaphragm; **mc**, mantle cavity; **opr**, optic retractor muscle; **ph**, pharynx; **phr**, pharyngeal retractor muscle; **pre**, posterior retractor muscle; **prm**, penial retractor; **ter**, tentacular retractor muscle. (After Solem 1974, modified from Trappman 1916)
[C. Eadie]

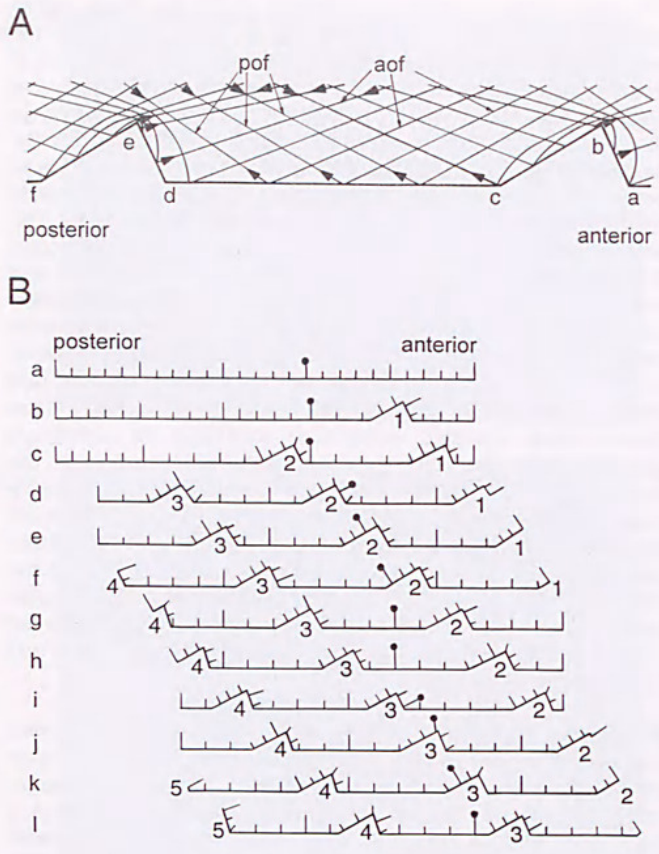

Figure 17.6 Methods of locomotion in pulmonates. **A**, *Agriolimax* sp. (Limacidae), contracting muscle fibres bear large arrow heads; the posterior oblique fibres (**pof**) contract between waves (c–d) pulling the body of the slug forward and exerting backward thrust on the substratum; the anterior oblique fibres (**aof**) contract to pull the epithelium of the sole forwards and to form each pedal wave (a–b–c and d–e–f). **B**, an animal such as a slug which uses direct locomotory waves; a hypothetical diagram to illustrate the commencement of locomotion. Vertical lines represent arbitrary division of foot into sectors with every fifth being highlighted and one marked with a dot to emphasise direction of uplift. (After Jones 1973) [C. Eadie]

In the Onchidiidae, a family of primitive pulmonates, only one monotaxic direct wave passes along the sole at a time. In all other pulmonates using direct monotaxic waves, more than one wave is seen at a time on the sole during locomotion. Two or three waves at a time are seen on the sole in the two small introduced species *Oxychilus alliarius* and *Cionella lubrica*. In the large introduced slug, *Limax maximus*, 11 to 19 waves may be present on the sole at any one time.

The musculature of the foot has a very distinct arrangement. Immediately ventral to the supra-pedal mucous gland lies a layer of longitudinal muscle fibres. A relatively unrestricted haemocoelic space lies between this muscular layer and the more ventral epithelium of the sole. This space is crossed by two sets of oblique longitudinal muscle fibres, continuous at their dorsal end with the longitudinal fibres and attached at their ventral end to the epithelium of the sole. One set (the anterior oblique fibres) applies an anteriorly directed upward force to the epithelium, whereas the other (the posterior oblique fibres) applies a posteriorly directed upward force to the epithelium (Fig. 17.6). The forces exerted at the dorsal end of each set are in the opposite direction to those exerted at the epithelial ends.

This system is thought to function in locomotion as follows. The anterior oblique fibres contract and lift the epithelium upwards and forwards relative to both the body and the substratum, producing a wave. As the region of contraction of the fibres continues forwards, each fibre then relaxes and the epithelium is re-applied to the substratum. Once the epithelium is back on the substratum it adheres to the mucous trail and becomes stationary. The posterior fibres then contract, thus moving forward the layer of longitudinal muscle and the body of the animal above it, since the epithelial end of each fibre is stationary on the substratum. This movement restores the anterior fibres to their original length. Another pedal wave follows, again moving the sole forward by contraction of the anterior fibres and restores the posterior fibres to their original length. Thus the two sets of fibres are mutually antagonistic (Jones 1973).

In a few species, a form of more rapid muscular locomotion does not involve successive muscular waves. This locomotion is called 'looping' or 'galloping' and involves a forward progression by flexing and extending the whole of the head-foot region.

Ciliary locomotion is used by almost all basommatophorans, many of the smaller stylommatophorans and, to some extent, by juveniles of the larger pulmonates. The critical factor seems to be the effective weight of the animal in the medium in which it lives (Jones 1973). The pulmonate foot is covered with cilia. Locomotion is achieved by the beating of the cilia in the mucus under the sole, propelling the body along. The two important factors are length of cilia and frequency of the beat. Very few detailed studies have been carried out to describe the exact functioning and control mechanisms of this form of locomotion.

Feeding and Digestion

Very little is known about the anatomy and physiology of feeding and digestion in any native Australian pulmonate. This section is based on an excellent review of the pulmonate alimentary canal by Runham (1975). This in turn is based largely on studies on *Lymnaea stagnalis* by Carriker (1946) and others, and *Agriolimax* (= *Deroceras*) *reticulatus* by Walker (1969) and others. Both these species have been introduced into Australia. Pulmonate alimentary systems conform to a general pattern (Figs 17.2B, 17.7). The mouth leads into the buccal mass (Fig. 17.8), a complex muscular structure containing the radula and the jaw, where food receives the secretions from the salivary glands. Food is then passed via the oesophagus and ancillary structures of crop and gizzard to the stomach, which also receives ducts from the large and complex digestive gland. After most of the digestion and food absorption has taken place, the residue is then passed down the intestine where faeces are formed to be passed out via the rectum and anus.

The structures used for feeding form the buccal mass. This is a globular organ at the front of the head that consists of the radula, jaw, odontophore 'cartilage' and associated muscles. No true cartilage is found in any heterobranch (Haszprunar 1985). The buccal cavity is continuous with the mouth anteriorly, via the oral

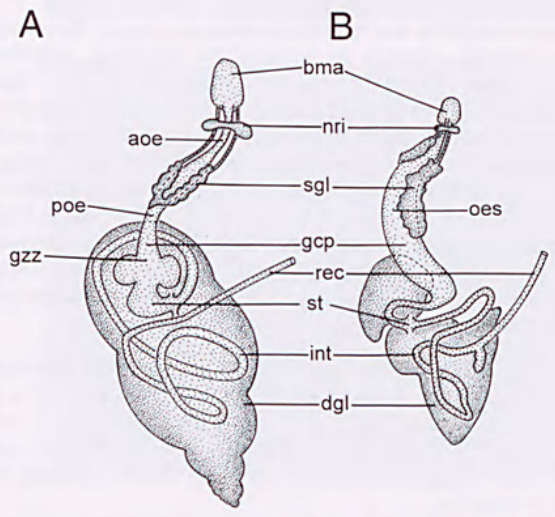

Figure 17.7 Pulmonate digestive systems. **A**, *Lymnaea stagnalis* (Lymnaeidae), a basommatophoran. **B**, *Deroceras reticulatum* (Limacidae), a stylommatophoran. **aoe**, anterior oesophagus; **bma**, buccal mass; **dgl**, digestive gland; **gcp**, gastric crop; **gzz**, gizzard; **int**, intestine; **nri**, nerve ring; **oes**, oesophagus; **poe**, posterior oesophagus; **rec**, rectum, **sgl**, salivary gland; **st**, stomach. (After Runham 1975) [C. Eadie]

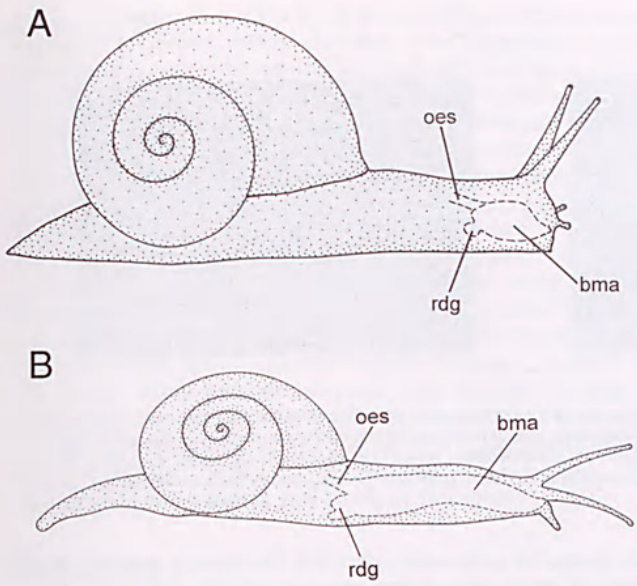

Figure 17.8 The pulmonate buccal mass varies in size according to feeding habit. **A**, *Helix* sp. (Helicidae), a herbivore; the buccal mass is short. **B**, *Strangesta* sp. (Rhytididae), a carnivore; the buccal mass is greatly enlarged as a modification for carnivory. **bma**, buccal mass; **oes**, oesophagus; **rdg**, radular gland. [C. Eadie]

tube, and with the oesophagus postero-dorsally. The mouth is surrounded by a series of sensory lips with associated mucous glands. At the anterior end of the buccal cavity part of the cuticle is thickened by chitin to form the single, dorsal jaw. The jaw varies in structure from group to group and is absent in specialised carnivorous groups. Dorsally, posterior to the jaw, a groove – the dorsal food channel – leads directly back into the oesophagus. This groove is bounded laterally by a narrow band of ciliated epithelium and numerous mucous glands.

Bulging into the buccal cavity from its floor is the large movable odontophore. This consists of the so-called odontophore 'cartilage', muscles and the radula which covers most of its surface (Fig. 17.9). The odontophore contains many muscle fibres and vesicular connective tissue cells which are fluid-filled and may act as a hydrostatic skeleton. The radula consists of a highly flexible membrane to which hard teeth are attached in rows. The size, shape and form of the teeth usually vary across a transverse row. In many species it is easy to distinguish a central tooth and fields of lateral and marginal teeth, whereas in others these intergrade. The various forms and numbers of teeth can be used in identification, and radula formulae can be defined for taxa; the formula for *Helix aspersa* is 45–50.20.1.20.45–50, and indicates a central tooth with 20 lateral teeth and 45–50 marginal teeth on each side. Teeth in any longitudinal row are more or less identical in size and shape. The radula is secreted at its posterior end by the radular gland. This gland is folded up to form a tubular structure such that its lateral edges nearly meet dorsally. A rod of connective tissue, the collostyle, fills the centre of this tube. At the posterior tip of the gland are specialised cells, the odontoblasts, that secrete much of the radula. Details of the mechanism of secretion and formation of the teeth are given by Runham (1963, 1975). The action of the radula in feeding (Fig. 17.9) has been described for *Lymnaea stagnalis* by Hubendick (1957) and for several slug species by Runham & Hunter (1970). The backward-pointing teeth can either be used as a rasp to crop the surface film of algae from a hard substratum (Fig. 17.10A), to 'bite' off pieces of a solid plant food (Fig. 17.10C) or to hold and to ingest large whole prey in carnivorous forms (Fig. 17.10B).

The salivary glands consist of many sacs of cells (acini), from which small collecting ducts merge to form the large, paired salivary ducts that empty into the postero-dorsal part of the buccal cavity. The glands produce an amylase together with small amounts of trypsin-like protease, and mucus (Evans & Jones 1962). The saliva provides lubrication during feeding, assists with the removal of food from the radula and initiates extracellular digestion (Runham & Hunter 1970).

Food is passed back from the buccal cavity into the oesophagus, which broadens out in many species into a holding sac or crop (Fig. 17.7B). In most stylommatophorans the crop is filled with a reddish brown liquid known as crop juice. This contains a rich soup of enzymes which are active against a wide range of polymers, such as carbohydrates, proteins and lipids (Runham & Hunter 1970). These enzymes are derived largely from the digestive gland which empties into the stomach and it is thought that during periods of inactivity the juice is passed forward from the stomach into the crop where it is held in readiness for the next period of feeding activity. Food is held in the crop for up to several hours, during which extensive extracellular digestion takes place (Walker 1969).

The crop leads directly into the stomach, a sac with various ciliary tracts and grooves forming transport pathways. Ducts carrying enzymes from the digestive gland open into it and from it the food passes into the intestine. *Lymnaea stagnalis* has a large, highly muscular gizzard, which normally contains sand grains (Fig. 17.7A; Carriker 1946). A caecum is also present and has a sorting area leading to the two digestive gland openings. In most stylommatophorans both gizzard and sorting area are absent and the stomach is largely an area of food transport and exchange with no trituration function (Fig. 17.7B). The variation in the structure of the gastric region within the different superfamilies of pulmonates is described by Tillier (1989). In particular he describes the differences associated with carnivory where the digestive tract is shorter and simplified compared to the herbivorous groups. The differences in digestive tract morphology associated with the process of limacisation are described by Tillier (1984a).

Suitable fine particles and soluble materials are passed from the stomach into the digestive glands (Walker 1969) by muscular pulsations of the stomach and digestive gland. Larger particles are excluded by ciliated folds. Waste material from the stomach and from the digestive gland is passed, via grooves in the walls of the stomach and digestive gland ducts, to the intestinal groove.

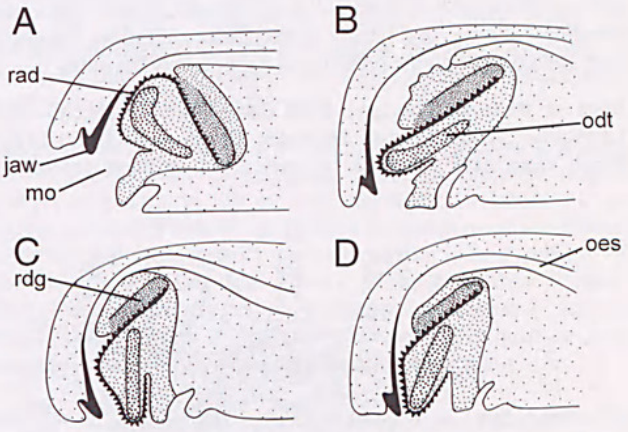

Figure 17.9 Sagittal sections through the buccal mass of *Lymnaea stagnalis* (Lymnaeidae) showing the movements during the feeding cycle. **A**, resting phase; the mouth is closed, the jaw retracted into the buccal cavity and the odontophore has an almost vertical position. **B**, phase 1: the buccal mass is rotated, the mouth is opened and the median jaw moves anteriorly and downwards; the odontophore also rotates, and the odontophore cartilage is pulled into a horizontal or forward tilting position and then is moved forward and pressed towards the mouth; contraction of the cartilage muscles straightens the cartilage and makes it rigid; the radula is stretched tight over the surface of the cartilage. **C**, phase 2: the vertically held odontophore is protracted through the mouth against the substratum and is ready for its feeding stroke. **D**, phase 3: the tip of the odontophore now in contact with the substratum moves forward and the forwardly directed teeth on the outside of the odontophore are dragged through the food material; as the odontophore moves forwards the median jaw is pulled back and held against the radula at the end of the feeding stroke; the mouth begins to close. **jaw**, jaw; **mo**, mouth; **odt**, odontophore cartilage; **oes**, oesophagus; **rad**, radula; **rdg**, radular gland. (After Runham 1975) [C. Eadie]

Figure 17.10 Pulmonate radulae from different feeding groups. A, *Cystopelta petterdi* (Cystopeltidae), central section of radula showing the many very small, fine teeth; this species probably feeds on bacteria or microalgae. B, *Austrorhytida capillacea* (Rhytididae), several tooth rows across the radula showing the lanceolate teeth grading in size to a large dagger-like tooth towards the outside of each side; this species is an active predator, feeding on other snails and slugs. C, *Stenacapha hamiltoni* (Charopidae), section of radula showing the variation in shape between the central (top right) and lateral teeth; this species probably feeds on microfungi.
[A, A. Daniell; B, C, B.J. Smith]

The digestive gland is the largest organ in the pulmonate body and is composed of a series of branching ducts ending in complex, blind tubules into which the gland cells empty. The main functions of the gland are absorption of food materials at various stages in its digestion, the secretion of enzymes, storage of reserve materials and excretion. Very small particles (less than 0.01 µm) enter the gland and are passed into the cells for intracellular digestion. The range of enzymes produced by the gland (Runham 1975) includes cellulase and chitinase. These two unusual enzymes are found in very few animals; their action is mainly extracellular in the lumen of the crop and stomach.

