# Evolutionary patterns and consequences of developmental mode in Cenozoic gastropods from southeastern Australia

UNIVERSITY OF LIVERPOOL

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**Kirstie Rae Thomson**
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# ABSTRACT

Gastropods, like many other marine invertebrates undergo a two-stage life cycle. As the adult body plan results in narrow environmental tolerances and restricted mobility, the optimum opportunity for dispersal occurs during the initial larval phase. Dispersal is considered to be a major influence on the evolutionary trends of different larval strategies. Three larval strategies are recognised in this research: planktotrophy, lecithotrophy and direct development. Planktotrophic larvae are able to feed and swim in the plankton resulting in the greatest dispersal potential. Lecithotrophic larvae have a reduced planktic period and are considered to have more restricted dispersal. The planktic period is absent in direct developing larvae and therefore dispersal potential in these taxa is extremely limited. Each of these larval strategies can be confidently inferred from the shells of fossil gastropods and the evolutionary trends associated with modes of development can be examined using both phylogenetic and non-phylogenetic techniques. This research uses Cenozoic gastropods from southeastern Australia to examine evolutionary trends associated with larval mode.

To ensure the species used in analyses are distinct and correctly assigned, a taxonomic review of the six families included in this study was undertaken. The families included in this study were the Volutidae, Nassariidae, Raphitomidae, Borsoniidae, Mangeliidae and Turridae. Phylogenetic analyses were used to examine the relationships between taxa and to determine the order and timing of changes in larval mode throughout the Cenozoic. Traditionally, planktotrophy has been considered the ancestral mode of development. However, using maximum parsimony and maximum-likelihood analysis, this research suggests that the ancestral developmental mode cannot be confidently determined in gastropods from southeastern Australia. Similarly, evidence that transitions between larval strategies might be reversible contradicts the general view that regaining the specialised structures associated with planktotrophy is so difficult that it is considered extremely unlikely to occur. When the timing of switches in larval mode was examined they were found to be scattered at different points in time rather than clustered to specific periods and therefore no inference can be made as to the likely factors driving transitions between larval modes. The correlation between mode of development and macroevolutionary trends was examined using non-phylogenetic techniques. The results do not concur with the hypothesis that species with planktotrophic larvae will exhibit wider geographic ranges, longer species durations and lower speciation rates then lecithotrophic or direct developing taxa. The analyses are thought to be hindered by a strong preservation bias and gaps within the fossil record. The quality of the fossil record and the congruence between phylogenies and stratigraphy is examined using the Stratigraphic Consistency Index, the Relative Completeness Index and the Gap Excess Ratio.

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# CHAPTER 1

# INTRODUCTION

A great deal of research has concentrated on the biological mechanics of larval development in marine invertebrates (e.g. Thorson, 1950; Mileikovsky, 1971; Shuto, 1974; Jablonski & Lutz, 1980, Wray, 1992, 2006; Raff & Byrne, 2006) but considerably less is known about the evolution of larvae and the factors that influence early development. It is well documented that the dispersal ability of a species during its larval stage may have a profound influence on its geographic distribution (Shuto, 1974; Hansen, 1980; Jablonski & Lutz, 1983; Scheltema & Williams, 1983; Jablonski, 1986; Johannesson, 1988; Ó Foighil, 1989; Martel & Chia, 1991; Emlet, 1995; Hoskin, 1997; Collin, 2001; Jeffery & Emlet, 2003; Jablonski & Hunt, 2006; Paulay & Meyer, 2006; Arellano & Young, 2009), species longevity (Hansen, 1978, 1980; Koch, 1980; Scheltema & Williams, 1983; Jablonski, 1986; Gili & Martinell, 1994; Jeffery & Emlet 2003; Jablonski & Hunt, 2006) and speciation rates (Shuto, 1974; Hansen, 1978; Murphy, 1978; Collin, 2001; Jablonski & Roy, 2003; Paulay & Meyer, 2006) but these ideas are yet to be adequately tested, either in living or fossil taxa. Studies to date have concentrated on limited taxonomic examples at few geological time periods (e.g. Hansen, 1982; Jablonski, 1986; Jeffery, 1997; Gili & Martinell, 1994; Cunningham & Jeffery Abt, 2009).

