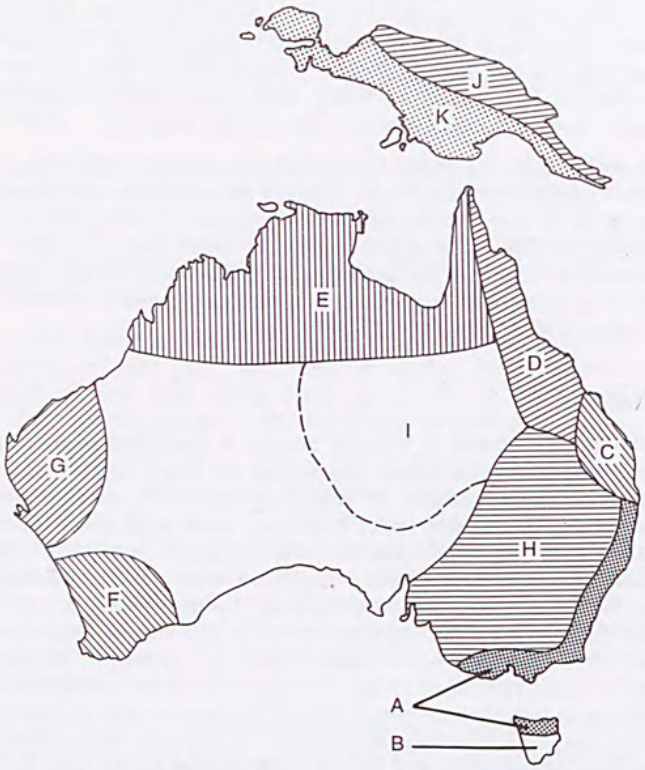

Figure 1.89 The fluvifaunal provinces of Australia and New Guinea. A, Lessonian. B, Tobinian. C, Krefftian. D, Jardinian. E, Leichhardtian. F, Vlaminghian. G, Greyian. H, Mitchellian. I, Sturtian. J, Gaimardian. K, Riechian. (After McMichael & Hiscock 1958) [I. Hallam]

the amalgamation of others by lowered sea levels. Subsequent recolonisation of estuaries from the relatively few remaining populations may explain, in part, why some estuarine species are relatively uniform genetically over large areas.

Deep Water Regions

Although the benthic marine molluscs of shallow waters (< 50 m depth) are relatively well known, benthic animals from depths greater than about 50 m are more difficult to collect, as trawls or dredges operated from vessels are required. Some general aspects of the zoogeography of deep-sea animals were outlined by Ebeling (1967).

The macro-molluscan fauna of the south-eastern continental shelf (50–200 m depth) has been studied in some detail, but very little is known about the shelf fauna from other parts of Australia. The upper slope fauna (200–500 m) from the east and north-west coasts of Australia has been collected in recent years but little work has been done on this material to date. In other parts of Australia the slope faunas are still essentially unknown.

Molluscs living at greater depths (500–2000 m or more) off the Australian coasts are largely unsampled, and much of the material from the handful of stations sampled to date is still unworked.

Pelagic Molluscs

The vast majority of marine mollusc species have benthic juvenile and adult stages. Apart from the bulk of cephalopods, only a few species belonging to four gastropod groups are holopelagic, that is, they complete the entire life cycle in the water column. Holopelagic gastropods include the heteropods, the thecosomatous and gymnosomatous pteropods and a few species of nudibranchs, and comprise fewer than 150 species across all groups (see Holopelagic Gastropods, this Chapter).

Different assemblages of pelagic organisms inhabit tropical, temperate and polar regions. Within these broad zones, defined largely by temperature, species are widespread, often occurring worldwide in areas with the appropriate temperatures. Some of the colder water species are thought to be bipolar, occurring in the northern and southern temperate or polar areas but not in the intervening tropics. The holoplanktonic molluscs recorded from the waters around Australia, including those found off the southern coast of the continent, are almost all tropical species. Further south, temperate species occur, of which two – *Limacina retroversa* and *L. helicina* – are recorded from southern Australia (Wells, F.E. 1989).

A very few molluscs are neustonic, actually living on the surface of the sea. They include the caenogastropod genus *Janthina* and members of the small nudibranch family Glaucidae. Both groups are tropical, though, like the pelagic molluscs, they have been found along the southern coast of Australia. Swimming cephalopods, such as squids, are usually widely distributed but the benthic octopuses, especially those with direct development, are typically more localised.

The developmental mode of a species is often correlated with its distribution, the relationship between planktonic larvae and large geographic ranges being well known (for example, Scheltema, R.S. 1971, 1978, this Chapter; Scheltema, R.S. & Williams 1983).

Introduced molluscs

A few marine molluscs are known to have been introduced to Australia. Several species, including *Neilo australis* (Neilonellidae), *Paphirus largillierti* (Veneridae) and *Maoricolpus roseus* (Turritellidae), may have become established successfully in Tasmania (Greenhill 1965; Dartnall 1974) following an apparently unsuccessful attempt to introduce the New Zealand Foveaux Strait oyster (*Ostrea lutaria*) (Dartnall 1974; Pollard & Hutchings 1990). The Pacific oyster, *Crassostrea gigas*, was introduced successfully into Tasmania during the 1940s, and is now well established in Victoria and New South Wales. *Maoricolpus roseus* is now the dominant molluscan species in parts of south-eastern Tasmania. The New Zealand gastropod *Zeacumantus subcarinatus* was introduced to the Sydney area in the 1930s (Iredale 1936). A listing of known introduced marine invertebrates was given by Pollard & Hutchings (1990).

Many marine animals and plants have been transported around the world on the hulls of ships (*cf.* Allen, F.E. 1953) and, more recently, in bulk carriers in ballast water (Hutchings, van der Velde & Keable 1987; Jones, M.M. 1991; Hutchings 1993). In addition to the sessile animals carried on the hulls of ships, other animals feeding or sheltering in these organisms, such as several nudibranch gastropods, have been distributed widely by such means (see Pollard & Hutchings 1990).

DISTRIBUTION AND AFFINITIES OF NON-MARINE MOLLUSCS

In contrast to the marine mollusc fauna, the non-marine fauna is much less diverse and most species have relatively restricted ranges. Most of the families which occur in Australia also occur on other continents, but there is a substantial degree of endemism at the generic and species level. Because of their generally poor powers of dispersal, freshwater molluscs (for example, Starobogatov 1970; Taylor, D.W. 1988) and terrestrial molluscs (Solem & van Bruggen 1984; van Bruggen 1987) make ideal subjects for biogeographic studies.

Non-marine Zoogeographical Regions

Most of the published studies on the zoogeography of Australian non-marine molluscs have referred separately either to freshwater or terrestrial forms, but they have not considered the two groups together. Tate (1887) was the first to attempt to delineate zoogeographical regions on the basis of the composition and distribution of the Australian terrestrial fauna. Subsequent rearrangements were made by Hedley (1884), Iredale (1937a,

1937b) and McMichael & Iredale (1959). Iredale & Whitley (1938) introduced the concept of a 'fluvifaunula' for a group of species that can be used to characterise each of the various freshwater zoogeographic areas of Australia. The concept was originally based on freshwater molluscs and fish, reflecting the taxonomic interests of the authors.

These two sets of zoogeographic regions have entirely distinct series of names for the different regions, despite the fact that Iredale & Whitley (1938) and McMichael & Iredale (1959) recognised that the patterns for freshwater distribution are in general agreement with those of terrestrial snails.

McMichael & Hiscock (1958) provided a modified version of the fluvifaunal provinces first proposed by Iredale & Whitley (1938) and revised by Iredale (1943) and Whitley (1947, 1959). This is based largely on major drainage systems (Fig. 1.89). Nine fluvifaunal areas are recognised in Australia and two in New Guinea.