Undigested and waste particulate material is passed via ciliary pathways at the start of the intestine, where it is consolidated and mixed with further mucus to form fairly solid faeces for defecation. Passage of material along the intestine is comparatively slow, taking about seven hours in *Agriolimax* (= *Deroceras*) (Walker 1972). Strong intracellular enzymes are present in the epithelial cells but these are not secreted into the lumen of the tract. The long stay of material in the intestine may allow further time for the cellulase and chitinase, in particular, to act, and absorption of further digestive products takes place in the intestine followed by further intracellular digestion. Faeces are then passed through the rectum and expelled via the anus.

Most of these studies have been carried out on species of the Limacidae, Arionidae and Helicidae (Runham & Hunter 1970). Much more work needs to be carried out on these processes in other groups of pulmonates, since the few species that have been studied in detail have shown many significant differences from one another, and all are higher stylommatophorans. Studies, particularly of Australian endemic families and lower pulmonates, may bring to light major new observations.

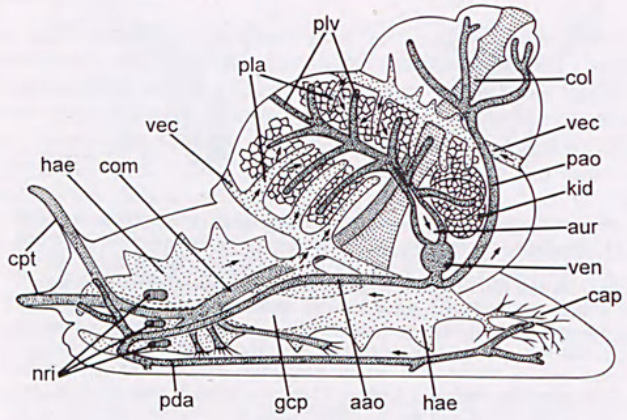

Figure 17.11 Circulatory system and haemocoelic spaces of *Helix pomatia* (Helicidae). **aao**, anterior aorta; **aur**, auricle; **cap**, capillaries; **col**, columella; **com**, columellar muscle; **cpt**, cephalic tentacle; **gcp**, gastric crop; **hae**, haemocoel; **kid**, kidney; **nri**, nerve ring; **pao**, posterior aorta; **pda**, pedal artery; **pla**, pulmonary arteries; **plv**, pulmonary veins; **vec**, venous circle; **ven**, ventricle. (After Borrodaile *et al.* 1958) [C. Eadie]

Circulation

The pulmonate heart is a simple, two chambered (ventricle and auricle), muscular organ situated just in the roof of the pulmonary cavity (17.11). All venous blood eventually reaches the venous circle along the edge of the pulmonary cavity and around the pneumostome. Pulmonary arteries then conduct the blood to the capillary network in the lung roof where it is oxygenated. The capillaries link with pulmonary veins which drain into a main pulmonary vein. This vessel conveys the blood to the auricle of the heart. It then passes to the ventricle which pumps the blood via the anterior and posterior aortae into beds of capillaries associated with various organs. Here the vessels end in ostioles which are surrounded by a dense network of muscle fibres capable of occluding the opening and so regulating the flow of blood into the haemocoel. The presence of septa within the haemocoel allows differential pressures to be built up. The transverse septum separates the visceral haemocoel from the cephalopedal haemocoel, and other septa occur at different places in the anterior haemocoel (Fretter 1975). Kisker (1923) described two horizontal septa in *Helix pomatia* with ostia controlled by muscle fibres. The more dorsal of these leads forward from close to the anterior end of the transverse septum beneath the thick layer of connective tissue of the neck and head, enclosing a space exclusively for blood. Anteriorly, before it inserts on the head, it fuses with the second septum which crosses the haemocoel to isolate the buccal mass and anterior oesophagus from the reproductive ducts lying above them.

Retraction of the head-foot into the shell is achieved by contraction of the various retractor muscles attached to the columellar muscle. During this sequence air is expelled from the pulmonary cavity and some blood is redistributed to allow room for the head-foot to be housed within the shell. Retraction and protrusion of the head have been investigated by Sommerville (1973) and Dale (1974). Unlike retraction, protrusion takes place in a number of steps or cycles and is not continuous.

The haemocoel of many pulmonates is thought to act as hydrostatic skeleton. It provides for antagonism of musculature, support of the shell and visceral organs, and erection of the tentacles (Dale 1973; Jones 1975). Aquatic forms tend to have the musculature of the body wall less well developed than terrestrial pulmonates (Plesch, Janse & Boer 1975). This is thought to reflect the greater hydrostatic pressure required to support the body of land-based forms.

Phase 1 of protrusion starts when the pneumostome is opened and the foot is pushed slowly outwards. The diaphragm contracts downwards, forcing blood into the head and sucking air into the pulmonary cavity (Dale 1974). In phase 2, the diaphragm is raised to its resting position, the pneumostome is closed and a pressure develops within the pulmonary cavity which forces air into the most posterior part of the cavity. The foot ceases protruding and retracts slightly which may cause a high pressure in the cephalic sinus and push the diaphragm upwards. Phases 1 and 2 are alternated six or seven times to effect full protrusion. For the head to evaginate there must be a redistribution of blood within the haemocoel and blood is shifted from the sub-renal sinus and visceral sinus into the head. Dale (1974) has shown that heart rate and ventricular systolic pressure increase during protrusion, but the venous return pressure does not. Thus the heart increases its output to pump up the head by a redistribution of the aortic blood through constriction of the visceral artery. The disposition of other internal organs during retraction and extension has been investigated in Australian land snails by Emberton (1989).

Excretion

Pulmonates are soft bodied animals which contain considerable amounts of water. They have colonised both marine and freshwater habitats and many have been particularly successful in terrestrial environments including harsh desert conditions. Problems associated with water loss (land snails) and water accumulation (freshwater species) have led to the enhanced development of the ureter. The ureter (Fig. 17.2A) is involved in water and ion resorption, and has been developed as a specialisation of the kidney. The ureter may be a simple tubular structure as in basommatophorans or, as in stylommatophorans, a complex arrangement involving a primary and ectodermal secondary ureter which has arisen as an adaptation to terrestrial life (Andrews 1988).

Pulmonates have a single renal organ or kidney which is a coelomoduct characterised by deeply folded walls. It is usually located posteriorly in the roof of the mantle cavity and is linked to the pericardial sac through a renopericardial pore (Fig. 17.2A). In freshwater pulmonates the hydrostatic pressure of the blood in the heart results in the continuous transfusion of a clear filtrate into the pericardium and subsequently into the kidney where it is mixed with nitrogenous waste from the lining cells of the kidney. The final composition of the urine is determined by a combination of renal secretion, ionic resorption in the kidney and water resorption in the ureter. In terrestrial pulmonates the filtration is direct, from the renal capillaries into the kidney. The renopericardial aperture is small and little if any fluid is lost from the pericardium to the kidney.

The structure and shape of the excretory organs (kidney and ureter) of pulmonates are highly variable. Delhaye & Bouillon (1972a, 1972b, 1972c) compared the excretory organs of various Basommatophora and examined their evolutionary and adaptive significance. The most primitive basommatophorans, the shore-dwelling Ellobiidae and Otinidae, have a simple kidney with no ureter. The marine siphonariids have a simple, large sac-like kidney (Hubendick 1978). In primitive limnic Basommatophora, the kidney may be divided into a proximal saccular region and a distal tubular portion (nephridial pouch) which contains the ureteric pore. This anterior tubular extension of the kidney is involved in osmoregulation. In the higher limnic Basommatophora, for example, Planorbidae, a ureter has developed (Delhaye & Bouillon 1972a) and the kidney shape correlates with changes in the shape of the mantle cavity. In sinistral Planorbidae, the kidney forms a loop at the left side of the last whorl and the ureter is a short, reflexed, anterior termination of the nephridial pouch. In the Ancylidae, the ureter is very long and loops backwards and forwards before it gives rise to a posterior renal opening.

The extent of osmoregulation in the Basommatophora varies. In the marine intertidal species of *Siphonaria* the body fluid is normally isotonic with seawater (Machin 1975). They have little ability to regulate their haemolymph concentration but can tolerate a wide range of external concentrations. This is important in an environment where seawater can be either diluted by rain or concentrated by the sun. Behaviourally, *Siphonaria* species cope with extremes in external media concentration by exclusion, by clamping the limpet-like shell tightly to the substratum.

The freshwater pulmonates face a somewhat different problem. They have a much lower body fluid concentration than marine species but are still hypertonic with respect to the outside environment and are subject to a continuous osmotic inflow of water through the body wall. The problem is overcome by producing an almost continuous flow of urine to 'bale' themselves out, and by hyperosmotic regulation through the active uptake of inorganic ions, for example, sodium and chloride, at the body surface (Andrews 1988). Water is not voided solely by the kidney and the production of 'wet' faeces and associated mucus are two further means of eliminating water from the body.

In both marine and freshwater pulmonates, water currents produced by cilia sweep the excretory products from the mantle cavity.

Among the Systellommatophora, the marine Onchidiidae have a typical renal pouch that opens through a long renal papilla into a diverticulum of the mantle cavity. In the terrestrial Rathouisiidae and Veronicellidae, the papilla is replaced by an elongate ureter which has similar histological features to the ureter of stylommatophorans (Delhaye & Bouillon 1972c). The ureter in the Veronicellidae is a straight tube which opens at the posterior end of the body, adjacent to the anus.

Land pulmonates, in contrast to freshwater groups, are primarily concerned with water conservation. Although equipped with a basic pre-adaptation to life on land (the shell), desiccation is an ongoing problem (Table 17.1). There is no free flow of water from the kidney and the excretory product consists almost entirely of insoluble uric acid (see Fig. 1.64A). White crystalline deposits accumulate in the kidney and are discharged at intervals (Andrews 1988). Pallial water or a 'squirt' of excreted water must be used occasionally to flush the products through the pneumostome.

Table 17.1 Loss of water through the shell in terrestrial pulmonate snails (based on weight loss of distilled water through empty shells with the aperture sealed). (From Machin 1975)

Species	Temperature (°C)	Relative humidity (%)	Shell loss (mg/g body wt/h)	% of total inactive loss	Authority
Arianta arbustorum	26	45	0.0139	2.3	Cameron 1970a
Cepaea hortensis	26	45	0.0084	2.2	Cameron 1970a
Cepaea nemoralis	26	45	0.0059	1.8	Cameron 1970a
Helix aspersa	22	70	0.0079	4.6	Machin 1967
Otala lactea	22	70	0.017	25.8	Machin 1967
Sinumelon remissum	20	dry air	0.014	70.0	Warburg 1965
Sphincterochila boissieri	22	70	0.0086	61.5	Machin 1967

Table 17.2. Oxygen consumption (Q_{O_2}) of some pulmonates. (After Ghiretti & Ghiretti-Magaldi 1975)

Species	Q_{O_2} µl O_2/g wet wt/h	Temperature (°C)
Cepaea hortensis	80	15
Cepaea vindobonensis (summer)	125	20
Cepaea vindobonensis (winter)	51	20
Helicigona lapicida	96	15
Agriolimax agrestis	194	23
Helicella obvia	180	23
Helix pomatia	20–80	15
Lymnaea stagnalis	11	-

The main sites of resorption in stylommatophorans are the primary and secondary ureters, with conditions favouring resorption in the distal parts (Andrews 1988). The primary ureter resorbs water and salts creating a urine hypotonic to the haemolymph. The secondary ureter then resorbs additional water. The final composition of excretory products has been found to vary in stylommatophoran slugs and snails. In the European slug *Agriolimax reticulatum*, less than 1.5% of nitrogenous waste is lost as gaseous ammonia and 92% as uric acid and xanthine. In active snails, gaseous ammonia constitutes 5% of the waste products and rises to 30% in hibernating snails (Andrews 1988).

Among stylommatophoran ureters, there are several different structural patterns, correlated with the progressive evolution of land snails (Solem 1976, 1978a). Some of these patterns have been used to define major subgroupings.

The orthurethran ureter differs significantly from that of the Sigmurethra and resembles that of the Basommatophora in that the ureter is a secondary specialisation of the kidney and is not clearly separated from it. The ureter lacks ciliated cells and ends in a retrograde groove (Delhaye & Bouillon 1972b). The ureteric pore is some distance from the pneumostome and pallial water is needed to flush out the excretory products. In a few taxa (some Enidae), a pseudosigmurethrous condition has developed in which a series of rectal and renal folds form a structurally closed sigmoid 'ureter' which opens at the pneumostome (Fig. 17.12).

The sigmurethran ureter begins at the anterior tip of the kidney and reflexes posteriorly along its margin before reflexing anteriorly along the hindgut to the pneumostome. The reflexed portion of the ureter (secondary ureter) may be an open groove (most Holopodopes) or a closed, heavily vascularised tube. A further variation is seen in the 'mesurethran' kidney which lacks an anterior extension and has the ureteric pore as a simple opening at the kidney tip. An open, reflected, ciliated excretory groove runs to the pneumostome (Delhaye & Bouillon 1972b). Some authors consider this development to define an additional subgrouping – the Mesurethra. In slugs, the ureter and kidney configurations are often highly modified to accommodate the spatial requirements of visceral hump reduction. An incomplete secondary ureter has been recorded in the Endodontidae (Solem 1976) and some Australian Charopidae (Stanisic 1990). The closed tube or distinct groove assist water conservation by obviating the need to use pallial water to eliminate waste products. At the same time, water is presumably resorbed from the excretory products along the entire length of the secondary ureter.

The development of a closed secondary ureter has been considered a major advance in land snail evolution and a necessary pre-adaptation for the development of terrestrial slugs (Solem 1978a).

Respiration

A major characteristic of pulmonates is the development of a pulmonary cavity (pulmonary sac or 'lung') from the pallial cavity (Figs 14.19A, 17.2A). The anterior mantle edge has fused to the foot and neck and there is only a small opening to the exterior – the pneumostome. Although a shell may be absent, the mantle cavity invariably maintains an anterior position. The mantle skirt, which forms the roof and sides of the pulmonary cavity is highly vascular, and blood passes from it directly to the heart (Figs 14.19A, 17.11). The cavity thus functions as a lung in which the network of capillaries effects oxygen exchange and the muscles of the floor of the pulmonary cavity (dorsal body wall or diaphragm) allow its volume to be controlled. The small opening to the exterior (pneumostome) can be closed by a muscular sphincter.

In aquatic Basommatophora, respiration involves the lung, skin and secondary gills, but never true ctenidia (Haszprunar 1985). In the marine groups, Siphonariidae and Amphibolidae, the pulmonary cavity becomes filled with seawater and acts as a water lung. A secondary gill, consisting of epithelial folds, has developed within the mantle cavity of siphonariids (Fig. 14.19B). In freshwater groups respiration is essentially cutaneous and the respiratory function of the pulmonary cavity is reduced. The Planorbidae and Ancylidae have developed a 'secondary gill' – through enlargement of the pallial fold. In the Ancylidae which lack a pulmonary sac this gill is external; it is internal in the Siphonariidae and Planorbidae. An osphradium is present in limnic Basommatophora, but absent in terrestrial forms.

Among systellommatophorans, the intertidal Onchidiidae have a small pulmonary chamber which forms a vestibule for the anus (Fretter 1943). In contrast, the terrestrial Veronicellidae lack a mantle cavity and rely on cutaneous respiration.