The lack of knowledge about larval evolution is in part due to preservation biases within the fossil record of different developmental stages (more fragile stages are not often preserved) but also a result of inadequate linking of larval and adult forms and poorly resolved phylogenies for different groups of marine invertebrates. By approaching our understanding of larval strategies from a palaeontological perspective, as opposed to a biological one, we are able to include the dimension of time from the fossil record that is unavailable in biological studies that focus on living taxa only. This thesis aims to fill a gap in our understanding by focusing on larval strategies of fossil marine gastropods from the Cenozoic sedimentary rocks of southeastern Australia which will complement a similar data on echinoids in this region (Jeffery & Emlet, 2003). The study will examine the macroevolutionary consequences of different larval strategies and resolve phylogenies to a sufficient level that switches in larval mode can be mapped and the plesiomorphic larval condition determined.

Gastropods from the Cenozoic sedimentary strata of Australia provide an ideal study group for a number of reasons. Gastropods are one of only a few groups of marine invertebrates whose larval strategy can be inferred from the adult shell. It is therefore possible to unravel the evolutionary history of larval strategies in gastropods without the need to make direct observations of larvae. In addition, a variety of larval strategies are found within the Gastropoda making it possible to review the macroevolutionary consequences of varying larval strategies. This study will provide a complementary dataset to similar echinoid data from the Cenozoic of southeastern Australia (Jeffery & Emlet, 2003). The widely outcropping carbonate rocks of southeastern Australia are stratigraphically well constrained and contain abundant, diverse and very well preserved gastropod specimens. As there has been no relative movement of localities since deposition, geographic ranges can be better constrained. In addition, the excellent and well curated collections of both type and non-type material housed within Museum Victoria in Melbourne, the South Australia Museum in Adelaide and The Natural History Museum in London provide a useful source of specimens to be included in this study. Lastly, there is scope for taxonomic revision of families within the Gastropoda of this region and development of phylogenies using morphological characters to better resolve the relationships between taxa and to improve our understanding of the evolutionary history of larval strategies in the Cenozoic.

## 1.1 LARVAL STRATEGIES

Many marine invertebrates, including gastropods, possess a two-stage life cycle, initially hatching from eggs as planktic larvae before metamorphosing into benthic adults (Figure 1.1). The adult body plan hampers mobility and the organism often develops narrow environmental tolerances during this life stage. As a result the larval stage provides the optimum opportunity for dispersal. From examination of living taxa, a number of different larval strategies are recognised in marine invertebrates. However, these can be broadly grouped into two types: planktotrophs and nonplanktotrophs. Species with larvae that have the ability to feed in the plankton (planktotrophs) are shown to have greater dispersal abilities as a result of their prolonged survival in the water column, whereas species with nonfeeding larvae (nonplanktotrophs) have more restricted dispersal abilities as they metamorphose into benthic adults more quickly. The ability to disperse is arguably the most influential factor controlling evolutionary trends (see Jablonski & Lutz, 1983 for review).