The Lessonian fluvifaunula occurs in the southern half of the eastern coastal drainage system, that is, the rivers which flow mainly eastwards off the Great Dividing Range from northern New South Wales to western Victoria and including northern Tasmania. It is characterised by species of *Hyridella*, although the genera *Cucumerunio* and *Alathyria* from the north and *Velesunio* from the inland also occur in the region.

The Tobinian fluvifaunula occurs in southern Tasmania, and lacks hyriids.

The Krefftian fluvifaunula, in the coastal streams of the east coast of southern Queensland, is similar to that of the Lessonian but the genera *Alathyria* and *Cucumerunio* are characteristic; *Hyridella* only occurs in the southern part.

The Jardinian fluvifaunula, which occupies the eastern drainages of Cape York and the rest of northern Queensland, contains no characteristic hyriids, although *Velesunio* is present.

The Leichhardtian fluvifaunula occurs in northern Australia from the western side of Cape York to northern Western Australia; characteristic hyriid genera are *Velesunio* with some occurrences of *Alathyria*, and, in the north-western part, *Lortiella*.

The Vlaminghian fluvifaunula of south-western Australia is characterised by the endemic *Westralunio carteri*.

The Greyian fluvifaunula in the north-west of Western Australia has no hyriids.

The Michellian fluvifaunula occupies the Murray-Darling River system and includes *Velesunio ambiguus* and *Alathyria jacksoni*.

The Sturtian fluvifaunula occupies the Lake Eyre drainage system and contains only *Velesunio wilsonii*.

McMichael & Hiscock (1958) also included New Guinea in their scheme – with two fluvifaunulae recognised – a northern Gaimardian fluvifaunula, with *Velesunio sentaniensis*, and a southern Riechian fluvifaunula which contains species of *Alathyria*, *Hyridella*, *Westralunio* and *Microdontia* as well as two endemic genera, *Virgus* and *Haasodonta*.

B.J. Smith & Kershaw (1979) outlined six faunal regions for non-marine molluscs. These zones are not distinct; there are transitional areas between adjacent zones (Fig. 1.90).

The Leeuwinian Region, in south-western Western Australia is the most distinct of these faunal regions. Characteristic molluscs are the land snail genus *Bothriembryon* and the freshwater mussel *Westralunio carteri*.

The Dampierian Region in northern Western Australia includes the Kimberley and Pilbara areas, and is characterised by a number of camaenids, including the genus *Rhagada*. Previous authors have tended to include the Kimberley in a northern Australia unit with the Pilbara as a related area.

The Solanderian Region includes the northern part of the Northern Territory through eastern Queensland. The dominant snails are the camaenid genera *Bentosites* (= *Varohadra*) and *Xanthomelon*.

The Centralian Region covers the centre of the continent and almost all of South Australia. Characteristic genera include the camaenid genera *Sinumelon*, *Pleuroxia* and *Semotrachia* and the viviparid genus *Centrapala*. In Palm Valley, *Bothriembryon spenceri* is an important relict species.

The Oxleyan Region extends across south-eastern Queensland and north-eastern New South Wales. The dominant genera are *Meriodolum* (Camaenidae), *Hedleyella* and *Pedinogyra* (both Caryodidae).

The Peronian Region of south-eastern Australia, Victoria and Tasmania is characterised by charopids and hydrobiids.

Lord Howe Island and Norfolk Island both have largely endemic faunas which are quite distinct from those on the mainland and thus these islands could be regarded as separate regions also.

Whereas the recognition of provinces such as those outlined above may be a convenient way of viewing a fauna, there is a danger that they can be taken too seriously, with the assumption that they have real biological meaning. This they may have, but to date it has not been demonstrated rigorously. In fact, the utility of these non-marine provinces is probably not much greater than their somewhat discredited marine counterparts.

Doubts have been expressed about the concept and the division of Australia into zoogeographic regions. K.F. Walker (1981b) tested the distributions of freshwater mussels (Hyriidae) against the fluvifaunal provinces and concluded that the earlier literature considered 'faunal distributions only with a preconception of distinctive fluvifaunulae' and that 'the degree of overlap appears too great to warrant recognition of separate zoogeographic provinces'. He contended that 'authors apparently worked from the assumption that discrete fluvifaunulae do in fact occur, each assemblage having a geographic range more or less distinct from that of its neighbours. The selection of "characteristic" species on this basis provides spurious support for the concept as all members of the group must be considered'. Bishop (1981) pointed out the lack of published information on Australian zoogeographic patterns of terrestrial taxa, and suggested that obtaining data on phylogenetic relationships on a global basis within a family would be more fruitful.

Our lack of knowledge of Australian non-marine molluscs is amply illustrated by the monographic works on camaenid land snails in the Kimberley region of Western Australia by Solem

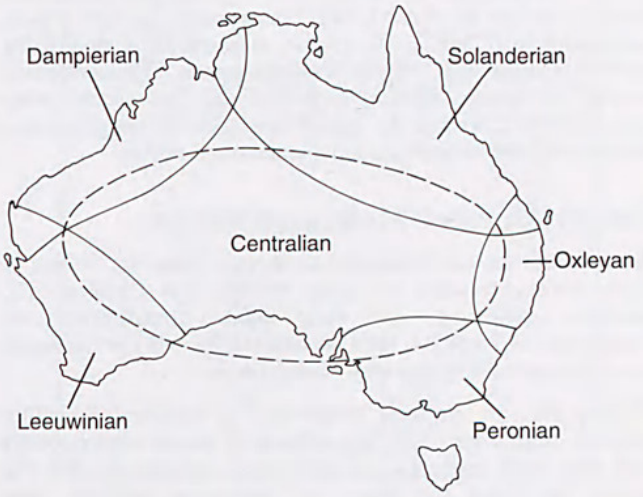

Figure 1.90 The six major faunal regions of Australia, with their transition zones. (After Smith, B.J. & Kershaw 1979) [I. Hallam]

Table 1.4 Freshwater mollusc families found in Australia. Those marked with an asterisk include at least one introduced taxon.

	Order	Family
Class Bivalvia		
Subclass Palaeoheterodonta	Unionoida	Hyriidae
Subclass Heterodonta	Veneroida	Sphaeriidae
		Corbiculidae
Class Gastropoda		
Superorder Neritopsina		Neritidae
Superorder Caenogastropoda	Architaenioglossa	Viviparidae*
	Sorbeoconcha	Thiaridae
		Hydrobiidae*
		Assimineidae
		Bithyniidae
		Pomatiopsidae
Superorder Heterobranchia	Pulmonata	Glacidorbidae
		Lymnaeidae*
		Planorbidae*
		Ancylidae
		Physidae*

(1979, 1981a, 1981b, 1984a, 1985, 1988a). In these papers, Solem monographed 139 species in 29 genera, of which 89 species (64%) and 12 genera were previously undescribed. He suggested in 1985 that only half of the living species had been described. Similarly, Ponder *et al.* (1993) described the freshwater snails of the *Beddomeia* group (Hydrobiidae); these include four genera and 67 species, of which 87% were new taxa, mostly Tasmanian.

The indigenous land and freshwater molluscan fauna of Australia comprises some 1020 described species – 224 freshwater and 796 terrestrial species (Smith, B.J. 1992 and subsequent papers to June 1995; see Table 1.7 in Conservation), excluding species from Lord Howe and Norfolk Islands. In addition there are 52 introduced taxa (Smith, B.J. 1992).

The Australian non-marine molluscan fauna is reasonably well known when contrasted with most other non-marine invertebrate groups, although B.J. Smith (1992) estimated that 30–40% of taxa, particularly small land snails, remain undescribed. A more likely estimate is about 50%, with the total non-marine fauna comprising around 2000 species. Most of the named freshwater species-group taxa (72% of 176) and the named terrestrial species-group taxa (81% of 642) are restricted to a single State or Territory.

The Freshwater Molluscan Fauna

An overview of the freshwater molluscan fauna by Walker is given under Molluscs of Inland Waters (this Chapter). The families represented, and their higher classification, are summarised in Table 1.4. Here we deal briefly with the taxonomic composition and biogeography of each family.