Stylommatophorans typically have a pulmonary cavity with a well-developed vascular net and contractile pneumostome. The closed mantle cavity, in addition to its role in respiration, also acts as an important water storage area (Solem 1978a). Air is inhaled by opening the pneumostome and lowering the muscular floor of the cavity and although the pneumostome opens and

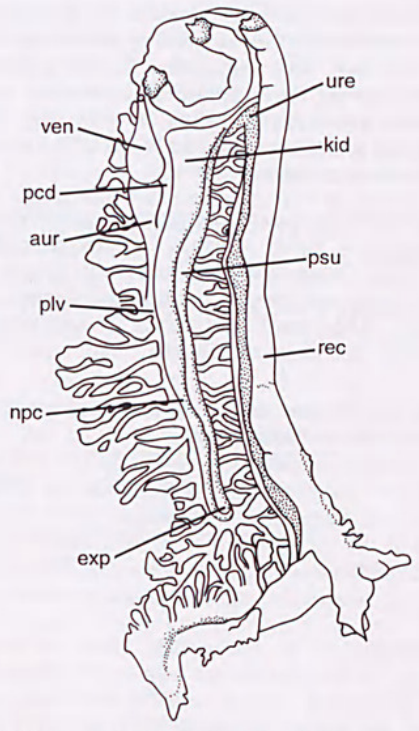

Figure 17.12 The pseudosigmurethrous ureter of *Amimopina macleayi* (Buliminidae). **aur**, auricle; **exp**, excretory pore; **kid**, kidney; **npc**, nephridial sac; **pcd**, pericardium; **plv**, pulmonary vein; **psu**, primary pseudo-ureter; **rec**, rectum; **ure**, ureter; **ven**, ventricle. (After Delhaye & Bouillon 1972c)
[C. Eadie]

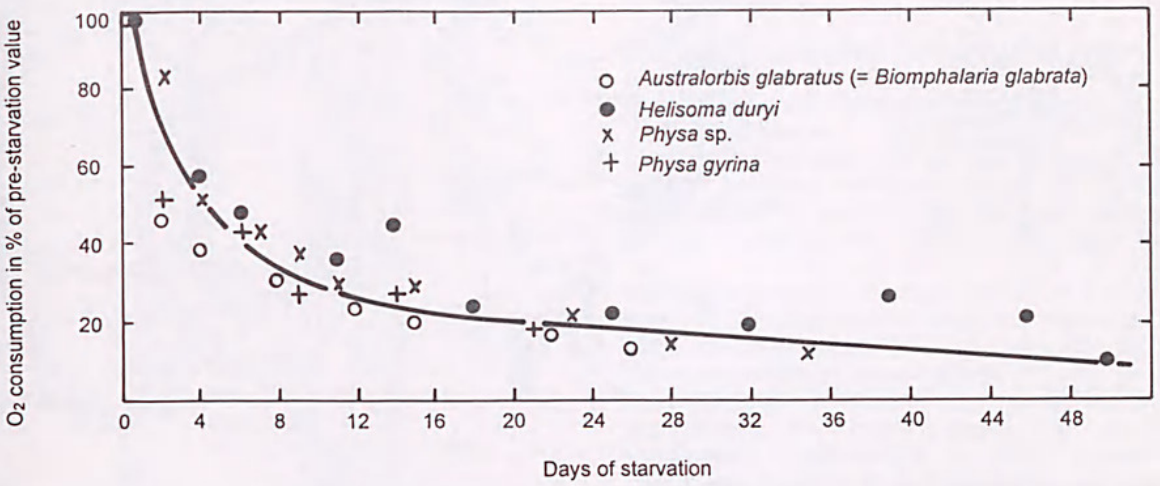

Figure 17.13 Effect of starvation on the rate of oxygen consumption of four pulmonate snail species. (Modified from Ghiretti & Ghiretti-Magaldi 1975) [C. Eadie]

closes in rhythmic sequence it is questionable as to whether each movement is related to respiratory ventilation (Ghiretti & Ghiretti-Magaldi 1975). Repetitive closing of the pneumostome may serve solely to reduce evaporation. Since the internal pressure of oxygen in the lung is lower than the ambient pressure, respiration by diffusion is also a possible mechanism for animals living at low metabolic levels.

Within the Stylommatophora, numerous variations on the typical mantle cavity form have arisen. In the Athoracophoridae, the pneumostome opens into a cavity from which numerous blind tubules extend into surrounding tissues in close association with blood vessels. The arrangement of the tubules is akin to the tracheal system of insects and although this arrangement is unusual, Solem (1959a, 1978a) considered that the 'tracheopulmonates' are merely highly modified sigmurethrans.

In more typical, derived slug-like taxa a discernible pattern of variation occurs (Solem 1978a; Tillier 1984a). Reduction in the visceral hump has caused compaction of the mantle cavity, resulting in relatively drastic changes in the arrangement of pallial organs. Compensation for the diminution of respiratory space takes two forms. Firstly, vascularisation of the remaining space is increased. Secondly, when compaction is severe, the available respiratory surfaces are increased in size either by internal rearrangement, as in the Athoracophoridae, or by the more commonly encountered condition seen in some semi-slugs (Tillier 1984a). In these, highly vascularised mantle lobes and shell laps, have evolved, thereby increasing the total gas exchange area (Solem 1978a).

Efficiency of respiration also depends on the oxygen-carrying capabilities of the respiratory pigments present. The only pigments that occur in pulmonates are haemocyanins and haemoglobins (Ghiretti & Ghiretti-Magaldi 1975). Among the pulmonates studied, most have haemocyanins. Several species lack respiratory pigments. Haemoglobin is present only in the Planorbidae, but its oxygen carrying capabilities are low and oxygen transport in these species is more likely to be dependent on the rapid movement of body fluids from the respiratory surface to the tissues and back (Ghiretti & Ghiretti-Magaldi 1975).

Among pulmonates, metabolic rates do not vary greatly from species to species, but oxygen consumption varies extensively (Table 17.2; Ghiretti & Ghiretti-Magaldi 1975). The rate of oxygen uptake during aestivation is not known, but is probably minimal. Other factors, such as physiological activity and biochemical changes in body tissues due to seasonal influences, can also affect oxygen uptake (Fig. 17.13).

Sense Organs and Nervous System

Pulmonates are euthyneurous. The central nervous system is detorted, and the ganglia are concentrated into a ring around the digestive tract. However, traces of chiastoneury in which connectives are crossed, are present in some Basommatophora, for example, the Ellobiidae. The degree of chiastoneury is variable. In higher pulmonates, such as the Helicidae, the various circumoesophageal ganglia are highly condensed and the connectives between them very short, but there is much variation among stylommatophoran pulmonates (Tillier 1989). In some basommatophorans, for example, the genera *Lymnaea* and *Chilina*, the various ganglia are well separated, but in others there is a tendency for shortening of connectives and fusion of ganglia (Fig. 17.14; Hubendick 1978).

Bargmann (1930) detailed the visceral nerve chain of pulmonates and concluded that eight types can be recognised. On the basis of functional cerebral-ganglion morphology, Van Mol (1967) proposed four main groupings – Archaeopulmonata (Ellobiidae, Otinidae), Basommatophora (remaining families), Soleolifera and Sigmurethura (all stylommatophoran families). Haszprunar & Huber (1990) recognised three basic types which define the Basommatophora, Systellommatophora (Gymnomorpha and Otinidae), and a new order, the Eupulmonata (= Trimusculidae, Ellobiidae, Stylommatophora). Tillier (1989) surveyed the visceral-chain morphology of most stylommatophoran families, and Emberton (1991) surveyed 17 stylommatophoran subfamilies, obtaining data which conflict in part with those of Tillier (1989).

In *Helix aspersa*, the circumoesophageal ring consists of nine ganglia and their connectives (Fig. 17.14C). The main ganglia are two cerebral ganglia, two pedal ganglia, two pleural ganglia, two parietal ganglia and an unpaired visceral ganglion (Hyman 1967). Additional ganglia connected to the oesophageal ring are the buccal ganglia and the tentacular ganglion. The ganglia forming the ventral part of the visceral ring are fused and consist of two pleural ganglia, two parietal ganglia, and a visceral ganglion (Fig. 17.14C); this pentaganglionate condition of the so-called visceral ring is also seen in opisthobranchs (Haszprunar 1985). Van Mol (1967, 1974) identified the procerebrum as the main synapomorphy of pulmonates. The procerebrum is assumed to be homologous with the rhinophoral gland of the Opisthobranchia (Haszprunar & Huber 1990) and has a neurosecretory function. It comprises small, globineurous cells, or large cells, or both (Van Mol 1967, 1974), features that correlate with modes of breathing. Contrary to the view of Van Mol (1967, 1974), Haszprunar & Huber (1990) considered the presence of large cells as primitive in the Pulmonata.

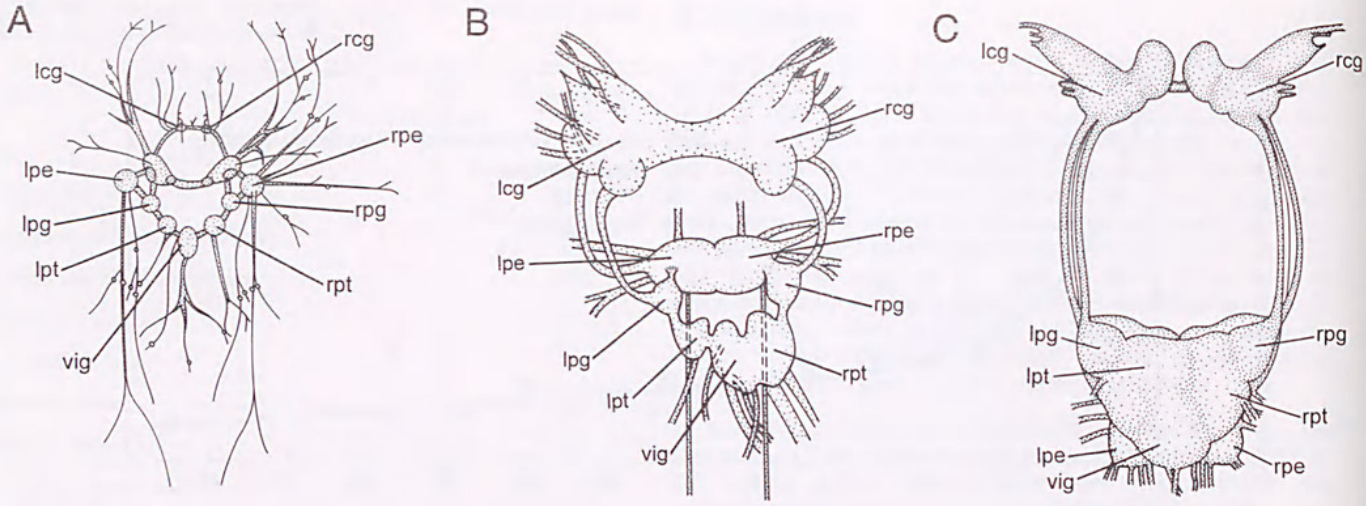

Figure 17.14 The circumoesophageal ganglia exhibit varying degrees of fusion. A, *Lymnaea* sp. (Lymnaeidae), in which the ganglia are all discrete. B, *Stenogyra* sp. (Subulinidae), exhibiting a moderate degree of fusion. C, *Helix* sp. (Helicidae), exhibiting the maximum extent of fusion. **lcg**, left cerebral ganglion; **lpe**, left pedal ganglion; **lpg**, left pleural ganglion; **lpt**, left parietal ganglion; **rcg**, right cerebral ganglion; **rpe**, right pedal ganglion; **rpg**, right pleural ganglion; **rpt**, right parietal ganglion; **vig**, visceral ganglion. (After Kerkut & Walker 1975) [C. Eadie]

Two additional neurosecretory centres are closely associated with the cerebral ganglion in the Pulmonata – the cerebral gland and the dorsal bodies. The presence of the cerebral gland is a synapomorphy for the pulmonate group, but is internalised in various lines (Van Mol 1967, 1974). The dorsal bodies are constant in shape and structure throughout the Pulmonata but display variability in innervation among the various subgroups (Boer, Slot & Van Andel 1968; Vincent, Griffond, Wijdenes & Gomot 1984).

The nerve trunks emanating from a particular ganglion may indicate its functional role, but the pattern of nerves radiating from particular ganglia varies from species to species. In some taxa, the cell bodies for a particular nerve axon are not necessarily within that ganglion; they may be situated in another ganglion, some distance away, as a result of condensation (Kerkut & Walker 1975).

The ganglia are covered by the epineural sheath, composed of dense, tough, white connective tissue, and each ganglion is supplied by symmetrically arranged arteries from the anterior aorta. A number of compounds, including those which are considered to be transmitter agents, have potent actions on pulmonate neurones. Studies have indicated similarities between pulmonate neurone receptors and the neurone receptors of other animal groups and there is strong evidence that acetylcholine is a transmitting agent between neurones in the pulmonate central nervous system (Kerkut & Walker 1975).

The major pulmonate sensory organs are the tentacles, eyes (Fig. 17.15) and statocysts (Fig. 17.16). The tentacles are either invaginable or contractile (Fig. 17.4) and their mode of function has been used by some authors to imply possible affinities between groups (for example, Burch & Patterson 1969).

The retractor muscle which invaginates the optic tentacle of stylommatophorans is a branch of the columellar muscle. It is covered with a thick cuticle overlying a columnar epithelium penetrated by the numerous distal neurosensory cell processes (Hyman 1967).

The single pair of tentacles present in the Basommatophora (Hubendick 1978) are contractile and are typically slender, cylindrical and pointed. The tentacles are reduced in certain marine groups. Within the Ellobiidae a pair of papillae present on the dorsal surface of the snout has been interpreted as a second pair of rudimentary tentacles.

Pulmonate eyes are vesicular, converse, and located either at the base of the tentacles (Basommatophora) or at or near the tip of the superior tentacles (Stylommatophora). The cornea is formed by flattened and transparent epidermis and the retina is composed of pigment and retinal cells (Fig. 17.15; Hyman 1967). The retinal cells are sensory and give rise to a nerve fibre which penetrates the connective tissue of the eye capsule before becoming part of the optic nerve. There is no optic ganglion (Kerkut & Walker 1975).

Pulmonate statocysts are generally situated laterally between the pleural and pedal ganglia. They are spherical in shape, covered by a layer of connective tissue and lined by hair-bearing epithelial cells; the lumen is filled with fluid and calcareous statoliths (Fig. 17.16; Kerkut & Walker 1975).

Reproduction

Pulmonates are hermaphrodites. The reproductive system is complex and variable (Figs 17.17, 17.18A), but conforms to a basic plan (Fig. 17.2C). The variability arises partly because the reproductive system is free to coil within the haemocoel (Duncan 1975). This allows for changes in the shape and size of various structures and the addition of various flagella, caeca and sacs to the basic reproductive system without the need for major spatial adjustments.

In some basommatophorans, the ovotestis is located in the visceral hump with the digestive gland. Protandric hermaphroditism is common among the more primitive forms (Hubendick 1978), whereas advanced groups, including the Lymnaeoidea, display simultaneous hermaphroditism (Geraerts & Joosse 1984).

A hermaphroditic duct, which may have one or more seminal vesicles attached, conducts the gametes to the fertilisation pocket at the base of the albumen gland. This region – the fertilisation pouch–seminal receptacle complex – including the carrefour region, is variable in structure. The subapical genitalia display variability in the extent of separation of the male and female ducts. In some species, such as *Pythia scarabaeus* and *Ovatella myosotis*, the genital duct is incompletely divided into 'semi-canals' (see Hubendick 1978). The female and male tracts are lined with glandular epithelium and prostatic epithelium, respectively. Gonopores are separate and the vas deferens is connected to the genital vestibule by an open ciliated groove. The spermatheca is inserted on the vagina.

In the Amphibolidae and Siphonariidae the hermaphroditic duct is long with a single lumen and there is a single genital pore in the typical anterior male position.

The freshwater basommatophorans have separate male and female ducts and the prostate gland is a series of invaginations of the male duct. The male copulatory organ (Fig. 17.18B, C) comprises a sheathed penis traversed by the vas deferens, frequently with a

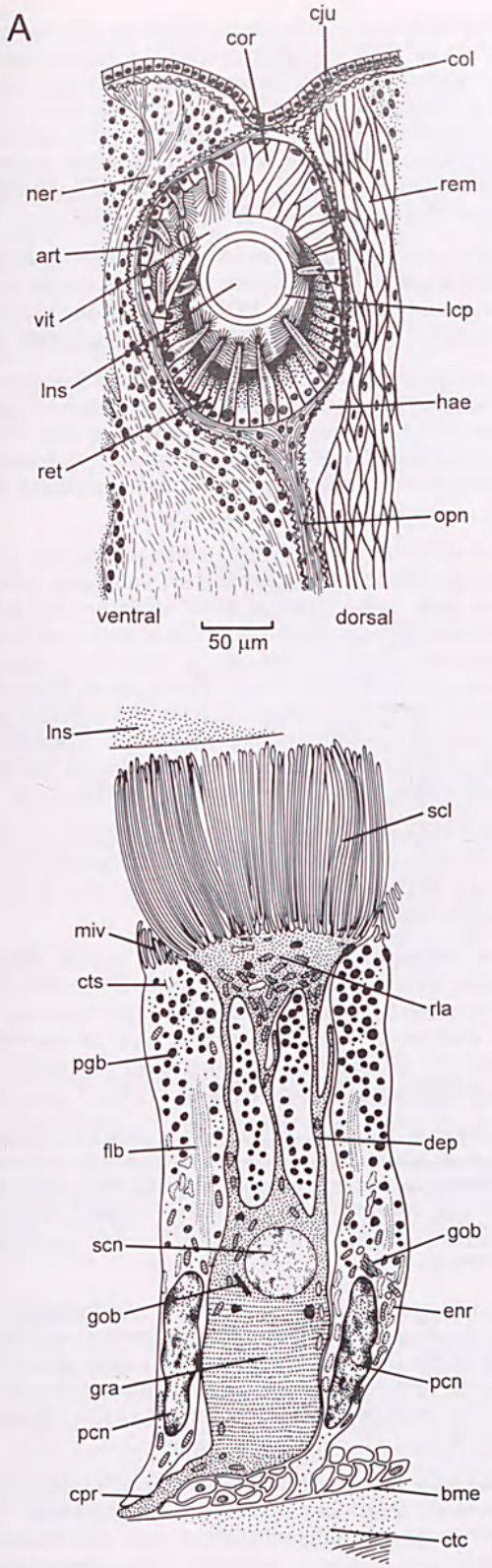

Figure 17.15 A, the eye of *Agriolimax* sp. (Limacidae), in longitudinal section, showing the main features. B, the fine structure of the retina of *Helix pomatia* (Helicidae), a sensory cell is shown surrounded by a pigment cell; the peripheral processes of the sensory cell join to form a receptor lamella from which projects the striated border; the central process arises from the base of the sensory cell. **art**, 'accessory retina'; **bme**, basement membrane; **cju**, conjunctiva; **col**, collagen; **cor**, cornea; **cpr**, central process; **ctc**, connective tissue capsule; **cts**, centrosome; **dep**, 'dendritic process'; **enr**, endoplasmic reticulum; **flb**, filament bundle; **gob**, golgi body; **gra**, granules or vesicles in base of sensory cell; **hae**, haemocoel; **lcp**, lens capsule; **lns**, lens; **miv**, microvilli; **ner**, tentacular nerve; **opn**, optic nerve; **pcn**, pigment cell nucleus; **pgb**, pigment body; **rem**, retractor muscle; **ret**, retina; **rla**, receptor lamella; **scl**, sensory cells; **scn**, sensory cell nucleus; **vit**, vitreous body. (After Kerkut & Walker 1975) [C. Eadie]

distal extension called the praeputium. A number of major penis types, each with its own set of variations, have been recorded (Hubendick 1978).

The Systellommatophora have the male and female genital openings separate. The male opening is situated at the anterior end of the animal and the female gonopore is located posteriorly either in the pedal grooves or the hyponotum. In the Onchidiidae the female opening is adjacent to the anus at the posterior end of the animal. Additional structures include dart glands in some onchidiids and a penial (Simroth) gland in the Rathouisiidae. The penis of veronicellids has a 'stimulator' (Bishop 1977).

The stylommatophoran ovotestis consists of a single or multiple group of follicles situated in the apical whorls of the digestive gland. Simultaneous hermaphroditism is typical though protandry has been recorded in several groups including some Australian camaenids (Solem & Christensen 1984). However, in terms of the differentiation of the primary gametes they are probably also simultaneous hermaphrodites. A coiled hermaphroditic duct connects the gonads to the carrefour region which varies in detail from family to family (Bayne 1973; Tompa 1984).

The structural arrangement is simple and similar in the Endodontidae and Charopidae (Solem 1976; Stanisic 1990). The carrefour region is a barely noticeable swelling in the gonoduct, partially buried in the albumen gland, and receives ducts from the gonad (hermaphroditic duct), talon and albumen gland. A separate duct exits to the prostate–uterus complex. The gonoducts distal of the carrefour region may be separate or fused. Solem (1972a, 1976) considered that having fused pallial gonoducts is a derived condition, and is a recurrent trend within the Stylommatophora. Duncan (1960) held an opposite view, stating that a single fused duct was followed by separation and specialisation of the male and female tracts. Tompa (1984) suggested that evolution of fused and separate tracts may be related to egg retention and the development of ovoviviparity in various pulmonate groups. In the Partulidae, other orthurethrans and the Succineidae there is partial fusion of the tracts. In the Charopidae, and most zonitids and helicoidean taxa, there is almost complete fusion of the gonoducts. In those groups with separate gonoducts the prostate gland is a thin tube and receives ducts from a number of prostatic alveoli which are usually arranged along its length in a specific pattern. Where the prostate gland and uterus are fused, as in the Charopidae, the prostatic duct, into which the prostatic alveoli discharge, is a lateral outpocket of the common gonoduct lumen. The uterus is a sac-like structure which may be differentiated along its length (Solem 1976; Stanisic 1990).

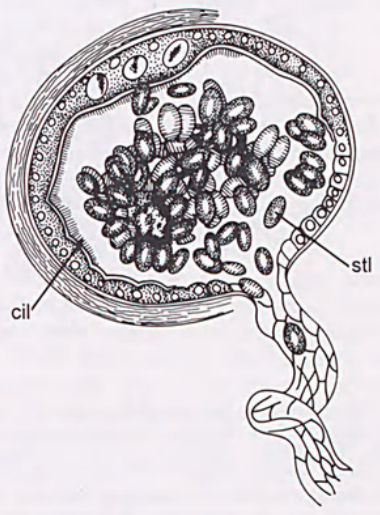

Figure 17.16 Structure of the pulmonate snail statocyst. **cil**, cilia; **stl**, statoliths. (After Kerkut & Walker 1975) [C. Eadie]

The terminal female genitalia consist of a relatively short muscular tube (= free oviduct) that gives rise to a muscular vagina. The stalk or duct of the spermatheca which enters the vagina or atrium, varies from long (as in charopids) to very short (as in enids). In the male genitalia the vas deferens leaves the prostate gland and either enters the penis directly, or expands to form a non-eversible muscular epiphallus which enters the penis through a simple pore or elaborate verge. The epiphallus assists in spermatophore formation.

The penis (Fig. 17.18B) is usually a muscular tube, often with a muscular sheath, and internal pilasters which show extensive structural variation particularly among sympatric congeneric species (Solem 1976, 1992; Emberton 1988, 1991; Stanisic 1990). A penial retractor muscle inserts on the penis or epiphallus. The penis may be reduced or absent (aphally) in some orthurethran and non-orthurethran groups (Cooke & Kondo 1960; Pokryszko 1987; Baur & Chen 1993). In these species the genital apertures are opposed at copulation.

In addition to the basic set of reproductive structures there are accessory mucous glands, dart sacs, appendices and flagella which have been derived independently in various taxa (Solem 1978a; Tompa 1984).

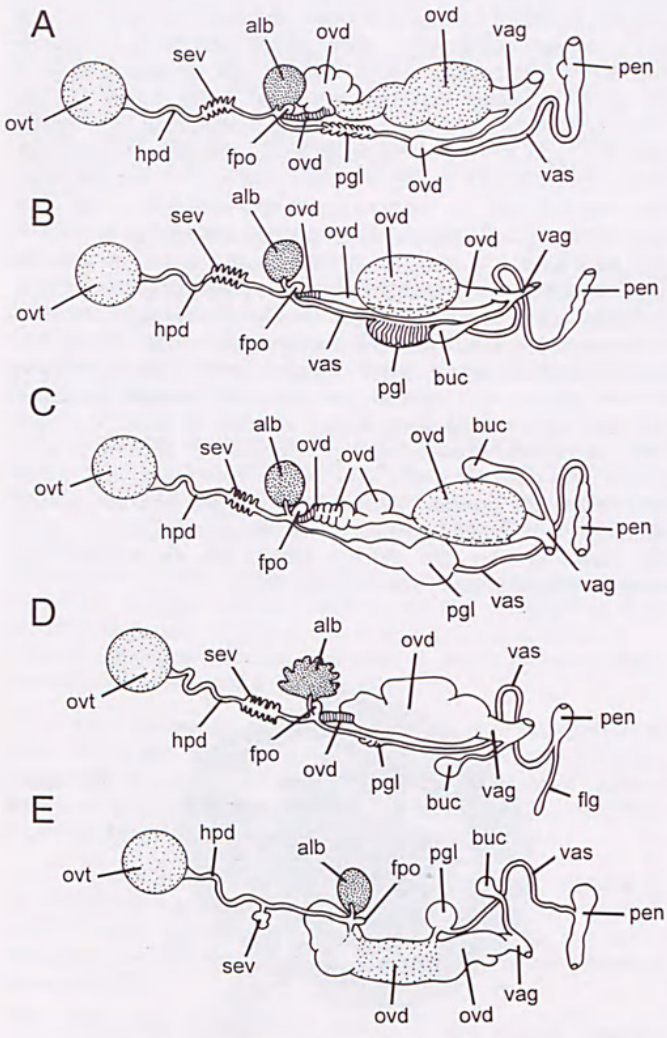

Figure 17.17 The organisation of the reproductive systems of representatives of freshwater basommatophoran families. Homologous organs of the female tract are shown by different shading. **A**, *Physa fontinalis* (Physidae). **B**, *Planorbarius corneus* (Planorbidae). **C**, *Lymnaea peregra* (Lymnaeidae). **D**, *Ancylus fluviatilis* (Ancylidae). **E**, *Acroloxus lacustris* (Acroloxidae). **alb**, albumen gland; **buc**, bursa copulatrix; **flg**, flagellum; **fpo**, fertilisation pocket; **hpd**, hermaphroditic duct; **ovd**, oviduct; **ovt**, ovotestis; **pen**, penis complex; **pgl**, prostate gland; **sev**, seminal vesicle; **vag**, vagina; **vas**, vas deferens. (After Duncan 1975) [C. Eadie]

In advanced taxa such as helicoideans the use of 'love darts' in the mating ritual has most probably developed to ensure successful coupling, and among the limacoideans, complex courtship procedures presumably have a similar purpose. Special recognition features include the stimulatory structures on the functioning surface of the penis and vagina, and head warts which are present in some advanced helicoids, African urocyclids and some camaenids (Tompa 1984; Solem 1985a, 1992).

Transfer of sperm may involve an exchange of unorganised sperm masses, or the transfer of distinctive chitinised envelopes of sperm or spermatophores (Solem 1974, 1978a). These sperm packets have variable and often complex species-specific shapes (Solem 1974).

Mating can take some time, and snails may be united for several hours (Tompa 1984). Fertilisation is usually reciprocal, although self-fertilisation has been reported in some species (Whitney 1940). In populations with aphallic individuals it is possible that self-fertilisation may be favoured over cross-fertilisation (Tompa 1984).

Compared with the eggs of most other gastropods, those of stylommatophorans are few in number, extremely yolky and sometimes quite large. The egg shell is elastic and partly or completely calcified, but not impermeable to water and the hazard of desiccation is partially obviated by behavioural adaptations which ensure oviposition in damp, shaded places or in the soil. Retention of the egg and subsequent birth of live young are also efficient adaptations for avoiding desiccation. Oviparity (egg laying) is most common but ovoviviparity and viviparity have been recorded for numerous species (Tompa 1979).

Most basommatophoran young hatch as crawling snails (Geraerts & Joosse 1984), but free swimming larvae are produced in some families such as the Amphibolidae, Onchidiidae (Raven 1975) and the Ellobiidae (Morton 1979).

Pulmonate ova are generally small and poor in yolk. When they are laid, each is surrounded by an egg capsule filled with albumen. In freshwater groups, these capsules are usually combined into a common mass by an outer membrane or jelly. In contrast, land pulmonates lay single eggs that are usually surrounded by a calcareous membrane (Fig. 1.20H; Raven 1975).

Egg formation is follicular and growth proceeds in two stages. Previtellogenesis leads to an increase in the amount of protoplasm and is followed by an accumulation of yolk (vitellogenesis). The yolk and egg capsule fluid (albumen) contain proteins and polysaccharides which play an important role in embryonic nutrition (Raven 1975).

Maturation of the pulmonate egg leads to the formation of the female pronucleus and involves two maturation spindles. The formation of the first maturation spindle is relatively similar in most taxa that have been studied, but four different ways in which the secondary maturation spindle is formed can be distinguished (Raven 1975).

Spermatogenesis and spermatozoa have been examined at the fine structural level in a number of pulmonate groups (Systellommatophora, Basommatophora and Stylommatophora: for reviews and principal references see Thompson 1973; Healy 1983, 1986; Healy & Jamieson 1989; Griffond Dadkhah-Teherani, Medina & Bride 1991). The spermatozoa (Fig. 17.19) most closely resemble those of opisthobranchs and certain 'allogastropod' groups such as the Pyramidelloidea, Rissoelloidea and Omalogyroidea (Healy 1993, 1996). Characteristic features of this type of internally fertilising spermatozoon include a distinctive acrosomal complex (consisting of a round vesicle supported basally by a columnar pedestal), a helical nucleus and a helical, highly elongate midpiece. In the midpiece, the 9 + 2 pattern axoneme is associated with nine coarse fibres (showing striated substructure) and enveloped by a complex mitochondrial derivative composed of matrix and paracrystalline layers and one or more enclosed, glycogen-filled helical spaces – the glycogen helices. A glycogen piece usually occurs posterior to

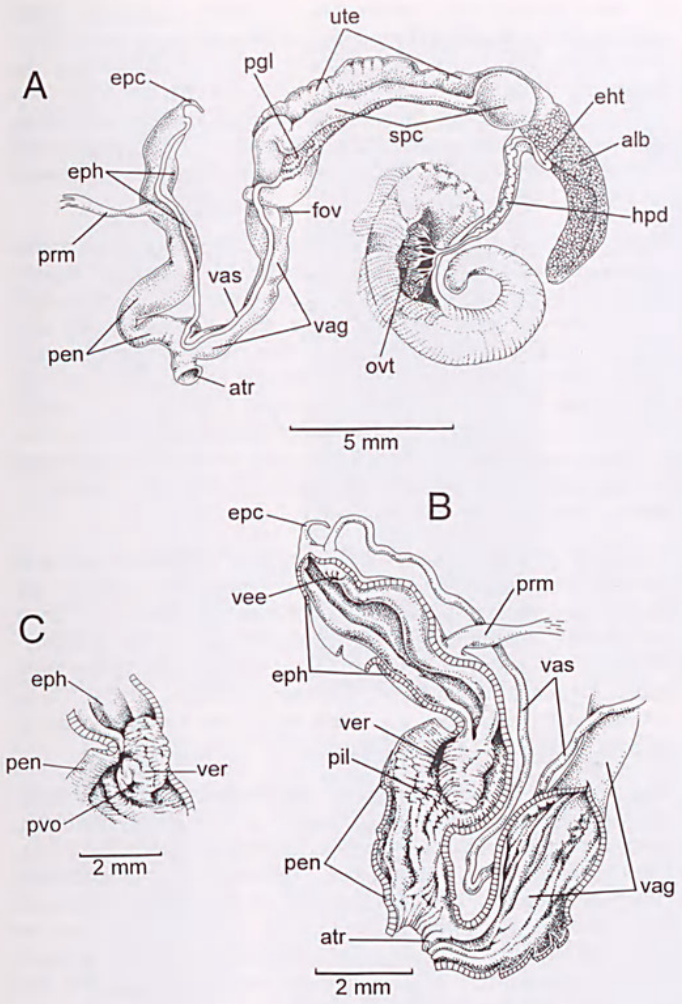

Figure 17.18 Genitalia of *Semotrachia esau* (Camaenidae). **A**, whole reproductive system; **B**, the interior of the epiphallus, penis and vagina; **C**, detail of verge. **alb**, albumen gland; **atr**, atrium; **eht**, entrance of hermaphroditic duct into talon; **epc**, epiphallic caecum; **eph**, epiphallus; **fov**, free oviduct; **hpd**, hermaphroditic duct; **ovt**, ovotestis; **pen**, penis; **pgl**, prostate gland; **pil**, pilaster; **prm**, penial retractor muscle; **pvo**, opening of verge into penis; **spc**, spermatheca; **ute**, uterus; **vag**, vagina; **vas**, vas deferens; **vee**, vas deferens entering epiphallus; **ver**, verge. (After Solem 1993) [R. Plant]

the midpiece, but is evidently absent in stylommatophoran pulmonates (Healy & Jamieson 1989; Giusti, Manganelli & Selmi 1991). Pulmonate taxa at and above the generic level show substantial differences in morphology of the acrosomal complex, nuclear keels and midpiece glycogen helices – to such an extent that sperm features have proved of taxonomic and potential phylogenetic usefulness (Thompson 1973; Healy 1983, 1988a, 1988b, 1996).