The Hyriidae are the most conspicuous of the bivalve families found in fresh water. They are rather well known taxonomically and show some interesting biogeographic patterns. To date this family has been the group of freshwater molluscs most commonly used for determining biogeographic patterns (see McMichael & Hiscock 1958; McMichael & Iredale 1959; Walker, K.F. 1981a).

Hyriids are also found in South America, New Guinea and New Zealand. Triassic fossils are known from North America (Banarescu 1990) and Australia (McMichael 1957; Ludbrook 1961). Of the Australian genera, *Alathyria* (four Australian species), *Westralunio* (one Australian species) and *Velesunio* (four Australian species) are also found in Papua New Guinea, and *Cucumerunio* (one Australian species) and *Hyridella* (four Australian species) also occur in New Zealand. Only *Lortiella* (two species) is restricted to Australia.

The Corbiculidae are represented by a few large species living in mangroves and in brackish water, and some tropical Australian species also extend into fresh water. The only truly freshwater taxon is *Corbicula* found in rivers through much of mainland Australia, but not Tasmania. B.J. Smith (1992) recognised two species, but the taxonomy of the Australian species of *Corbicula* is greatly in need of revision. The genus is also found in Asia.

Members of the third bivalve family, the cosmopolitan Sphaeriidae, are found mainly in temperate Australia, including Tasmania, the Murray-Darling Basin, coastal Queensland (Kuiper 1983) and the Northern Territory (W.F. Ponder personal observations). The only modern review (Kuiper 1983) is based purely on shell characters and substantial changes to the existing taxonomy are likely following revision based on a wider suite of characters. Presently the Australian representatives of the family are thought to represent only two genera, both of which are cosmopolitan. There are seven species of *Pisidium* (one introduced); one species is in the subgenus *Afropisidium* which has a wide distribution outside Australia. The three species of *Sphaerium* are all currently included in the endemic subgenus *Sphaerinova*.

Only two or three species of the widespread family Neritidae occur in freshwater habitats in Australia. They are restricted to the near coastal reaches of rivers and streams in tropical north-eastern and northern Australia (Smith, B.J. 1992). Very little is known of their biology.

The Viviparidae are represented in Australia by at least six species in three indigenous genera (Smith, B.J. 1992). They are mainly associated with major river systems in the northern half of Australia and in the Murray-Darling system (Cotton 1935b, 1935c; Stoddart 1982; Smith, B.J. 1992; Sheldon & Walker 1993b). In addition, an introduced Chinese species has been recorded recently from the Sydney region (Shea 1994). No viviparids are known from Tasmania. Viviparids are found on all continents (Banarescu 1990) and, at the least, it is likely that the genera *Notopala* and *Larina* (?= *Centrapala*) are closely related to taxa in New Guinea and Asia.

The cerithioidean family, Thiaridae, is found throughout Asia, Africa, and the tropical Indo-Pacific islands. In Australia it is represented by five genera (*Brotia*, *Melanoides*, *Ripalania*, *Sermylasma* and *Thiara*) and several subgenera (Smith, B.J. 1992). This arrangement is tentative, as the taxonomy of the Australian members of this family is generally poorly understood. The group is most diverse in northern Australia, but *Thiara (Plotiopsis) balonnensis* is found in the Murray-Darling system and many large coastal rivers, and a similar species, *T. (P.) lirata* occurs in south-western Western Australian rivers. *Thiara amarula*, typical of the genus, occurs across northern Australia and is also found from East Africa and Madagascar to New Caledonia, Fiji and Samoa (Starmühlner 1976). At least one species, *Melanoides tuberculata*, has colonised other tropical areas successfully, including the southern United States of America. Like some other members of this family, it is parthenogenetic and ovoviviparous. It is not clear whether this species, found through much of tropical Australia, has become established in Australia or is native to the area. Other *Melanoides* species, members of the subgenus *Stenomelania*, are native to Australia; two species are found in Queensland, and another in northern New South Wales. According to the present classification (Smith, B.J. 1992), two endemic monotypic genera, *Ripalania* and *Sermylasma*, are confined to rivers in tropical eastern Queensland, and *Brotia (Pseudopotamis) supralirata* occurs on the Torres Strait islands.

Several rissooidean families live in inland waters – the Hydrobiidae, Assimineidae, Pomatiopsidae and Bithyniidae. The Hydrobiidae are by far the most diverse and the most speciose of all Australian freshwater molluscan families. This family is found mainly in south-eastern Australia but has also undergone significant radiations in artesian springs associated with the Great Artesian Basin (Ponder 1986b; Ponder *et al.* 1989; Ponder & Clark 1990) and on Lord Howe Island (Ponder 1982).

Two major hydrobiid groups are represented in Australia (Ponder 1992a). The *Hemistomia* group comprises several genera including *Fluvidona*, *Angrobia*, *Posticobia*, *Jardinella*, *Fonscochlea* and the estuarine *Tatea* which is related to faunas in New Zealand and New Caledonia. The *Beddomeia* group comprises the second major radiation and includes *Beddomeia*, *Phrantela*, *Nanocochlea* and *Victodrobia*; the last of these is found only in Victoria and the remainder occur in Tasmania (Ponder *et al.* 1993).

Within Tasmania, species of *Phrantela* and *Beddomeia* are restricted to the western and northern areas respectively, with the exception of one atypical species of *Beddomeia* found in the Franklin River drainage (Fig. 1.91). This group of genera has no obvious close relationship with any extralimital taxa. The genus *Ascorhis*, which is normally estuarine, was recorded from brackish temporary pools near Lake Eyre South (Ponder & Clark 1988) to which, presumably, it had been transported from the coast by birds. The Hydrobiidae are found in Europe, the Americas, northern and western Africa, Sulawesi, New Zealand, New Caledonia, New Guinea and on a few Pacific oceanic islands.

A New Zealand species, the parthenogenetic, ovoviviparous *Potamopyrgus antipodarum* (Ponder 1988), is widespread in disturbed areas in south-eastern Australia, and is probably now the commonest freshwater snail in south-eastern Australia, including Tasmania; it is also well established over much of Europe and, more recently, has been found in the United States of America. Hydrobiids often have very restricted distributions and can show high levels of genetic structuring in very small areas (Ponder *et al.* 1994).

The cosmopolitan Assimineidae occur mainly in the marine supralittoral, typically in estuarine habitats. The family is represented in fresh waters of south-western Australia by *Austroassiminea letha* (Solem *et al.* 1982), which is found in a few coastal springs and seepages, and by several unnamed taxa from springs in north-western Australia and the Northern Territory (W.F. Ponder personal observations).

The Pomatiopsidae have undergone major radiations in Asia (Davis, G.M. 1979 and subsequent papers) and are also found in the Americas and Africa. In Australia, this Gondwanan family is represented by only a single genus, *Coxiella*, which is confined to salt lakes and saline coastal lagoons and rivers over much of the mainland and, in Tasmania, to coastal ponds. *Tomichia* from southern Africa is a probable sister taxon to *Coxiella*; *Aquidauania* from South America is also related (Davis, G.M. 1979).

Species of the family Bithyniidae are found throughout much of the mainland, but not Tasmania. They are usually found in muddy pools, billabongs and slow, muddy streams or rivers. B.J. Smith (1992) listed only a single species (*Gabbia australis*) but several unnamed taxa are known from northern Australia (W.F. Ponder personal observations). The family is also found in Eurasia, Africa and India and parts of South-East Asia. The genus *Gabbia* is known from Australia and southern New Guinea; although Asian taxa are placed in this genus, according to Starobogatov (1970) they belong to different genera. At present the biogeographic and taxonomic relationships of the Australian taxa have not been determined and more definitive conclusions await further study.

Australian members of the family Stenothyridae are generally found in estuarine waters (Smith, B.J. 1992). However a few taxa occur in the lower reaches of tropical Australian rivers just upstream of brackish areas.