Embryology

Fertilisation in pulmonates involves the penetration of a single or of several sperm (polyspermy) into the egg. If more than one sperm enters, only one forms a pronucleus and the others eventually break down. The male pronucleus does not form until the second polar body is extruded. When male and female pronuclei come into close proximity, a spindle forms between them, the nuclear membranes of the pronuclei dissolve and their chromosomes become arranged in the first cleavage spindle (Raven 1975).

The egg undergoes determinate spiral cleavage (Raven 1975) and the coeloblastula develops following the formation of a small lumen in the blastula. Gastrulation is embolic and the archenteron is formed from the four primary endoderm cells. The blastopore becomes the mouth or site of stomodeal invagination and much of the stomodeum forms the oesophagus. The radular sac is a ventral invagination of the oesophagus. The foot arises as a protuberance below the mouth and a circular area of ectoderm gives rise to the shell gland which secretes a cap-like shell of organic material (Hyman 1967; Verdonk & Biggelaar 1983).

The pulmonate embryo has several structures which regress before hatching. These include the cephalocyst which accommodates the albumen sac, the podocyst which may be circulatory in function, and the protonephridia which have different origins in basommatophorans and stylommatophorans.

The mantle is formed from the shell gland. The shell is cup-shaped at first but becomes spirally coiled through more rapid growth on one side. In shelled pulmonates, the shell continues to grow and the mantle cavity originates as an invagination under the mantle which becomes closed by fusion to the neck region. In slugs, such as *Arion* and *Limax* species, the shell is encapsulated by the mantle and remains in a rudimentary condition. In *Onchidella celtica* the larval shell and larval operculum are shed at metamorphosis (Fretter 1943).

The stomach and crop develop from the archenteron and the pericardium, heart, and definitive nephridium develop from the mesodermal bands of the archenteron. In *Achatina fulica* these organs develop from the right mesodermal band (Ghose 1963), whereas the left band is involved in the basommatophoran *Planorbarius corneus* (Pötzsch 1904). Blood sinuses arise as spaces in the mesenchyme.

The nervous system is derived from the ectoderm and the ganglia are formed by proliferation of ectodermal cells that sink to the interior. The commissures and connectives are formed by secondary outgrowth from the ganglia.

The great majority of pulmonates hatch as young snails which are anatomically complete except for their reproductive system which originates as a single ectodermal invagination of the mantle cavity in the Stylommatophora. In the Basommatophora two separate primordia are involved (Fraser 1946). The reproductive structures are a system of vague tubules at birth and develop to maturity quite rapidly in some freshwater groups, but can take one to several years in some terrestrial species.

NATURAL HISTORY

Life History

Very little is known about the life histories of Australian pulmonates and available information is largely anecdotal. Most studies have been taxonomic, especially so for marine and freshwater species.

McLauchlan (1951) detailed the life cycles of several land snails from the Sydney region, New South Wales, and included incidental notes on the growth and habits of some Queensland species. Egg laying was documented for species of *Vercularion*, *Strangesta* and *Meridolum*, although some *Meridolum* species were reported to produce live young.

Kimberley camaenids, living in a highly seasonal monsoon climate with unpredictable wet seasons, have a four year maturation period before life as a true hermaphrodite (Solem & Christensen 1984). *Amplirhagada* species reach half adult size in the wet season of birth, attain adult size and become mature males at the end of their second wet season and function as males at the beginning of the third wet season. The female genitalia do not mature until the end of the third wet season. Hence the snail does not function as a hermaphrodite until the fourth and subsequent years. This specialised life cycle was probably derived from a more general pattern present among monsoonal land snails (Solem & Christensen 1984).

Adaptations to the monsoonal climate include morphological changes which may be peculiar to this fauna. The size of the ovotestis and hermaphroditic duct reduce midway through the wet season, probably to allow for increased nutrient storage before dry-season aestivation. Allosperm, produced during the wet season, are not immediately digested but are stored until late in the following dry season. This may contribute to more efficient sperm production in the following season or provide an additional source of nutrients for the snail. In addition, the species have the ability to respond rapidly to the onset of rain, leading to a frenzied pattern of feeding, mating and egg laying (Solem & Christensen 1984).

Growth in a monsoonal climate can be sporadic due to the variability of rainfall. Although the Kimberley camaenids reach adulthood at the end of their second wet season, the length of feeding activity, which is governed by the rains, varies from year to year and affects the final adult size in populations. In shorter and drier wet seasons and in situations where snails live in poor moisture-retaining microhabitats, the adult size of individuals is smaller because the snails become adult at a lower whorl count. In contrast, favourable moisture conditions allow extended growth time and greater numbers of whorls, and hence, larger individuals.

The seasonal adaptations and changes that have been documented for Kimberley land snails, could have application to many other Australian snail species. The seasonally related size differences reported by Solem & Christensen (1984) have been noted in Queensland land snails that inhabit the northern monsoon forests and those living in the seasonally dry subcoastal vine thickets of mid-eastern and south-eastern Queensland (J. Stanisic personal observation).

Data on longevity of Australian pulmonates are virtually non-existent. A life span of greater than eight years was postulated for Kimberley camaenids (Solem & Christensen 1984). Solem (1982) predicted a two year life cycle for the Kimberley helicarionid *Westracystis lissus*, based on presence of different size morphs among some populations of this species. McLauchlan (1951) estimated a life expectancy of six to seven years for some *Strangesta* species and McMichael & Iredale (1959) reported that specimens of the northern Queensland camaenid, *Chloritisanax banneri*, came to life after six years in a box at the Australian Museum.

Ecology

Australian Pulmonata can be divided into three basic ecological groups – marine, freshwater and terrestrial. With few exceptions basommatophorans are aquatic. The Ellobiidae (with a few terrestrial exceptions) and Amphibolidae are largely confined to mangroves (Fig. 1.47) or saltmarshes with some species on high energy shores in the supralittoral or upper littoral zones, whereas the limpet-like Siphonariidae and Trimusculidae are rocky shore dwellers. The higher limnic Basommatophora, which include the Lymnaeidae and Planorbidae, are found in both lentic and lotic freshwater environments and some, such as the Lymnaeidae, prefer mainly lentic habitats (slow or non-flowing waters) and even thrive under eutrophic conditions (Smith & Kershaw 1979). Freshwater species attach to weed and other suitable substrata such as rocks and timber and generally feed on algae. *Smeagol* species live among gravel and pebbles in the upper littoral zone (Tillier & Ponder 1992).

The Systellomatophora includes the marine Onchidiidae and two terrestrial slug families. Stylommatophorans are exclusively land dwellers.

Retention of moisture is the primary physiological problem for land snails. Hence in eastern Australia the majority of the land pulmonates are found in closed forests (= rainforest) where moisture levels in the form of rainfall and humidity are high. These forests also provide ample food and shelter. Comparatively few east coast species have made the transition to the drier eucalypt forests. In the arid parts of central and Western Australia snails live in isolated, moisture-conserving microhabitats and rely on patchy, predictable but variable monsoonal rains for survival. In each situation, the faunas are peculiarly adapted to their environment. Reproductive and behavioural strategies allow several species to survive in a single pile of rock talus in the Kimberley (Solem & Christensen 1984; Solem 1985b). In the eastern rainforests, snail diversity is high and slugs and semi-slugs have evolved. These species have reduced their dependence on the moisture-conserving features of a shell in response to relatively continuous high rainfall.

Limestone outcrops are also important refugia for land snails, particularly in eastern Australia and the Kimberley. In eastern Australia the outcrops frequently occur among drier sclerophyll forests, but the rocks trap available moisture in crevices and provide protection from wildfires. In these habitats, peculiar snail communities, often remarkably different from those in the surrounding forests, have developed. The land snails (Fig. 17.20A) that inhabit these exceptional refugia benefit from an ample supply of calcium and, because of long term isolation and the need to adapt to life among and on rocks, show shell and radular specialisations (Stanisic 1990).

Popularly, Australian land snails have been segregated into tree and litter species. Although the former is a practical category, the latter encompasses groups with a number of significantly different microhabitat preferences. For example, the 'litter-dwelling' Charopidae live on trees, rock surfaces, among moss, under bark, under logs and among dirt particles (Stanisic 1990). These microhabitat preferences are often significant systematically at both the generic and species levels.

Snails exploit a wide range of microhabitats in rainforests. Arboreal species include members of the Achatinellidae, Enidae, Helicarionidae, Charopidae (*Hedleyoconcha*, *Oreokera*), Cystopeltidae, and Camaenidae (*Bentosites*, *Chloritisanax*, papuinines; Fig 17.20B). They may live on trunks and branches of trees (Enidae, papuinines), under bark (*Chloritisanax*) or on leaves (*Hedleyoconcha*, Achatinellidae). *Triboniophorus graeffei* (Athoracophoridae) and Cystopeltidae live on the ground but forage on rocks and tree trunks at night.

The microhabitats of most ground-dwelling rainforest species have not been well documented and much of the available information is anecdotal and based on inference from few examples. Charopids have diverse microhabitat preferences (listed above). Helicarionids live under logs (*Melocystis*, *Helicarion sensu lato*; Fig. 17.20D), arboreally or among leaves in litter (*Nitor*). Some helicarionids are ground-dwelling but forage on the leaves and trunks of shrubs and trees. Rhytidids appear to live free in the litter/soil layer under logs. *Pedinogyra* (Caryodidae) and *Coelocion* (Megaspiridae) species live in litter among rock talus. Camaenids demonstrate an equivalent microhabitat diversity to that of charopids. Species of *Austrochloritis sensu lato*, *Meridolum* and *Galadistes* species seem to prefer living under logs. *Torresitrachia* and *Hadra* species (Fig. 17.20C) live either under rocks or logs, and species of *Trachiopsis* live in the top layer of litter and soil under logs and rocks. The minute pupilloid snails usually seal to the underside of logs, rocks, or bark on trees (*Pupisoma* species).

In central and western Australia, camaenids are usually associated with rock talus or vegetation clumps such as spinifex, and live buried deep in the talus or in soil, emerging only in response to the onset of rain.

Limestone outcrops provide a secondary, above-ground habitat and species such as the pupillid *Gyliotrachela australis* and some charopids (Stanisic 1990) live attached to the limestone rock, usually along driplines and in shaded areas.

The feeding habits and dietary preferences of the terrestrial pulmonates are poorly understood. The literature abounds with references to detritivores and fungivores. These terms have been loosely applied to entire groups of snails (Colman & Burch 1977) but not usually on the basis of direct observations of individual species.

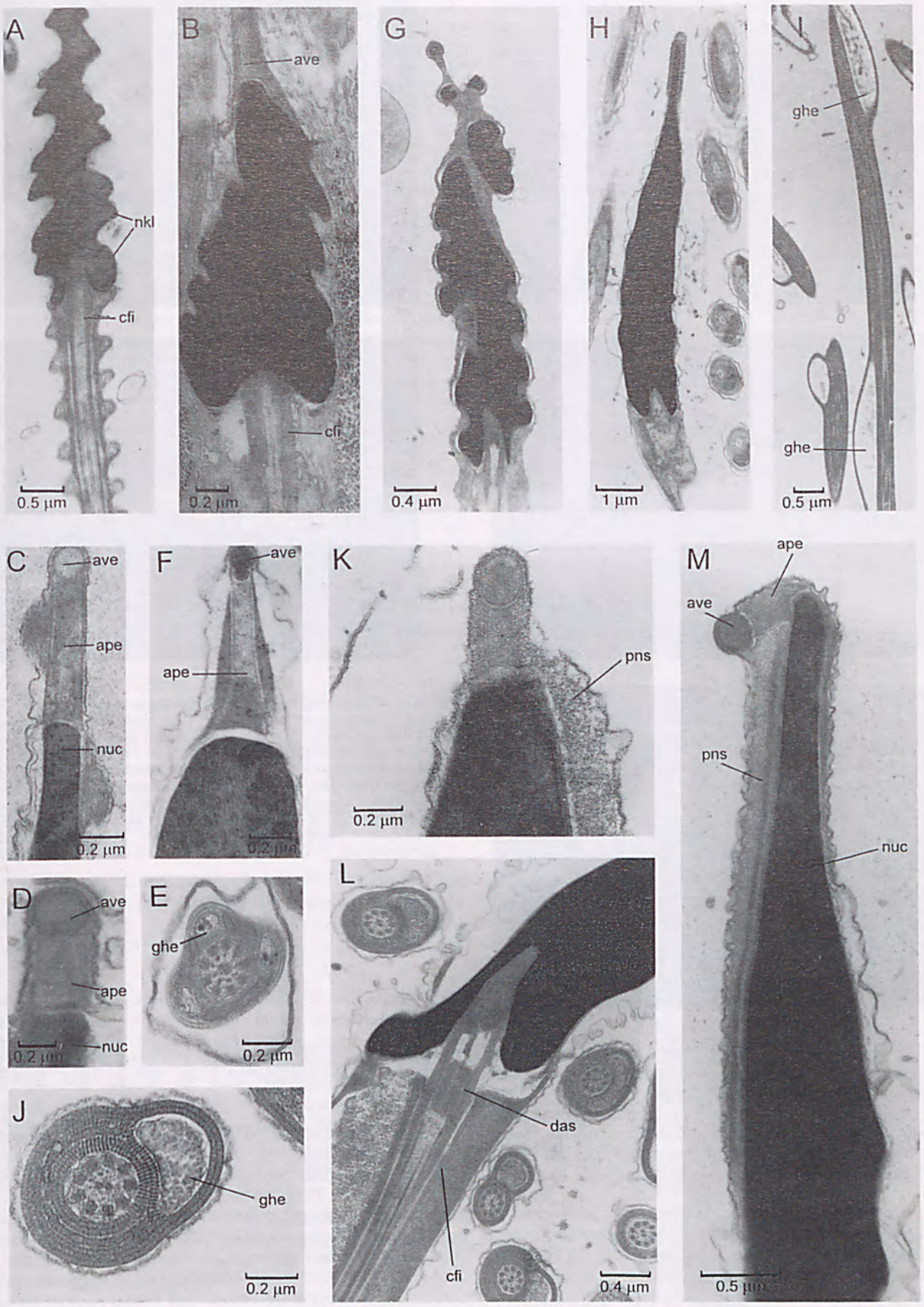

Figure 17.19 Pulmonate sperm ultrastructure. **A**, *Ophicardelus ornatus* (Ellobiidae), nucleus and portion of midpiece; **B**, *Austropeplea lessoni* (Lymnaeidae), acrosome, nucleus and portion of midpiece; **C**, *Salinator solida* (Amphibolidae), acrosome and nuclear apex; **D**, **E**, *Ophicardelus ornatus* (Ellobiidae), acrosome and transverse section of midpiece; **F**, *Onchidium damelii* (Onchidiidae), acrosome; **G**, *Helicarion australis* (Helicarionidae), nucleus; **H**, *Helix aspersa* (Helicidae), nucleus and portion of acrosome; **I**, *Helix aspersa*, spiralling glycogen helix in midpiece; **J**, *Sphaerospira bloomfieldi* (Camaenidae), acrosome and nuclear apex; **K**, *Sphaerospira yulei*, transverse section of midpiece; **L**, *Sphaerospira yulei*, longitudinal section of midpiece; **M**, *Helix aspersa*, acrosome and nuclear apex. **A**, **D**, **E**, Eupulmonata, Actophila; **B**, **C**, Basommatophora; **F**, Systellommatophora; **G–M**, Eupulmonata, Stylommatophora. **ape**, acrosomal pedestal; **ave**, acrosomal vesicle; **cfi**, coarse fibres; **das**, distal accessory sheath; **ghe**, glycogen helix; **nkl**, neck keel; **nuc**, nucleus; **pns**, perinuclear sheath. (A–E, from Healy 1983; H, L, M, from Healy & Jamieson 1989)

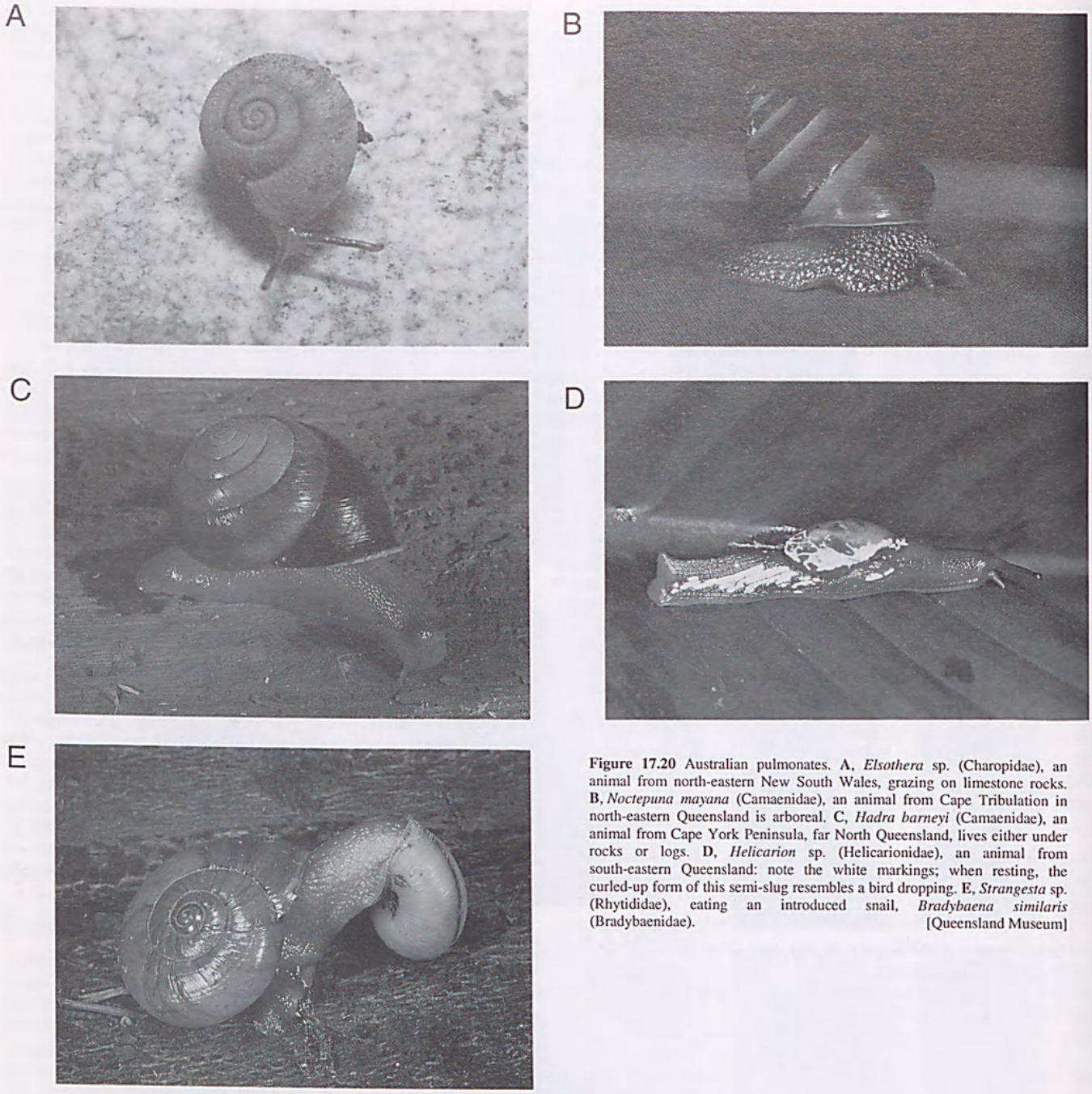

Figure 17.20 Australian pulmonates. **A**, *Elsothera* sp. (Charopidae), an animal from north-eastern New South Wales, grazing on limestone rocks. **B**, *Noctepuna mayana* (Camaenidae), an animal from Cape Tribulation in north-eastern Queensland is arboreal. **C**, *Hadra barneyi* (Camaenidae), an animal from Cape York Peninsula, far North Queensland, lives either under rocks or logs. **D**, *Helicarion* sp. (Helicarionidae), an animal from south-eastern Queensland: note the white markings; when resting, the curled-up form of this semi-slug resembles a bird dropping. **E**, *Strangesta* sp. (Rhytididae), eating an introduced snail, *Bradybaena similaris* (Bradybaenidae). [Queensland Museum]

McLauchlan (1951) reported that members of the carnivorous *Strangesta* feed on snails (Fig. 17.20E), worms and various other invertebrates. In the same study, a camaenid, *Meridolum* sp., was portrayed as an omnivore with a diet including vegetable matter, plant tissue, decaying vegetation and animal matter. Some charopids feed on microflora on limestone rocks (Stanisic 1990). Colman & Burch (1977) suggested that most are fungal feeders.

Feeding preferences, even within families, can be varied. In north-western Australia, species in the camaenid genera *Westraltrachia* and *Amplirhagada* are sympatric in limestone ranges. *Amplirhagada* species are generalised feeders on dead plant material. *Westraltrachia* species also feed on general plant debris except in limestone areas where they are sympatric with *Amplirhagada* species and graze on algal–fungal blooms on limestone seepage faces (Solem 1985b).

Cystopelta and *Triboniophorus* species and those helicarionids with arboreal habits probably feed on micro-algae and fungi that coat the stems, branches and leaves of trees. The Caryodidae are probably generalised feeders, although often caryodids have been collected while feeding on fungal mats under logs (J. Stanisic personal observation). On the basis of their dagger-like radular tooth shape, the rathouisiid slugs are possibly carnivorous (Burch 1976a).

Predators of snails are varied but there are few literature references to actual observations of snail predation. Birds are certainly significant predators, particularly in the rainforests of southern Queensland. The Noisy Pitta (*Pitta versicolor*) utilises a stone (anvil) to break the shell of larger snails (Camaenidae, Caryodidae) before extracting the animal (J. Stanisic personal observation). Mammals (rats and carnivorous marsupials) and reptiles also probably eat snails. Ants are considered to be important predators in shaping of the Pacific Island snail faunas (Solem 1976) and probably are also major snail predators in most areas of Australia. Other invertebrate predators include carabid beetles (Bishop 1981), glow worms (Scott 1990) and carnivorous snails.

Habitat destruction associated with human activity is ecologically catastrophic for snails and forest clearing, limestone mining and the predilection to burn on a cyclic basis (Colman 1987) all can have major impacts on the ultimate survival of individual snails and even entire species.

Behaviour

Paramount to the survival of a terrestrial snail is the need to conserve water (Machin 1975; Solem 1978a). Even though this need is reduced in aquatic species, certain behavioural traits and morphological adaptations assist them in maintaining correct water balance. Some of the marine pulmonates, in particular those inhabiting intertidal habitats, have developed limpet-like shells which are clamped to the substratum during periods of exposure. They become active and feed only on damp rocks or when submerged. Estuarine forms, such as *Salinator* species and the Ellobiidae, burrow to avoid the effects of freshwater immersion. *Salinator* also has an operculum.

Some freshwater species burrow and aestivate (Hyman 1967) to avoid desiccation whereas others secrete an epiphragm.

Terrestrial species are much more susceptible to the effects of water loss and employ a variety of means to reduce the effects of desiccation. Most pulmonates do not have an operculum and although the majority of species are able to withdraw into the shell, they still suffer water loss through the soft mantle tissue which is exposed to the elements, as well as through the shell itself (Machin 1975). Some species aestivate by sealing to the substratum (logs, rocks, leaves, other snails). However, a proportion are free sealers and secrete a calcium-impregnated mucous shield – the epiphragm (Fig. 1.62) – across the aperture. This structure performs the same function as an operculum and reduces moisture loss although it is permeable to oxygen. Depending on the severity of local conditions, snails may secrete numerous epiphragms as they retreat further into the shell (Solem 1974). Some species living in drier areas burrow into the soil (for example, *Xanthomelon pachystylum*), whereas others move deeper into rock crevices or talus piles (Solem 1992).

Slug and semi-slug species do not have a shell in which to withdraw and have evolved such that their activity periods coincide with the humid periods of the day (early morning/early evening) or periods of rainfall (*Cystopelta* and *Helicarion* species). Not unexpectedly some of these slug species secrete extremely thick mucus which possibly has anti-desiccation properties. Helicarionid semi-slugs can also reduce water loss by curling up into a tight ball when resting, thus exposing much less of the body surface to the effects of evaporation.

Desert snails, in particular, need to have behavioural and physiological characteristics to survive the very high temperatures of their surroundings. Warburg (1965) showed that the mainly arid zone *Themapupa adelaidae* was able to survive for eight hours at 50°C.

Defence against predators is varied. Burch (1976a) suggested that some slugs secrete a noxious mucus which, when combined with visual cues provided by bright colouration, may offer protection from predators. Some helicarionids wriggle their tail vigorously when handled, possibly to draw attention from the more vulnerable visceral mass (Scott 1990). Some slugs break off their tail deliberately (autotomy) when disturbed, enabling the slug to crawl to safety while the predator attacks the wriggling tail piece: the tail region subsequently regenerates (Hyman 1967). This has not yet been reported in Australian species.

Although slugs do not have the protective advantage of the shell, they are less restricted in their choice of hiding places. Without the encumbrance of a shell they can slip into the narrowest of crevices to hide from predators.

Snails depend on a sense of touch coupled with behaviour patterns and possibly pheromones to find a suitable mate. This problem is compounded when closely related species live in the same area (Solem 1974), and accessory structures have developed to assist successful mating. In the introduced *Helix aspersa* mating involves the exchange of love darts whereas courting behaviour in some limacids is highly ritualised and complex (Tompa 1984). Some members of the Camaenidae, for example, *Rhagada*, have developed elaborate head warts (Solem 1985a) which are situated between the superior tentacles. During mating these structures are intimately involved in the touching behaviour which is the lead-up to copulation. Head warts differ from species to species and presumably are species recognition devices.

Terrestrial pulmonates either produce live young or lay eggs that are subject to the same pressures of desiccation and predation as the adult snail. Few observations have been made on egg-laying behaviour. However, most land pulmonates are considered to lay clusters of rubbery eggs in depressions in the soil under logs or in rotting timbers (Tompa 1984). In contrast, *Strangesta* species and other rhytidids lay solitary, hard-shelled eggs (Colman & Burch 1977).

Economic Significance

In Australia, snails are of economic significance primarily as agricultural pests and carriers of disease. Their importance as a food item is minor in comparison with European countries (see also Chapter 1).

Most of the introduced snails and slugs feed on living plants and are pests either because they directly feed on crop seedlings and fruit, or because they can cause contamination to produce. Native species, however, are generally not regarded as pests as they are largely detritivores or fungivores.

Perhaps the most significant pulmonate pest species is the giant African snail, *Achatina fulica* (Fig. 17.21). A varied dietary menu, consisting of about 500 plant species, coupled with large size and voracious appetite, makes this species potentially the most dangerous for agriculturally based countries. It is present in Papua New Guinea and several other Pacific and South-East Asian countries. *Achatina fulica* was first recorded from Australia in the early 1970s. Fortunately, the single outbreak (Gordonvale, north-eastern Queensland) was successfully eradicated (Colman 1977).

Many introduced helicids and limacoidean slugs are pests of garden vegetables. The Asian snail, *Bradybaena similaris* (Fig. 17.22A), has become a pest in cucurbit crops in the Brisbane area where it feeds on young seedlings and causes faecal contamination of produce. In South Australia, the presence of the European helicid, *Cernuella virgata*, in wheat crops at harvest raises the water content of grain samples and reduces the monetary return to growers (Smith & Kershaw 1979); its control

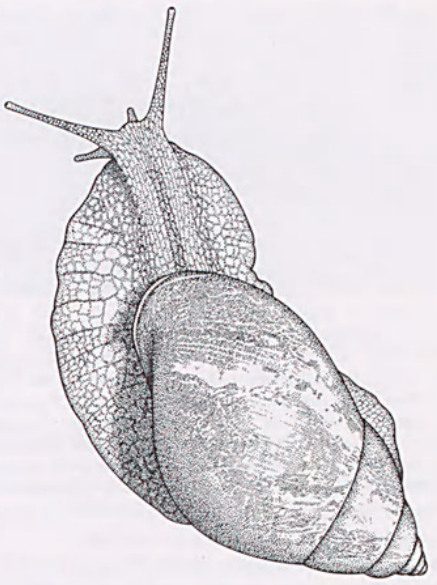

Figure 17.21 A native of East Africa, the giant African snail, *Achatina fulica*, is widely regarded as the world's most significant land snail pest. The one recorded infestation in Australia was eradicated. (After photograph from Watson 1985) [C. Eadie]

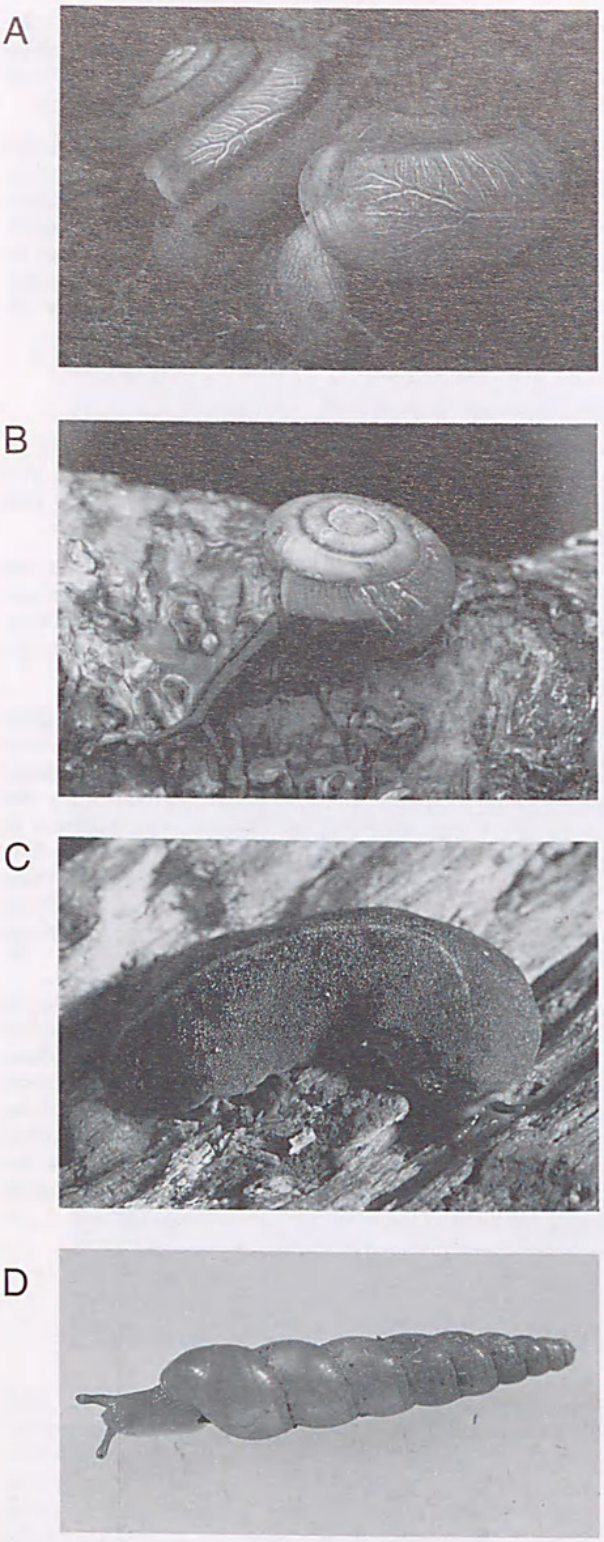

Figure 17.22 Pulmonates introduced to Australia. **A**, the Asian snail *Bradybaena similaris* (Bradybaenidae), animals from Brisbane; banded and unbanded forms. **B**, *Zonitoides arboreus* (Zonitidae), the orchid snail introduced from North America is a pest on orchid roots. **C**, *Laevicaulis alte* (Veronicellidae), is found in northern Australia. **D**, *Subulina octona* (Subulinidae), originally from tropical America, but now circumtropical, is a detritus-feeder which lives in coastal and adjacent areas of northern, eastern and south-eastern Australia. [Queensland Museum]

has become a major economic issue (Baker, G.H. 1986). The orchid snail, *Zonitoides arboreus* (Fig. 17.22B), which is established in eastern Australia, is a pest of orchid roots and seedlings and comes from the United States of America (Godan 1983). Some introduced European species, for example *Oxychilus* species and *Testacella haliotidea*, are carnivorous and can be beneficial by preying on introduced vegetarian snail species.