On the basis of our present understanding, it appears that most of the species in the freshwater pulmonate families have rather broad distributions. Members of the cosmopolitan family Lymnaeidae are widely distributed. *Austropeplea lessoni* ranges over much of the Australian mainland – although northern populations are sometimes regarded as a separate species, *Austropeplea vinosa* – and *A. tomentosa* occurs throughout south-eastern Australia and Tasmania into South Australia (Boray & McMichael 1961; Boray 1964; Smith, B.J. 1992). This species is also native to New Zealand (Boray & McMichael 1961; Climo & Pullan 1972). Fossils resembling *A. tomentosa* are known from New Zealand (Climo & Pullan 1972) and Australia (W.F. Ponder personal observations), and Australian and New Zealand populations are morphologically indistinguishable (Boray & McMichael 1961). However, it is unlikely that a freshwater species would maintain sufficient gene flow across the Tasman Sea for speciation not to have occurred so further studies are required to verify the relationships of the New Zealand and Australian populations. Several introduced species are recorded from Australia, four of which are well established (Boray 1978; Kershaw 1991; Smith, B.J. 1992); they include *Pseudosuccinea columella*, an intermediate host of liver fluke (Ponder 1975; Boray 1978),

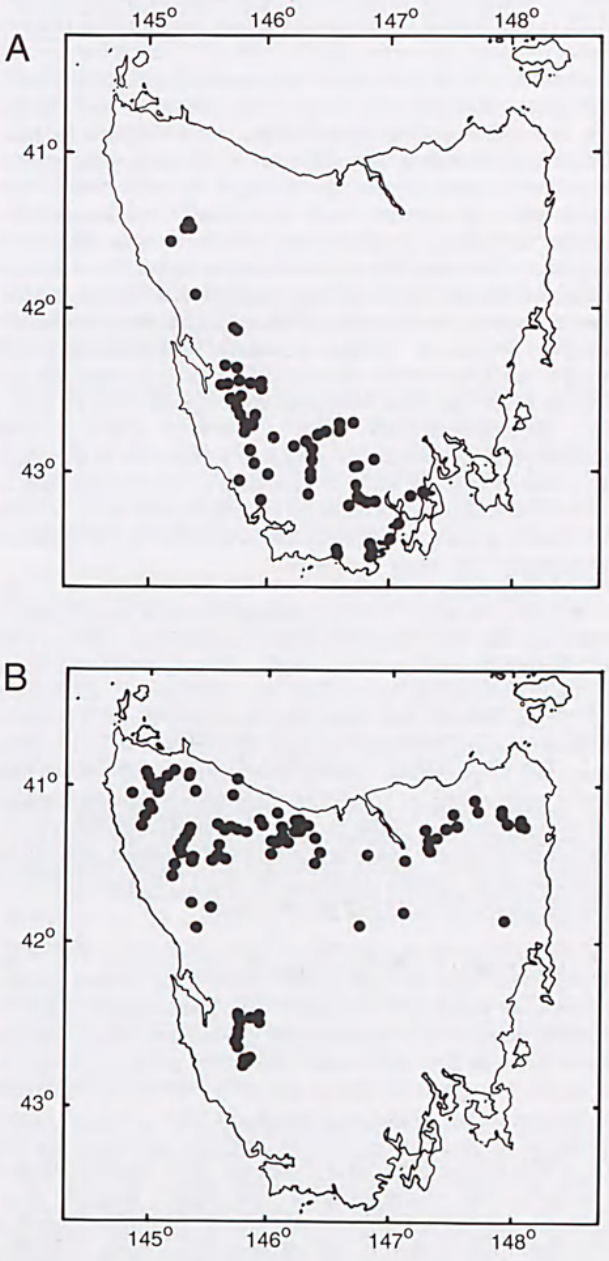

Figure 1.91 Distributions of two hydrobiid genera in Tasmania. A, records of *Phrantela* species. B, records of *Beddomeia* species. (After Ponder, Clark, Miller & Toluzzi 1993) [G. Ross]

Some lymnaeids have limited distributions, as shown by a few species in other parts of the world which have restricted distributions. The only known Australian example is an undescribed genus and species which appears to be restricted to limestone areas in the lower reaches of the Franklin River, south-western Tasmania (W.F. Ponder personal observations).

The cosmopolitan family, Planorbidae, is well represented in Australia by at least nine genera (Smith, B.J. 1992). *Planorbarius corneus* was imported as an aquarium animal and has become established in a few locations in Tasmania (Kershaw 1991; W.F. Ponder personal observations). The introduced and abundant *Physa acuta* (Physidae) is easily confused with species of *Glyptophysa*, with which it often occurs. Fossils attributed to *Glyptophysa*, *Syrioplanorbis* and *Gyraulus* are known from Miocene deposits in Australia (McMichael 1968; Ludbrook 1980; Walker, J.C. 1984). The species-level taxonomy of Australian planorbids is poorly understood as is evident from the listing by B.J. Smith (1992) of 85 available species names under *incertae sedis*.

J.C. Walker (1984) gave a detailed account of the biogeography of the non-planate planorbid genera. The genus *Isidorella*, with two species, is endemic and is found through much of the Australian mainland except coastal Queensland; the only possible near relative is *Protancylus* from Sulawesi. *Glyptophysa*, with several species, is found throughout Australia, including Tasmania, and is distributed through parts of South-East Asia, New Guinea, some Pacific islands, New Caledonia and New Zealand. A monotypic subgenus, *Oppletora*, is restricted to the north-west of Australia. One species of the endemic genus *Bayardella* occurs in the north-west of the mainland, and another mainly in the east. The Tasmanian endemic genus *Ancylastrum* is limpet-shaped but is closely related to *Glyptophysa*. Two species of *Amerianna* occur in northern Australia and the genus is distributed through New Guinea and the Philippines, with a few records in Thailand and Indonesia where it is probably introduced. Walker concluded that *Isidorella* and *Bayardella* are Gondwanan elements. *Glyptophysa* may also be Gondwanan, and this genus may have spread north more recently; whereas *Glyptophysa* may share a common ancestry with *Ancylastrum* and *Oppletora*, the origin of *Amerianna* is uncertain but may have been to the north of Australia. Of the planate genera, *Gyraulus* is cosmopolitan, *Helicorbis* occurs through much of Asia and the Pacific islands and *Pygmanisus* is endemic to the southern half of Australia, including Tasmania.

The Ancylidae are also virtually cosmopolitan but poorly known in Australia. The only revision, that of Hubendick (1967), was based on a small amount of material and only shell characters were used. Hubendick recognised two widespread Australian species groups but did not refine the taxonomy further. Currently the two recognised Australian species are included in a subgenus (*Pettancylus*) of *Ferrissia*, a genus distributed through North and Central America, Africa, South-East Asia and the Pacific islands; the subgenus also has a Pacific distribution (Hubendick 1967). A supposedly endemic genus and species, *Stimulator consetti*, is restricted to north-western Australia. Ponder (1981a) recorded an unidentified ancylid from Lord Howe Island.

The Glacidorbidae (Ponder 1986a) are known from Australia, Chile and South America (one species in the genus *Gondwanorbis*; Meier-Brook & Smith 1975; Ponder 1986a; Starobogatov 1988). In Australia, species of *Glacidorbis* occur in Tasmania, south-western Australia and in the south-east, extending north to southern Queensland. The genus is known also as a Miocene fossil, from South Australia (Buonaiuto in Bunn & Stoddart 1983). A single specimen of an undescribed species probably belonging to this family is also known from New Caledonia (W.F. Ponder personal observations). The distribution of this family suggests it is Gondwanan and that the family might also be expected to occur in New Zealand, but to date it has not been found there. Currently there are four named species from Australia, all included in *Glacidorbis*, but several unnamed species are known from Tasmania and the south-eastern Australian mainland.