Snails are important vectors for human and stock diseases (Malek & Cheng 1974; Godan 1983) but fortunately few of the native species have been implicated as serious problems in this regard (Table 1.3). An exception is the native freshwater snail, *Austropeplea tomentosa*, which acts as an intermediate host for the sheep liver fluke, *Fasciola hepatica* (Boray & McMichael 1961; Boray 1964, 1969). The species ranges widely in eastern Australia, from Tasmania to Queensland (Boray 1964). The same snail species has been implicated in schistosome dermatitis (swimmers itch) caused by *Cercaria longicauda* in New Zealand (Featherston, Weeks & Featherston 1988). A similar dermatitis in northern Queensland involves *Austropeplea lessoni* from freshwaters as a secondary host (Blair & Islam 1983). A more important vector for liver fluke, the introduced *Lymnaea columella*, is now well established in New South Wales (Ponder 1975), and Victoria, Tasmania and Western Australia.

Schistosomiasis (bilharzia), a debilitating disease of humans in Asia and Africa, has the potential to be introduced through the importation of exotic freshwater snails. Some local species of the family Planorbidae may also be potential secondary hosts of this tropical parasite. However, a combination of high hygiene standards and low population density around most of Australia's tropical waterways probably mitigates against the disease becoming a serious and widespread problem among humans in Australia.

Meningoencephalic angiostrongylosis, a parasitic disease of man caused by the rat lung-worm, *Angiostrongylus cantonensis*, has been introduced to Queensland. The introduced slugs and snails, *Laevicaulis alte* (Fig. 17.22C), *Vaginulus plebeius*, *Bradybaena similaris* (Fig. 17.22A), *Subulina octona* (Fig. 17.22D) and probably many other pulmonates are secondary hosts for this parasite which has caused death in dogs and infects humans (Malek & Cheng 1974; Bishop 1977).

Australian culture has yet to accept 'escargot' as a part of its diet. Hence snail farming is not a major industry as it is in parts of Europe. Nevertheless, small scale operations, utilising the introduced garden snail, *Helix aspersa*, have been established in Victoria and New South Wales to supply a limited restaurant trade.

BIOGEOGRAPHY

The basic survey work needed to provide distributional data on most Australian pulmonate species has yet to be done. Checklists of the non-marine fauna were compiled by Iredale (1937a, 1937b, 1938, 1943a, 1944a, 1945) and Smith (1992) but an accurate estimate of the total number of non-marine pulmonate species is not yet possible. Detailed work on the semi-arid zone camaenids of central Australia, Western Australia and South Australia has increased the known number of species in that region from about 100 to over 350 species (Solem 1992). Stanisic (1990) revised 50 charopid species from Queensland and New South Wales, 27 of which were new, from an area traditionally regarded as having a low diversity for the family. A total fauna of over 1200 terrestrial species does not seem unrealistic.

Australia has comparatively few marine and freshwater pulmonates. McMichael & Iredale (1959) and McMichael (1967) presented overviews of the relationships of the freshwater species but without the basis of revisionary studies. Previously Hubendick (1951) had allied the Australian lymnaeids with South-East Asian stock. Walker (1984, 1988) completed a detailed revision of the non-planispiral planorbid genera and concluded that most (*Glyptophysa*, *Ancylastrum* species) are remnants of a Gondwanan fauna, but that at least one (*Amerianna*) arose in the Papua New Guinean–northern Australian region. Brown (1981) considered that the Australian planispiral planorbids are part of more widespread extralimital groups. Australian ancylids show morphological similarities to New Zealand species and are congeneric with species in New Caledonia, Hawaii, the Neotropics and the West Indies (Hubendick 1967).

The bulk of Australian pulmonates are land snails and their distribution over the continent is not homogeneous. Along the east coast (from the Torres Strait Islands to Tasmania) species diversity is high in the rainforests. The main reason for this is that rainforests are now, and have been in the past, important refugia for land snails (Stanisic 1990). The fact the rainforest has persisted and diversified in the face of post-Miocene aridity phases has enabled moisture dependent snails to develop complex sympatric communities in some areas, such as the Border Ranges of southern Queensland and northern New South Wales where more than 60 species occur with 30 to 40 species living at individual sites (J. Stanisic personal observations).

The drier rainforests (vine thickets and vine forests) of south-eastern Queensland, also support around 40 species per site. Mosaic diversity, in which the total faunal complement of an area consists of species clusters confined to particular plant communities has been noted in the tropical rainforests of northern Queensland. The high mountains of this region, such as Mount Bellenden Ker (Fig. 1.102B) and Mount Bartle Frere, have altitudinally segregated rainforest communities. The lowlands and foothills have typically tropical to subtropical vegetation, whereas the mountain summits (above 1000 m) are basically temperate in aspect. These upland environments are refuges for snail species not found at the lower levels (Stanisic 1987, 1990). Of a total of 45 species (from various families) recorded from Mount Bellenden Ker by Stanisic (1982), 14 were confined to the uppermost 500 m.

Development of high land snail diversity has not only involved sympatric communities in regions of high relative moisture. Limestone outcrops, with their ability to trap moisture and with an abundant supply of calcium, have been able to support island-like snail communities in a sea of snail-depauperate countryside. Solem (1988a, 1991) cites the extraordinary example of 28, mainly allopatric, camaenid land snail species from 52 km of limestone hills (Ningbing Ranges and Jeremiah Hills; Fig. 1.103) in the north-eastern Kimberley. The limestones of the Chillagoe–Palmerville area and the Rockhampton region of Queensland, and the many outcrops of the Great Dividing Range in New South Wales maintain diverse sympatric communities. The species complement comprises widespread, dry-adapted forms as well as a significant endemic component which displays relationships with the nearby rainforest fauna (Stanisic 1990).

In each of the above situations, the mechanisms of community evolution have been different. In the rainforests, local, short-term, climate-related barriers and subsequent dispersal in more favourable periods have led to allopatric speciation and the development of sympatric species pairs in some cases (Stanisic 1990). In the Kimberley, radiation into a region devoid of snail competitors, and with flood-assisted, seasonal dispersal, is considered to be the underlying mechanism (Solem 1985b).

At the regional level considerable attention has been paid to endemicity levels, resulting in the development of the regional faunal concept. Iredale (1937a) applied the concept to land snails and divided the continent into a number of faunal areas and regions characterised by particular land snail taxa which in turn inferred relationships with extralimital snail faunas: the faunal regions have been modified by McMichael & Iredale (1959) and Smith & Kershaw (1979) (see Fig. 1.90 and pp. 80–82). Hence in the north-east, the Solanderian Region is characterised by the papuinid tree snails, larger camaenids, and several neritopsines and caenogastropods which give it a distinctly Papua New Guinean character. In the south-east, the southern part of the Peronian Region is dominated by charopids, punctids and rhytidids thus implying a New Zealand connection. However, this approach provides very little information on the multiple origins of the snail fauna and the different underlying causes of diversity in a particular area. Stanisic (1994b) proposed a system of smaller subfaunal units based on coincidence of species ranges.

Regional data currently available on the terrestrial pulmonates are shown to be inadequate when tested by rigorous survey work. Smith (1984) presented a contemporary summary, but for data other than on the south-east of the continent (Smith & Kershaw 1979, 1981), he relied on incomplete check-lists. An exception to this is the work on Kimberley and northern Australian land snails by Alan Solem (Solem 1988b, 1991; Solem & McKenzie 1991) which was based on collections from numerous and widespread collecting sites. Solem (1988b) recorded a total of 245 land snail species (including several neritopsines and caenogastropods) for the Kimberley. Most of these were shown to be endemic to the Kimberley: only several had extended ranges (Solem 1988a).

Hypotheses about the origins of the Australian land pulmonate fauna have been proposed, but because of the lack of basic comparative studies, these are largely speculative.

McMichael & Iredale (1959) extended the regional fauna concept and divided pulmonates into southern or Gondwanan and northern or Palaeo-Oriental families, complemented by a small component of endemics. However, the treatment was flawed because of the excessive splitting of single family units. Solem (1959a, 1959b) rationalised the taxonomy and placed a greater emphasis on connections with near Pacific Islands. Bishop (1981) presented an analysis which acknowledged the lack of basic family distribution data in many parts of Australia.

The southern or Gondwanan families (Bruggen 1980) include the Charopidae, Bulimulidae, Rhytididae and Athoracophoridae, and those families of northern origin include the Camaenidae and Helicarionidae. Families that are part of wider world distributions include the Pupillidae, Punctidae, Succineidae and possibly the Megaspiridae. Families endemic to Australia are the Caryodidae, although possibly part of a wider acavoidean Gondwanan pattern, and the Cystopeltidae, which has been variously related to the Helicarionidae (Hedley 1890) and Charopidae (Tillier 1989).

More rigorous biogeographic analysis requires the development of more robust phylogenies for pulmonate families (reviewed by Emberton *et al.* 1990). It is highly probable that current views on the origins of some groups will be modified significantly. Solem (1985b) concluded that the Kimberley camaenids represent a post-Miocene colonisation from the Indonesian–Timor region and considered that the camaenids of eastern Australia derive from a separate wave of immigrants through the Papua New Guinea area. The multiple origins of the family are supported by morphological data (Solem 1992). Similarly the concept of the Charopidae as a homogeneous, temperately diverse Gondwanan family, is in question. Stanisic (1987, 1990) has established the family as a significant faunal unit in the subtropical and tropical regions of eastern Australia and has reported the presence of a previously unrecorded Rotadiscinae which has North American connections.

Hence, although the origins and affinities of the Australian pulmonates are probably diverse, the validity of such hypotheses has yet to be tested rigorously in most cases.

Lord Howe Island and Norfolk Island have extensive land snail faunas (Iredale 1944a, 1945) which also have yet to be studied critically. The Lord Howe Island species show some connections with Australia, New Zealand and New Caledonia through genera such as *Palaina*, *Placostylus* (Fig. 17.23) and *Hedleyoconcha*. However, the Norfolk Island fauna includes a large number of helicarionids which bear superficial resemblance to Pacific Island species.

Fossil Record

The earliest known land snails occur in the Palaeozoic (Upper Carboniferous or Pennsylvanian) of Europe and North America and include four families (two orders) of stylommatophoran pulmonates (Solem & Yochelson 1979). In contrast, the earliest record of the Basommatophora is from the late Jurassic. The first terrestrial basommatophoran was the ellobiid genus *Carychium* and the first freshwater ellobiids include *Zaptychius*. The oldest known higher limnic Basommatophora (Physidae, Planorbidae and Lymnaeidae) have been found in the late Jurassic Morrison Formation (Solem & Yochelson 1979).

Figure 17.23 *Placostylus bivaricosus* (Bulimulidae), one of the endemic snails on Lord Howe Island. [I. Hutton]

The non-Australian pulmonate fossil record is relatively extensive (Zilch 1959). In comparison the Australian non-marine fossil record is poor. Of the 17 stylommatophoran families with Australian endemic representatives, only three have a Southern Hemisphere origin in the fossil record (see Table 17.3). Solem (1979a) summarised the first appearance of land snails in the fossil record and showed that 43 out of 60 pulmonate families have a known fossil record (Table 17.3). Most make their first appearance between the Cretaceous and Eocene and most of the known radiations occur in the Northern Hemisphere where there are better known fossil deposits.

In general, Australian records of pulmonate gastropod fossils are Late Tertiary or Quaternary in age and there has been no attempt to produce a detailed taxonomic analysis of the species which have been found. Generic and familial placements have been made on the basis of gross shell features rather than detailed analysis and any phyletic or ecological inferences which have been made are largely speculative. This problem is exacerbated by the incomplete knowledge of the extant taxa. Even the earliest Australian land snail fossil records (Sowerby in Strzelecki 1845) are still somewhat enigmatic. '*Bulinus gunni*' has been tentatively assigned to *Bothriembryon* (McMichael 1968; Ludbrook 1980) but the relationships of '*Helix tasmaniensis*' are still in doubt; sculptural features (fine arcuate radials and spiral cords) led to an uncertain association of this species with the Rhytididae (Harris 1897).

A suite of species were subsequently described from yellow limestone (travertine) beds, probably of Pleistocene age, at Geilston Bay, Tasmania (Johnston 1880). These included *Helix tasmaniensis*, the extant *Tasmaphena sinclairi* (Rhytididae) and two species of unknown affinity. Pleistocene calcareous beds in the Kent Group, Bass Strait, yielded the keeled '*Helix*' *simsoniana*. This species was initially compared with the extant Tasmanian caryodid *Anoglypta launcestonensis* and the New Zealand *Rhytida greenwoodi*. Kershaw (1988a) considered that it was more probably related to the extant caryodid genus, *Pedinogyra*. Kendrick & Wilson (1975) discussed the relationships of some fossil species of *Bothriembryon* in south-western Australia.

Several fossil pulmonates, from Tertiary limestone rocks of northern Australia, were described by McMichael (1968), among them both freshwater and terrestrial species. The basommatophorans were referred to *Physastra*, *Anisus*, *Gyraulus*, *Isidorella* and *Syrioplanorbis*, all members of the Planorbidae. The last of these is known as a fossil in the Oligocene of Europe and occurs in the Recent of Syria. Land snails included *Bothyriembryon praecursoris* (Bulimulidae) and *Meracomelon lloydi* (Camaenidae) but the generic placements were somewhat uncertain.

Ludbrook (1980) documented more fossil land and freshwater pulmonates from Miocene limestone deposits of the Etadunna Formation in northern South Australia. These deposits included species previously described by McMichael (1968). Ludbrook (1978, 1984) also listed a number of Quaternary land snail fossils from South Australia and the western part of the Eucla Basin. All were considered conspecific with extant species. Quaternary fossil land snails have been recorded from limestones at Chillagoe, north-eastern Queensland (Odhner 1917) and Rockhampton, mid-eastern Queensland (Hill, Playford & Woods 1970). Stanisic (1994a) recorded a fossil caryodid from the Eocene deposits in mid-eastern Queensland (Fig. 17.24).

Numerous Quaternary fossils have been recorded from calcarenite ('coral rock') beds on Lord Howe Island (Iredale 1944a) and from Nepean Island, near Norfolk Island (Iredale 1945). The Lord Howe shells were considered to be conspecific with living forms: the Nepean Island forms were distinct from the nearby Norfolk Island species (Iredale 1945).

METHODS OF STUDY

If a study programme requires the collection and subsequent examination of pulmonate specimens, whether simply for identification purposes or more advanced studies, the methods of collection and preservation employed will depend on the objectives of that study program.

Collection of Specimens

Field collectors should be guided by a general knowledge of the ecology and habitat requirements of the species sought. A good general principle to follow is that if dead shells are found live material may not by far away. Unless the animal is needed only empty shells should be collected. When species are taken alive the collector should know if any of them are carnivorous otherwise valuable specimens may be lost by predation in the container – even of the same species, as cannibalism may occur. Live specimens may also eat paper labels if they are confined in containers for long periods.