The freshwater molluscs of Australia show patterns of distribution which reflect their history, and the history of climatic change, as well as their ability to disperse and to withstand drought. Major elements of the fauna are endemic and, at least, are probably of Gondwanan origin. Some taxa, particularly hydrobiids, thiarids and many of the pulmonates are unable to withstand drying, particularly if it is prolonged. These groups are thus confined largely to permanent water in the eastern and south-eastern drainages of the mainland and Tasmania or are associated with large rivers or artesian springs. Their distributions are often a reflection of geomorphological and climatic history.

Some taxa can survive prolonged drying, for example, under experimental conditions, 25% of *Gabbia australis* specimens survived after being dried for 203 days (McKay 1926) and some hyriids survive for very long periods in dried mud or soil, or even in air (McMichael & Iredale 1959). Other taxa may be good dispersers, living in habitats frequented by birds and adopting behaviour that makes accidental dispersal more likely. Aerial transportation of molluscs has been reviewed by Rees (1965), but none has been documented in Australia. Dispersal of glochidia larvae by their fish hosts is a factor in the distribution of hyriid mussels. Floods, cyclonic storms, and humans and stock also aid dispersal. Taxa that combine good dispersal capability with means of avoiding desiccation often have wide ranges over inland Australia.

The existence of only two species of Hyriidae in Tasmania, confined to only a single river system, is unexplained, especially as this group was present in Australia as early as the Triassic (McMichael 1957; Ludbrook 1961). Tasmania entirely lacks representatives of several families that occur on the mainland – Corbiculidae, Viviparidae, Bithyniidae and Thiaridae. However, all of these families have a predominantly tropical distribution, with high diversity in South-East Asia so their absence from Tasmania may simply be the result of climatic constraints, or their inability to cross Bass Strait, even during times of low sea-level coupled with glacial conditions. Their origin in Australia probably dates from contact of the Australian and Sunda Plates during the Tertiary. They are probably not Gondwanan, as suggested by the lack of these groups in New Caledonia (with the exception of Thiaridae and estuarine corbiculids) or in New Zealand.

One of the more unexpected aspects of Australian freshwater mollusc zoogeography is the absence of the Melanopsidae – an ancient cerithiodian family with freshwater members found in the Mediterranean area, New Caledonia and New Zealand. Australia also lacks radiations of freshwater taxa in families such as Stenothyridae and Neritidae, although these occur in brackish water in estuaries and mangroves. The lack of a conspicuous freshwater neritid fauna in particular is surprising given that they are common in New Guinea, the Pacific islands and throughout South-East Asia. Their presence on relatively recent Pacific islands suggests that they are capable of effective dispersal – so why have only two or three species reached the rivers of the tropical north? Possible explanations include historical accident, unfavourable physical conditions for dispersal, and major drying events with extinction of much of the endemic freshwater fauna in the northern rivers. There are several endemic freshwater fishes (several rainbow fish and gobies, Allen, G.R. 1989) in these drainages, but little is known of most of the invertebrate groups.

Analysis of the hydrobiid genus *Jardinella* suggests that the three closely related species found in coastal drainages are derived from a western radiation (Ponder 1991). If these river systems had been in continuous existence during the last few million years one might expect to see greater diversity and endemicity in groups such as Hydrobiidae.

Presently the analysis of freshwater mollusc biogeography in Australia is hampered by poorly resolved taxonomy and lack of detailed distributional data for many taxa. Given the current rapid changes to our freshwater ecosystems, with evidence that taxa have recently disappeared from some areas, it is essential that such work be undertaken urgently.

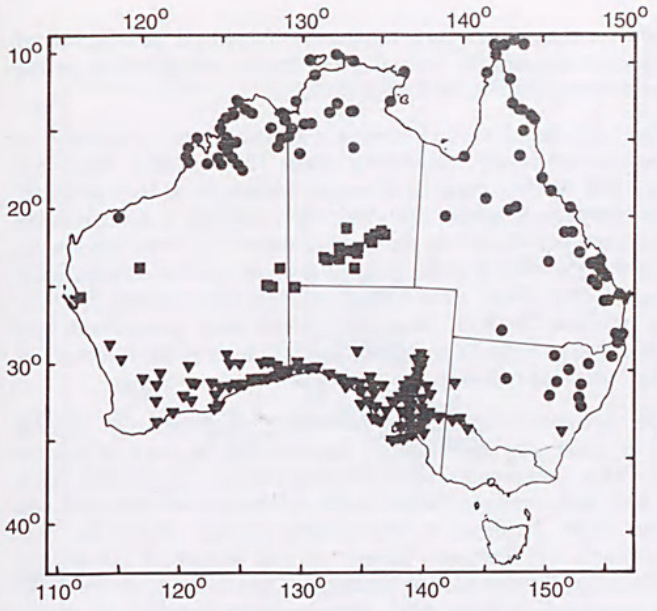

Figure 1.92 Distribution of three widespread species of *Pupoides* (Pupillidae) in Australia. ▼, *Pupoides adelaidae*; ■, *Pupoides beltjanus*; ●, *Pupoides pacificus*. (After Solem 1991) [A. Solem]

The Terrestrial Molluscan Fauna

It is not yet possible to make definitive statements concerning the biogeography of Australian land snails. Most of the basic survey work needed to provide raw distributional data has not yet been accomplished. 'Species' and 'genera' in many groups are recognised as artificial pigeon holes that do not reflect phylogeny, and the critical intercontinental comparative studies to determine genus and family category affinities are still needed. On the simplest distributional levels, major changes in knowledge can be anticipated. For example, two genera previously considered to be restricted to Queensland-northern New South Wales, *Glyptopupoides* and *Georissa*, were found recently in the Kimberley region of Western Australia (Solem 1988c).

Study by J. Stanisic of the spectacular radiation of charopid land snails from the tropical to temperate rain forest patches in Queensland and New South Wales is less advanced than work on camaenids (Stanisic 1990), but he has collected more than 200 species in the last few years. In all, 347 species of indigenous land snails have been described from eastern Australia (Stanisic 1994). Based on material in the Queensland Museum collections, a further 325 species in 16 families are unnamed as yet (Stanisic 1994); most of these are charopids (200), helicarionids (40) and camaenids (35). Based on these data, a total land snail fauna for Australia of 1200 to 1500 native species is a conservative estimate.

Several other families have also radiated extensively, among them the Punctidae, Bulimulidae and Helicarionidae; species and higher level revisions are needed to determine the full extent and directions of their diversification. Perhaps the most poorly known family is the Succineidae. Iredale (1937a) described two new genera and listed 13 species; *Arborcinea* is based on aestivating juvenile specimens, and *Austrosuccinea* has been synonymised with the worldwide genus *Succinea* (see Patterson 1971). None of the Australian species names has been characterised well enough that a series of populations can be grouped, assigned a meaningful range, and separated from other named forms, despite the fact that succineids have been collected in most parts of Australia.

Because of the limitations outlined above, only a 'broad brush' outline of land snail distribution and diversity can be presented. Of the 37 families of land snails and slugs recorded from Australia, 23 contain native species only, and 14 are represented only by introduced taxa (Table 1.5); the Enidae, Subulinidae and Helicarionidae include both native and introduced species.

The introduced taxa are largely synanthropic (associated with humans), restricted to cities, gardens, and field crop areas, where some become major nuisances, if not actual pests. A few species, such as the subulinid *Lamellaxis clavulinus*, several European slugs and the helicid *Theba pisana* have become feral with great success. Fortunately, these are the exceptions, rather than the rule. Their distributions within Australia today reflect the whims of history and commerce, temperature and humidity barriers and patterns of cultivation (Solem 1989).

The native taxa show a variety of distributions that can be clustered, in part at the family level, in part at the generic level. These clusters represent current restrictions of moisture, and thus ranges, during the currently arid period in which we live.

The largest number of families show northern tropical origins. These are mostly Indonesian-Polynesian groups that barely enter the wet coastal margin of Australia. There are a few records of the cyclophorid genus *Leptopoma* in northern Queensland, and recently the Indonesian *L. minus* has been found on Melville Island and the Cobourg Peninsula in the Northern Territory. The Trochomorphidae, which occur from South-East Asia to Tahiti are represented by *Trochomorpha melvillensis* on Melville Island (Solem 1988c) and *Amphidromus cognatus* from the same area. Solem (1983b) recorded a South-East Asian-Indonesian genus of Camaenidae as an Australian resident.

The charopid, *Pilsbrycharopa tumidus*, which belongs to an Indonesian-New Guinean complex, occurs further inland in the Fitzroy River, southern Kimberley (Solem 1988c). More arid areas have their own special taxa. Separate species of the South-East Asian pupilloid genus *Gyliotrachela* occur at Chillagoe Caves, Queensland, the Daly River area of the Northern Territory and both the Napier and Ningbing Ranges in Western Australia. Records of the hydrocenid genus *Georissa*, which occurs from India to Hawaii, are scattered from northern New South Wales to mid-Queensland; an isolated species occurs in the Ningbing Ranges of Western Australia.

The pupillid *Gastrocopta recondita* occurs on various Indonesian islands and as well as on an inland Kimberley range. Another member of the genus, *G. macrodon*, has been recorded from Milne Bay and the Louisiade Archipelago, Papua New Guinea, plus wetter parts of the Kimberley (Solem 1988c), but not from Queensland and the Northern Territory.

Some species known from Indonesia range more extensively into Australia. Both *Stenopylis coarctata* (Helicodiscidae) and *Discocharopa aperta* (Charopidae) occur in the Pilbara and central Australia. The helicarionids *Wilhelminaia mathildae*, *Coneuplecta calculosa*, *Coneuplecta microconus* and *Liardetia scandens* (an endemic), and the genera *Pleuropoma* (Helicinidae) and *Nesopupa* (Pupillidae) all occur inland of the Kimberley, Western Australia-Northern Territory-Queensland coast.

The above situations represent single species or taxa of low diversity with general northern Australian distributions. Other Indonesian-Melanesian taxa have crossed only at Torres Strait. The Diplommatinidae are represented by some seven species; the Pupinidae by 29 species in several genera; the Rathouisiidae by probably two species; and the Athoracophoridae by at most a few species in coastal Queensland and New South Wales; all are largely confined to the east-coast rainforests (Stanisic 1994). Most of the above genera reach a common southern limit of distribution in the Clarence River-Richmond River-Dorrigo area of north-eastern New South Wales.

Much more successful immigrants are members of the subfamily Camaeninae (Camaenidae). In both shell size and species numbers, this group dominates the land snails of the Great Dividing Range and adjacent hills, extending from Torres Strait to southern New South Wales, then with a western shift into the Flinders Ranges, Gawler Ranges, and Eyre Peninsula of South Australia, where a radiation into several genera has occurred (Solem 1992a).

Two essentially tropical Pacific groups require special comment. The Achatinellidae are basically a Polynesian group today, with a few small-sized species widely distributed by commerce. Australian records extend from Sydney north to Torres Strait and then west through the Northern Territory and wetter parts of the Kimberley of Western Australia. We do not know how much of this represents passive transport on plants, the true identity of the Australian populations, or even the proper generic classification for these few species. The taxonomy of the so-called Helicarionidae of Australia is in disarray. There are several wet forest endemics from Queensland to Tasmania, especially the 'semi-slugs' of the *Helicarion* group, but neither species nor generic limits have been established for the northern taxa, although R. Kershaw has clarified the status of several southern taxa. These Indonesian taxa in northern Australia provide evidence of habitat expansion. Similar radiations are seen in the dry country of the Kimberley, Western Australia and Northern Territory (*Westracystis*) and Gawler-Flinders Ranges (identity uncertain) taxa.

The taxa discussed previously have been characterised by relatively clear indications of northern origins and affinities, basically northern or eastern 'wet areas' distributions, and mostly low diversity (Pupinidae and Helicarionidae have moderate diversity). However, the origin and affinities of a few families provide unsolved puzzles.

The Cystopeltidae, occurring from southern Queensland to Tasmania, and comprising a few species, have not been allied convincingly to any other land snail family. The mid- to southern Queensland monotypic genus *Coelocion* is placed in the Megaspiridae together with the living species of *Megaspira* from southern Brazil and fossils from the Paris Basin Eocene; the little known New Guinea genus *Perrieria* may not be related.

The only native species of Enidae, *Amimopina macleayi*, from the northern fringes of Australia, is related to central and South African enids, rather than to the genera living today in India, South-East Asia, or Indonesia. The two species of *Eremopeas*, which range from the Timor Sea and Torres Strait south to the Pilbara, George Gill Range in central Australia, and Claude, New South Wales, cannot be allied at present to extralimital members of the Subulinidae.

The Pupillidae are basically a worldwide group with many species showing substantial ranges within Australia (Fig. 1.92). No anatomical studies have been completed, and the relationships of the Australian *Pupilla*, *Pupoides* and *Gastrocopta* are unknown.

Six further families – Caryodidae, Rhytididae, Punctidae (= Laomidae), Charopidae (= Flammulinidae), Bulimulidae (= Bothriembryonidae) and Camaenidae (= Hadridae, Papuinidae, Chloritidae, Xanthomelontidae and Rhagadidae) – are discussed in approximate order of increasing diversity. All represent significant faunal elements.

The Caryodidae, which Iredale (1937b: 14–19) split into four families, are part of the Gondwanan acavoid complex, which includes taxa from South Africa and Namibia, Madagascar, Mascarene Islands, Seychelles, Sri Lanka, mid-Queensland to Tasmania, and much of South America. Members of each of the several Australian genera are very different from each other in shape and size, and are well differentiated anatomically. Whether they should be maintained as an Australian endemic family or combined on a family level with some of the extralimital taxa remains to be determined. The caryodids form an old Australian group confined to wet forest litter along the east coast, with limited species diversity (13 species; Smith, B.J. 1992).

The Rhytididae (= Paryphantidae) show moderate diversity in areas of South Africa, Seychelles, Mascarene Islands, northern Queensland to Tasmania, New Caledonia, and New Zealand diversity. A few species are known from the Mount Lofty Ranges, South Australia, one from near Pemberton, Western Australia, and there are a few possible relatives from Indonesia to Samoa. No modern revision of inter-area affinities exists. The group may be polyphyletic: homoplasious features associated with adaptation for carnivory may have been mistakenly interpreted as evidence of common ancestry. In Australia, the family occurs mainly in the southern areas and is not very diverse.

The Bulimulidae (= Bothryembrionidae) are primarily a Neotropical family, numbering about 1000 species. There are two Old World centres of diversity: Melanesia to New Zealand, and Western Australia. The *Placostylus* complex is diverse in the Solomon Islands and on the main island of Fiji. Two species are known from New Caledonia and a few species are recorded from Lord Howe Island, Vanuatu (= New Hebrides), and the northern tip of New Zealand. Some apparently more generalised taxa restricted to Vanuatu are anatomically similar to the members of the Australian radiation, the *Bothriembryon* complex.

The last near-comprehensive revision of *Bothriembryon* (Iredale 1939) used only shell features. Intensive field surveys in Western Australia have revealed about 55 species (Solem unpublished data), which range from the Pilbara, south to Cape Leeuwin and then east into South Australia. A few endemic species fringe the Eyre Peninsula and Kangaroo Island, and one species, *B. tasmanicus*, lives along the east coast to Tasmania. Three colonies are known of a remarkable isolated relict, *Bothriembryon spenceri*, in central Australia. No phylogenetic hypotheses have been presented for the family, although the bulimulid distributions suggest intriguing problems for investigation.

The family Punctidae occurs worldwide, with major centres of diversity in New Zealand and south-eastern Australia. A few species live in South Australia, and the humid south-western corner of Western Australia; there are isolated montane records in Queensland and New Guinea, and several species live on Lord Howe and Norfolk Islands. The fauna comprises several hundred species, but nothing can be said about generic clusters or species ranges.