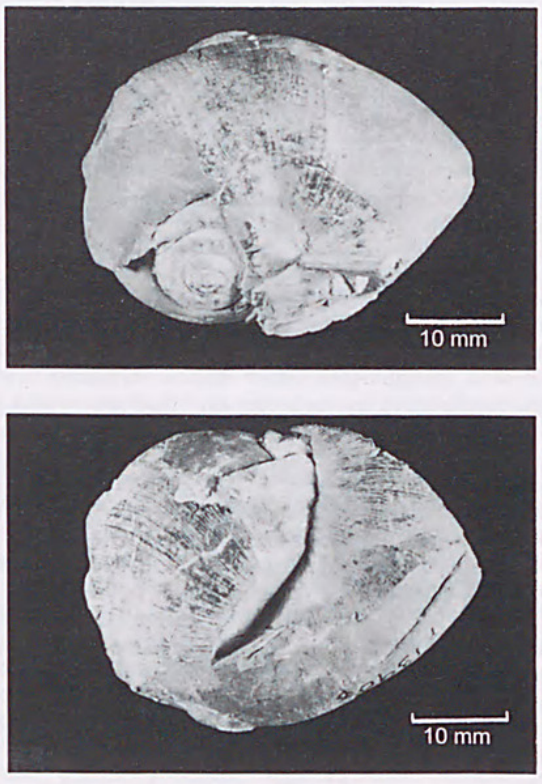

Figure 17.24 *Praecaryodes antiquata* (Caryodidae), a fossil land snail from the Tertiary deposits of mid-eastern Queensland. A, dorsal view; B, ventral view. (From Stanisic 1994a) [Queensland Museum]

Table 17.3 First appearance of native Australian eupulmonatan land snail families in the fossil record. (After Solem 1979a)

Group	Stratigraphic Time	Place
Suborder Stylommatophora		
Infraorder Orthurethra		
Superfamily Achatinelloidea		
Family Achatinellidae	Late Palaeozoic	North America, Europe
Superfamily Pupilloidea		
Family Pupillidae	Late Palaeozoic	North America
Superfamily Partuloidea		
Family Enidae	Late Palaeozoic	North America, Europe
Infraorder Sigmurethra		
Superfamily Achatinoidea		
Family Subulinidae	Palaeocene	Europe
Family Megaspiridae	Cretaceous	Europe
Superfamily Rhytidoidea		
Family Rhytididae	Pliocene	New Zealand
Superfamily Acavoidea		
Family Caryodidae	Eocene	Australia
Superfamily Bulimuloidea		
Family Bulimulidae	Eocene	South America
Superfamily Arionoidea		
Family Punctidae	Oligocene	Europe
Family Charopidae	Miocene	Micronesia
Family Helicodiscidae	Pleistocene	North America
Superfamily Succineoidea		
Family Succineidae	Palaeocene	Europe
Family Athoracophoridae	none	
Superfamily Limacoidea		
Family Helicarionidae	Lower Cretaceous	Europe
Family Cystopeltidae	none	
Family Trochomorphidae	none	
Superfamily Camaenoidea		
Family Camaenidae	Cretaceous	North America

All collections should be accompanied by information about where, when and by whom the specimens were collected. They should also include some note about the type of habitat in which the animals were found. This constitutes the minimum information necessary to accompany each collection in order to make the material of any use for subsequent study and reference. A collector should avoid collecting in any local, state or national parks or reserves. If collecting in such localities is necessary, collecting permits should be obtained as required and only the number of specimens needed for the project should be taken. Once the study has been completed the material should be lodged in a natural history museum.

Collectors of terrestrial species should be aware that different environmental conditions, such as climate can grossly affect the 'visibility or findability' of a population. For example, many specimens of the native slug, *Cystopelta purpura*, can be seen on the trunks of the snow gums in the Central Divide of Victoria on cool wet days when the cloud is low and everything is moist/wet. Even an experienced collector looking in the same habitat on a hot, dry, clear day would fail to find any specimens. Many terrestrial species are active in cool moist conditions, but others are only active in those conditions at night; it is therefore more convenient and pleasant for the collector to seek the animals in their places of shelter under logs, bark or rocks or in leaf litter. The most efficient way to collect the small litter-dwelling species is to collect a quantity of leaf litter and search it at leisure later using a microscope. This can be made semi-quantitative by collecting a standard amount of litter from each sample site.

Many aquatic species may be difficult to find by eye because of silt-laden water or dense vegetation. Hand nets or fine sieves can be used to strain out the larger species from mud and weed and small species can be efficiently collected by washing out weed or dead leaves into a bowl or bucket. The residue can be kept, if necessary, for microscopic examination. Deeper waters can be sampled by means of a small dredge or grab.

Marine pulmonates are collected using methods described in Chapter 1.

Transport of Live Material

Specimens are usually collected alive into small field vials and transported in these pending further treatment. However, even a few minutes in a small sealed tube in hot conditions can kill or seriously distress most species.

If specimens are to be kept alive for long periods, sent through the post or freighted over long distances, special precautions should be taken. It should be remembered that Australia and many overseas countries require permits for the import or export of live specimens. These permits can take time to obtain so the collector should, if possible, obtain the necessary documents before the material is collected to give the molluscs the best chance of survival as they may have to be held in transit while permits are obtained. Live specimens are best transported in moist, soft, non-living material such as dead leaves or damp (but not wet) tissue inside a sealed, inflated plastic bag. This in turn should be packed in soft packing inside a rigid box. Live plant material, such as grass or green leaves, should not be used as this respires in the container and depletes the available oxygen. Aquatic species also travel better in this way rather than in water, which quickly becomes foul, especially if one or two of the animals should die. Food is not usually necessary if the journey is only a day or two. Excessive heating or cooling is a problem and the rigid container and packing should be of some material which will prevent this. If in doubt, the inner plastic bag can be inflated with air to give the specimens a better chance of survival. Material packed in this way can be safely air-freighted to anywhere in the world.

Relaxation of Specimens

All pulmonates should be fully relaxed before killing as this allows better penetration of preservatives and presents the animal in a more convenient condition for dissection. It also allows external features to be examined easily. An evaluation of a number of narcotisation techniques was published by Runham, Isarankura & Smith (1965).

A reliable general technique is to drown the specimens in water with the aid of menthol crystals as a narcotising agent. A vial containing the specimens is filled completely with fresh water, a few small menthol crystals added and the vial sealed to exclude all air and left overnight. Next morning the water can be decanted carefully and fixative added to fix the relaxed specimens. In the case of terrestrial pulmonates, drowning the animals in a jar of freshwater alone, for 12–16 hours, has proved effective (J. Stanisic personal communication). Some slugs produce excessive amounts of very viscous mucus which should be gently removed before the animals are preserved. In an emergency, half a cigarette can be used as a narcotising agent. The tobacco should be removed from the paper, crumbled into the water and used as outlined above for menthol crystals. It is not quite as effective as menthol and has the disadvantage that tiny specimens may become lost in the strands of tobacco.

Preservation and Storage

The method adopted for killing, preservation and storage depends on the purpose for which the specimens have been collected. For use purely in identification of the species or as a general museum specimen, where general dissection is the only requirement, the relaxed animal can be killed by 'fixing' in 90% alcohol. After 24 hours the specimen should be transferred to a fresh solution of 70% alcohol for storage. This treatment gives a general preservation, keeps the internal organs soft, does not attack the shell, and preserves DNA for biochemical studies. Large specimens should be slit or injected to ensure good penetration. If any histological investigations are envisaged for the specimen the animals should be killed by immersion in 10% buffered formalin for six to 12 hours. They should then be washed in fresh, running water for five minutes, rinsed in 70% alcohol for five minutes and stored in fresh 70% alcohol. This method provides good general histological fixation of the tissues as well as preserving the natural colour of the organs and the shell sculpture. It does cause some hardening of the tissues and renders them more brittle in dissection, and tends to destroy DNA.

Other specialised cytological fixatives, such as Bouin's Fixative or Susa, can be used instead of buffered formalin. These preserve the fine structure of the cells and tissues better but are very poor for general dissection and many are acidic and quickly dissolve the shell, and destroy DNA.

The formula for 10% buffered formalin is one part concentrated formaldehyde solution, eight parts water and 5 gm/l of sodium bicarbonate powder. For a double buffered solution, add 6.6 gm of potassium dihydrogen orthophosphate and 31.0 gm of di-sodium hydrogen orthophosphate to 400 ml of concentrated formaldehyde solution, made up to 4 litres with water.

Sodium bicarbonate used with seawater is a good buffer. Ethyl alcohol is recommended for use rather than methyl alcohol as the latter tends to harden tissue.

Culture of Pulmonate Species

Most pulmonate species can be kept alive under artificial conditions for short periods of time. It is, however, a long step from there to either maintaining them in the laboratory for long periods of months or years, or getting them to breed in captivity, rearing several generations. In general, the culture conditions should mimic as closely as possible the natural conditions in which the species are found. The containers and contents should be kept as clean as possible to minimise contamination with such organisms as nematodes and mites.

Many Australian aquatic pulmonate species have been kept and bred in the laboratory (J. Burch & J. Walker personal communication). Conditions are kept favourable for them by providing clean water regularly and feeding with soft plant material such as lettuce. By contrast very few terrestrial species have been bred in captivity. McLauchlan (1951) provided valuable information on which to base further studies. Almost nothing has been published on the basic requirements and details of the life history of most terrestrial species.

Radular Preparation

Examination of the radula is very helpful in the identification of the family and generic placement of many pulmonate species.

The radula of any pulmonate can be extracted either from the buccal mass of large animals or after the shell of small animals is removed. Place buccal mass or entire animal of small species into about 25 ml of a 20% solution of sodium hydroxide in a test tube and heat in a water bath until the specimen has completely broken down – sabout 10 to 15 minutes or longer if necessary. Decant the material into a glass dish containing twice the volume of cold water, and place it on a dark, obliquely illuminated surface, such as a black tile, against which the radula will be easily seen as a fine silvery ribbon. Transfer the radula carefully with a mounted needle into a watch-glass of clean (preferably distilled) water for preparation for examination.

A Scanning Electron Microscope (SEM) provides by far the most useful and revealing technique of examining the radula. Details of the preparation of pulmonate radulae for examination by this method are given by Solem (1972b). Radulae can also be examined with a light microscope, for which the following method is quick and useful.

Extract the radula and transfer to clean water in a watch-glass. Mix a small amount of the powder stain Lignin Pink into a small quantity of polyvinyl lactophenol to produce a dark red solution. Place two drops of this solution onto one end of a glass microscope slide and transfer the radula into it using a mounted needle (picric acid is also a good stain for this purpose; W.F. Ponder personal communication). Leave the radula in the stain for about five minutes (depending on size). Transfer it gently to a drop of clear polyvinyl lactophenol on the same slide, for one minute. Transfer the stained radula to a fresh drop of clear polyvinyl lactophenol on a clean slide, arrange and cover with a cover-slip.

CLASSIFICATION

The classification of the Pulmonata given below (Table 17.4) incorporates the ordinal categories proposed by Haszprunar & Huber (1990) and the superfamily and family groupings of Solem (1978a) and Hubendick (1978). Tillier (1989) put forward a very different arrangement of families within the Stylommatophora from that of the more traditional system of Solem (1978a). Though Tillier (1989) demonstrated the artificiality of grouping the Sigmurethra on the basis of foot structure – Holopoda, Aulacopoda and Holopodopes – and proposed a division based on kidney shortening (Brachynephra *versus* Dolichonephra), this system has yet to achieve universal acceptance. Emberton *et al.* (1990) compared and assessed the levels of discrepancy of five stylommatophoran classifications, and evaluated the use of molecular sequence data in resolving stylommatophoran phylogeny. Adoption of the more traditional approach, which involves no subdivision of the sigmurethran superfamilies, reflects conservatism on the part of the authors.

Nordsieck (1992) further refined the system of Haszprunar & Huber (1990) by including the Systellommatophora in the order Eupulmonata and elevating the Basommatophora to ordinal rank.

Order SYSTELLOMMATOPHORA

Systellommatophorans are slug-like pulmonates which usually lack an internal or external shell or, rarely, have a reduced external shell. The mantle cavity is very reduced or absent. The dorsal mantle forms a notum which covers the head and sides of the body and extends into the hyponotum on the ventral surface (Figs 17.26A, 17.28B). The notum is separated from the hyponotum by a sharp keel or groove, the perinotum. The head usually bears one pair of tentacles. The procerebrum lacks large cells. The lung (pulmonary cavity) is posterior or absent and the pneumostome, anus and excretory pore are located behind the foot. The radula has mainly unicuspidate or bicuspidate teeth. The male gonopore is situated on the right side of the head and the female opening is located in the midline in the pedal groove, posteriorly near the anus or anteriorly near the right oral lappet.

The order is equivalent to the Ditremata, Gymnophila and Gymnomorpha with the addition of the Otinoidea following Tillier & Ponder (1992). Although various authors (Pilsbry 1948; Van Mol 1967, 1974; Solem 1978a; Tillier 1984b) have included the Systellommatophora among the Pulmonata, others, such as Salvini-Plawen (1970), have argued for an intermediate position between the Pulmonata and Opisthobranchia. However, Haszprunar (1988) presented evidence, based on a comparative analysis of the central nervous system, which indicated the monophyletic origin of the true Pulmonata and the Gymnomorpha. This view was further supported by Haszprunar & Huber (1990) and is followed here.

Table 17.4 Classification of the Pulmonata. Only those groups represented in the Australian fauna are included here. Ordinal classification follows Hazprunar & Huber (1990); superfamily and family groupings follow Solem (1978a) and Hubendick (1978). Families represented in Australia by introduced species are marked with an (I) and notes are appended where additional explanation of the classification has been considered necessary.

PULMONATA

Order SYSTELLOMMATOPHORA

- Superfamily OTINOIDEA (Note 1)
  - 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 (Note 2)
  - Family Planorbidae (I; Note 3)
  - Family Physidae (I)
- Superfamily GLACIDORBOIDEA (Note 4)
  - 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 (Note 5)
  - Family Pleurodiscidae (I)
  - Family Valloniidae (I)
- Superfamily PARTULOIDEA
  - Family Enidae
- Infraorder SIGMURETHRA
- Superfamily ACHATINOIDEA
  - Family Ferrussaciidae (I)
  - Family Subulinidae
  - Family Megaspiridae
  - Family Achatinidae (I; Note 6)
- Superfamily STREPTAXOIDEA
  - Family Streptaxidae (I)
- Superfamily RHYTIDOIDEA
  - Family Rhytididae
- Superfamily ACAVOIDEA
  - Family Caryodidae
- Superfamily BULIMULOIDEA
  - Family Bulimulidae (Note 7)
- Superfamily ARIONOIDEA
  - Family Punctidae
  - Family Charopidae
  - Family Helicodiscidae
  - Family Arionidae (I)
- Superfamily LIMACOIDEA
  - Family Limacidae (I)
  - Family Milacidae (I; Note 9)
  - Family Zonitidae (I)
  - Family Trochomorphidae (Note 10)
  - Family Helicarionidae
  - Family Cystopeltidae (Note 8)
  - Family Testacellidae (I)
- Superfamily SUCCINEOIDEA
  - Family Succineidae
  - Family Athoracophoridae
- Superfamily POLYGYROIDEA
  - Family Corillidae (Note 11)
- Superfamily CAMAENOIDEA
  - Family Camaenidae
- Superfamily HELICOIDEA
  - Family Helicidae (I)
  - Family Bradybaenidae (I)

Note 1. The inclusion of the Smeagolidae in the Otinoidea follows the suggestion of Tillier & Ponder (1992).

Note 2. The family Ancylidae is here kept as a separate entity following Zilch (1959) rather than combining it with Planorbidae in the new family Ancyloplanorbidae as proposed by Hubendick (1978). The name Ancyloplanorbidae is not valid as it is not based on an existing genus name.

Note 3. The status of the family Planorbidae and various subdivisions of the family are in a state of flux at present with work by Walker (1984) and others helping to clarify this difficult group.

Note 4. The superfamily Glacidorboidea and family Glacidorbidae are tentatively placed here as originally suggested by Ponder (1986) pending further assessment of the affinities of the group.

Note 5. The family Pupillidae is used here in the sense of Solem (1978a), to include the families Vertiginidae, Orculidae and Chondrinidae of Zilch (1959), following Smith (1992).

Note 6. The family Achatinidae is listed tentatively as part of the Australian fauna following the 'outbreak' of *Achatina fulica* in North Queensland recorded by Colman (1977). Although this population has now been eradicated, it is almost inevitable that this pest should become established in northern Australia in the near future, if it is not already there unrecorded. It is widely distributed on islands of the South-West Pacific and in New Guinea.

Note 7. Burch's (1976b) suggestion that the family Bulimulidae should be called Orthalicidae was followed by Smith & Kershaw (1979) in their work on the south-eastern Australian fauna. Here, however, the traditional use of the well-known name Bulimulidae is followed, as advocated by Solem (1978a).

Note 8. The omission of the family Cystopeltidae by Solem (1978a) was probably an oversight. The superfamily placement of this family is unsure, and until more work on its relationships has been done it is placed tentatively in the Limacoidea, an arrangement which possibly reflects its relationships.

Note 9. The family Milacidae is listed here separately from Limacidae, following Altena & Smith (1975), rather than as part of it, as treated by Solem (1978a).

Note 10. The family Trochomorphidae is included here as a separate family following Zilch (1950) rather than including it with the Zonitidae following Solem (1978a) and Smith (1992).

Note 11. The family Corillidae has been added to the listing given by Smith (1992) to accommodate *Craterodiscus pricei*, which was referred to this family by Tillier (1989).