Table 1.5 Land snail families found in Australia.

Class and ordinal groups	Native Families	Introduced Families
Class Gastropoda		
Superorder Neritopsina	Hydrocenidae	
	Helicinidae	
Order Architaenioglossa	Cyclophoridae	
	Diplommatinidae	
	Pupinidae	
Order Pulmonata		
Suborder Systellommatophora	Rathouisiidae	Veronicellidae
Suborder Eupulmonata	Achatinellidae	Cionellidae
	Pupillidae	Pleurodiscidae
	(+Vertiginidae,	Enidae
	Chondrinidae)	Valloniidae
	Enidae	Subulinidae
	Caryodidae	Ferussaciidae
	Subulinidae	Achatinidae
	Megaspiridae	Streptaxidae
	Rhytididae	Arionidae
	Bulimulidae	Zonitidae
	Helicodiscidae	Limacidae
	Punctidae	Helicarionidae
	Charopidae	Milacidae
	Helicarionidae	Testacellidae
	Succineidae	Bradybaenidae
	Athoracophoridae	Helicidae
	Cystopeltidae	
	Trochomorphidae	
	Camaenidae	

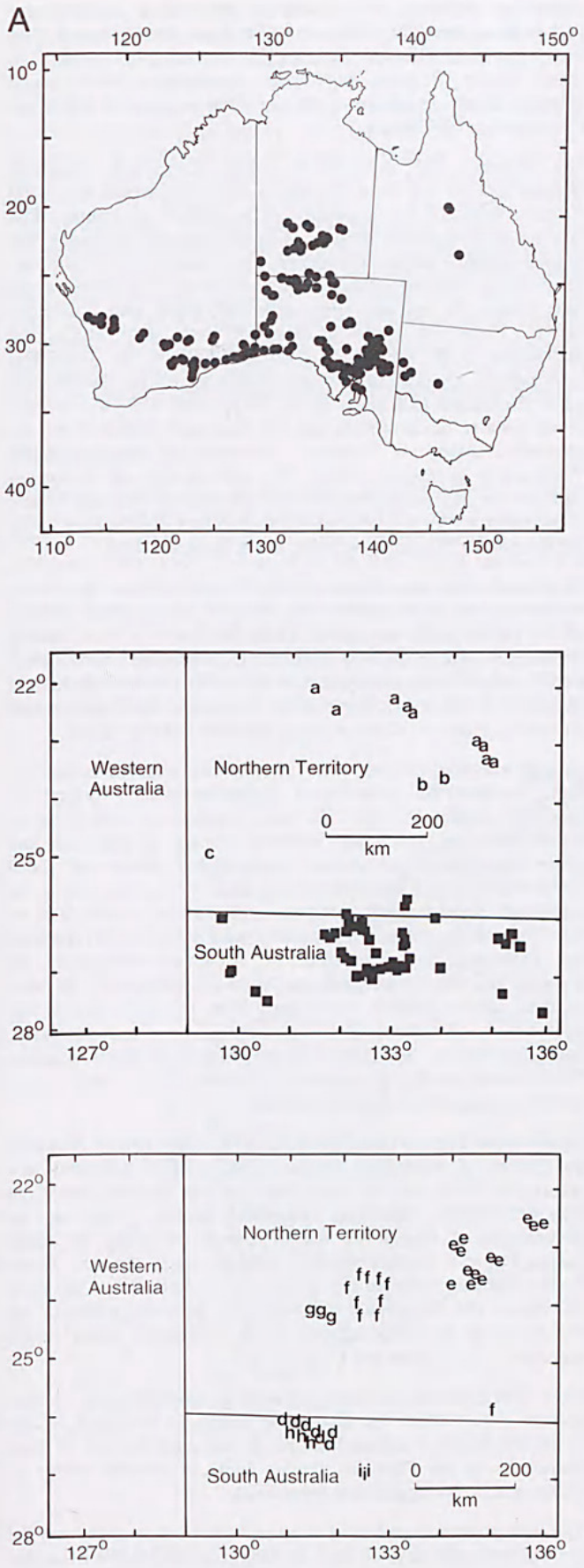

Figure 1.93 Distribution patterns in the camaenid genus *Sinumelon* (Camaenidae). **A**, overall distribution of all Australian species, based on 653 records. **B**, **C**, the northern records of the widespread species *S. pedasum* (squares) and the very limited ranges of nine other species in the same region of Central Australia. **a**, *S. perinflatum*; **b**, *S. bednalli*; **c**, *S. hullanum*; **d**, *S. amatensis*; **e**, *S. dulcensis*; **f**, *S. expositum*; **g**, *S. gillensis*; **h**, *S. musgravesi*; **i**, *S. pumilio*. (After Solem 1993) [G. Ross]

The Charopidae show an extensive Polynesian-Micronesian radiation (Solem 1983a). Species diversity is high in New Caledonia, New Zealand, Tasmania, Victoria, New South Wales, parts of Queensland and South Africa, and there are less extensive radiations in South America, Lord Howe Island, Norfolk Island, and the humid south-west of Western Australia (Solem unpublished). Stanisic (1990) demonstrated the diverse affinities of a number of subtropical east coast taxa. In general, shell and anatomical features were similar to those of New Zealand species. However, *Sinployea intensa* was shown to be a remnant of a large Pacific radiation and the mainly Pacific Basin-North American subfamily Rotadiscinae was recorded for the first time. A more comprehensive understanding of biogeography is dependent on the clarification of several hundred more species in the Australian-New Zealand fauna.

The Camaenidae are somewhat better known. This complex family arose from an early to mid-Tertiary immigrant from Indonesia-New Guinea, undoubtedly in several colonisation waves. In the Cretaceous, camaenids were present in both Utah, United States of America and central China. The extant New World distribution is from Cuba through the Lesser Antilles and from Costa Rica south into Amazonian Peru, substantially south of the Mesozoic distribution. In the Old World, camaenids range from Japan and China through Indonesia and New Guinea into the Solomon Islands, and then over much of Australia. B. Scott (1996) reassessed the family, and restricted the Camaenidae to only the Asian and Australian taxa.

No camaenids are known from Tasmania, much of Victoria, or the humid south-west corner of Western Australia. Because of pre-adaptation to a long dry season, during which the snails aestivate, they do very well in semi-arid regions. They are unique among the Australian biota in that one subfamily, the Sinumeloninae, has its centre of diversity in central Australia, with secondarily derived taxa in the Gawler-Flinders Ranges, on the Nullarbor, and along the west coast of Western Australia.

In summary, except for the Pupinidae and Helicarionidae, most families are derived through or via South-East Asia and are found along the wetter northern and eastern margins of Australia. These families show very low levels of diversity. The Cystopeltidae, Megaspiridae, native Enidae and native Subulinidae are relicts with limited Australian ranges and are of unresolved affinity. The Pupillidae show a low level of speciation, and taxa generally have wide ranges; their origin(s) is(are) unknown. Five families, Caryodidae, Bulimulidae, Rhytididae, Punctidae and Charopidae, show southern continent affinities and may have been involved in plate tectonic dispersions. The most speciose of Australian land snail families, the Camaenidae, appears to be a post-Miocene colonist from the north.

Two additional aspects of Australian land snail biogeography require brief mention. First, extensive geographic ranges are very unusual for Australian land snail species and genera, probably because of limited dispersal (*cf.* Molluscs on Land, this Chapter). Those of the Pupillidae (Fig. 1.92) and some species in the camaenid genus *Sinumelon* (Fig. 1.93A, B) are exceptions; other species of *Sinumelon* have very restricted ranges (Fig. 1.93C). The median linear species range for all Australian land snails is probably less than 40 km. The ranges of 29 camaenid species found in the Ningbing Ranges, in the Kimberley region of Western Australia (Solem 1988a), are 0.1–7 km (median 1.65 km) in length and 0.01–7.45 km^2 (median 0.825 km^2) in area; most are allopatric. A sample distribution of the short species ranges found in this radiation is given in Figure 1.94.

High levels of sympatry are found only in a very few places. In the areas between Dorrigo, New South Wales and Rockhampton, Queensland, J. Stanisic has found that up to 30 species of land snails may occur in patches of wet rainforest, but drier vegetation patches, such as vine thicket, may contain 40 to 45 species. The species diversity decreases in the less favourable country between Rockhampton and Mackay. Between Mackay and Proserpine, the diversity rises again to 30 to 35 species, but with fewer charopids,

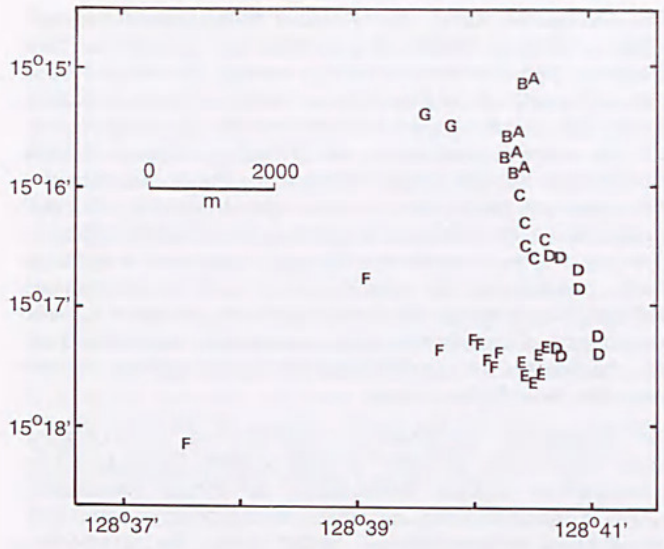

Figure 1.94 The restricted ranges of endemic camaenid species in the South Ningbing Ranges, north of Kununurra, Western Australia. **A**, *Cristilabrum simplex*. **B**, *Cristilabrum buryillum*. **C**, *Cristilabrum monodon*. **D**, *Cristilabrum primum*. **E**, *Cristilabrum grossum*. **F**, *Cristilabrum bubulum*. **G**, an undescribed *Cristilabrum* species. (After Solem 1988a) [G. Ross]

more camaenids, and the appearance of several pupininds. By Townsville, species numbers drop to 10 to 15, a level which continues north to Cape York, with the exception of some of the foothills and highlands of the Ingham-Cooktown rainforest massif, as described by Stanisic (1994).

In the Kimberley and Northern Territory north of the Roper River, rain forest patches have a mean diversity of 12.5 species/patch with a maximum of 18 to 20 species. In central Australia, species diversity rarely reaches ten. Although finding even six land snail species in one place over most of the rest of Australia is very unusual, reasonably high diversities are also found in some parts of Victoria, southern and mid-New South Wales, Lord Howe Island, Norfolk Island and Tasmania.

Thus the land snail diversity in Australia is derived from vicariance of a few groups, comprises species with very limited ranges, and shows high levels of sympatry in restricted areas of the continent.

THE FOSSIL RECORD

Because of the hard shell deposited by and housing most molluscs they have an excellent fossil record and are represented in Australia in each geological period during the 550 million years from Early Cambrian to the present day. Extensive marine transgressions through geological time over large parts of the Australian plate provided conditions suitable for deposition of fossils. Sedimentary basins so formed are shown in Figure 1.95, and timing and extent of the major transgressions are shown in Figure 1.96.

Documentation of the fauna, however, is less than adequate. Fossil molluscs which occur in all Australian States and territories, mostly represent marine species of all life habits and from most marine habitats, but only a few freshwater and terrestrial molluscs have been found. All molluscan classes are represented in the Australian fossil record, in relative proportions similar to those for the whole world (Sepkoski 1981).

Molluscan shells are commonly preserved as the original shell material, replaced by some other mineral, as extremely thin and faithful overgrowths or as a void within rock matrix. Soft tissues are preserved exceptionally rarely but muscle and ligament attachment sites and pallial lines on shells give some clues to soft anatomy. In many Tertiary limestones only calcitic molluscs such as oysters and scallops are preserved while aragonitic shells (for example, most gastropods) are not preserved.

Australian molluscs are referable to three major fossil faunas (Sepkoski & Sheehan 1983) – the Cambrian, the Palaeozoic and the 'modern' (or Mesozoic-Cainozoic). The extinction event at the close of the Permian is clearly represented while major diversifications are evident in the early Palaeozoic and at the late Cretaceous-early Tertiary.

The cratonic and intracratonic Perth, Carnarvon, Canning, Bonaparte, Daly and Georgina Basins of the Palaeozoic and Great Artesian Basin of the Mesozoic contain rich fossil faunas often dominated by molluscs. Eastern Australia including Tasmania was a geosynclinal – tectonically active – area during the Palaeozoic. Sedimentary piles on various shallow-water shelves around small land masses or volcanic arcs entombed many rich molluscan faunas. These are found in nearshore and shelf mudstones, sandstones and limestones. Rocky bottom or shoreline environments are deduced for some molluscs, such as the Permian genus *Eurydesma* (Runnegar 1979), but the only molluscs reported in deep-water environments are the few cephalopods from the graptolite shales of Victoria (Thomas & Teichert 1947; Vandenberg & Stewart 1983). The only records of freshwater molluscs are of unionid bivalves from non-marine Mesozoic basins in association with rich plant assemblages (Jack & Etheridge 1892; McMichael 1957; Ludbrook 1961; Jell & Duncan 1986).

In general, limestone faunas of the Palaeozoic have been more extensively and better studied than those of other periods because of the preservation of original shell and because latex casting techniques, facilitating study of the external moulds of many earlier fossils, only became widely used in the 1960s. Eastern Australian faunas are better known than cratonic faunas of central and western Australia, because of their proximity to centres of population.

Despite advances in many areas of specimen preparation and the high numbers of professional palaeontologists working in Australia during the last 50 years, numerous collections of undescribed and unstudied molluscs remain in museum and university collections; several postgraduate theses on fossil molluscan faunas completed during these years have yet to be published. A conservative estimate suggests that at least 50% of the fossil Mollusc fauna, particularly gastropods and bivalves, of the Palaeozoic and Mesozoic of Australia remains to be documented. The cephalopods are the best studied group because of their biostratigraphic importance from the Devonian to the Cretaceous, and probably 80–90% of species have been described. As noted below, the classes Monoplacophora, Rostroconchia, Scaphopoda and Polyplacophora are known in the fossil record but fossil forms are comparatively rare.

Most marine Tertiary rocks occur in the southern part of Australia in a series of continental basins in which shelf sediments are preserved. From west to east, these are the Bremer, Eucla, St Vincent, Otway, Bass and Gippsland Basins. There are no occurrences of deep-water deposits from the slope or ocean basins. Deposits of very shallow, subtidal origin are rare. Other factors that contribute to the absence of a fossil record are poor outcrop or lack of suitable sediments. For instance, molluscs are not found in the carbonaceous sands of shallow water origin common in the Eocene and Oligocene.

Early Tertiary sedimentation occurred in southern and western coastal basins from the Carnarvon Basin in the west to the Gippsland Basin of eastern Victoria. It continued in most of these basins up to the Pliocene, though local or basinal breaks in sedimentation are apparent in most areas.

The best preserved and most diverse faunas are known from the neritic marls and clays of the Late Oligocene to Middle Miocene. Faunas of shallow water sands and clays are more common in the Late Miocene through to Pleistocene. Fossil remains of rocky bottom dwellers such as chitons, *Haliotis* species, limpets and some trochids and turbinids are known from only a few localities and often are not well preserved. Molluscan biostratigraphy, biogeography and the nature of the Tertiary record have been summarised by Darragh (1985).