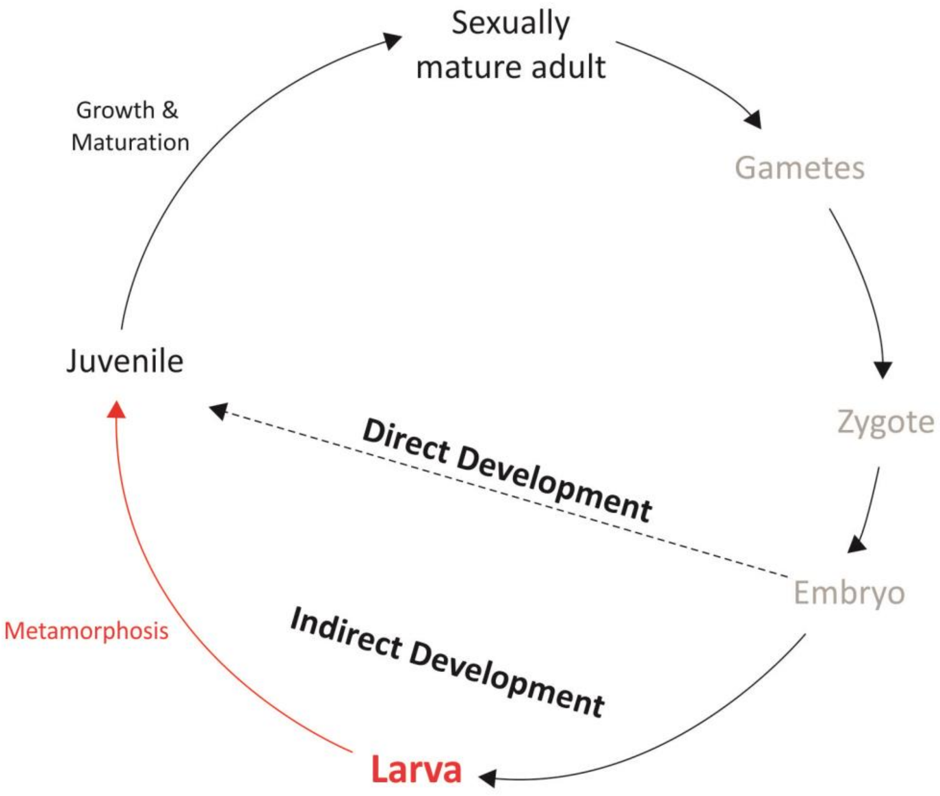


**Figure 1.1** Idealised metazoan life cycle with the larval life stage highlighted in red and life stages prior to hatching (and not observable in fossil specimens) highlighted in grey. Modified from Figure 2 in McEdward & Janies, 1993 (pg. 260).

### **1.1.1** PLANKTOTROPHY

Planktotrophic (or planktic) larvae are sometimes referred to as feeding larvae (e.g. Strathmann, 1974, 1978, 1985) and are capable of spending a significant time in the plankton. They are hatched from large numbers of small, yolk-poor eggs and have specialised structures for feeding and locomotion within the plankton. These structures are either lost or reabsorbed during metamorphosis into a juvenile. The number of eggs spawned by an individual parent organism can vary from thousands to millions. For example, the gastropod *Littorina irrorata* can spawn up to 85,000 eggs at any one time (Bingham, 1972) whilst up to 70 million eggs can be produced by a single spawning of the oyster *Crassostrea virginica* (Davis and Chanley, 1956). Once the eggs are released into the water column many factors, including predation and starvation, result in high mortality rates, as high as 99% in some cases (e.g. Thorson, 1950, 1966; Mileikovsky, 1971). However, the evolutionary success of this larval type was highlighted by Thorson (1950), who estimates that 70% of living benthic marine species undergo this type of development.

Planktotrophic larvae can spend long periods of time in the plankton and as a result are often subject to relocation by ocean currents. Many taxa spend two or three months as larvae, such as the echinoid *Strongylocentrotus pallidus* and the holothuroid *Parastichopus californicus* (Strathmann, 1978), whilst the phyllosoma larvae of the spiny lobster can remain in their pelagic, feeding state for up to a year (Mileikovsky, 1971). If larval behaviour causes no interference then dispersal by ocean currents can be heavily influenced by the length of the pelagic phase. Currents of 0.5km/h can transport planktotrophic larvae as far as 150km to 500km within a single breeding period (Scheltema, 1977) if unaffected by other factors, such as temperature (e.g. O'Connor et al., 2007; Scheltema, 1986), predation and the ability to find an appropriate settlement site (Strathmann & Branscomb, 1979).

Larvae which spend very long periods of time as pelagic, feeding organisms and which have the ability to be dispersed across great distances are referred to as teleplanic ("far wandering", Scheltema, 1971) and are often found among the tropical benthos (Jablonski and Lutz, 1983). Demersal development refers to species whose larvae swim or crawl near the substrate gaining nutrition from organic detritus in or close to the substrate (Jablonski & Lutz, 1983). Inclusion of this larval type under the planktotrophic umbrella is contentious as some demersal species do not feed at all and would therefore be better placed in the nonplanktotrophic category (Jablonski & Lutz, 1983). Demersal development is most often seen in high latitude, deep sea regions (Pearse, 1969; Mileikovsky, 1971; Clarke, 1979). This type of benthic dispersal can be advantageous as larvae are exposed to more stable benthic food resources and the less variable temperature and salinity regimes associated with upper part of the water column (e.g. Levinton, 1974; Hendler, 1977; Whitlatch, 1977; McCall, 1978).

### **1.1.2** NONPLANKTOTROPHY

Nonplanktotrophic (or nonplanktic) larvae are sometimes referred to as nonfeeding larvae (Strathmann, 1978; Marshall & Keough, 2003) and spend little or no time in the plankton prior to metamorphosis. The reduced pelagic period in this larval strategy has led to the hypothesis that nonplanktotrophic species have more limited dispersal abilities than planktotrophic species. Nonplanktotrophs gain all their nutrition from the large, yolk-rich eggs from which they hatch. As a result of this higher maternal input, the parent organism spawns a much smaller number of eggs than seen in planktotrophic species, usually thousands rather than millions. For example, the bivalve *Nucula proxima* spawns approximately 4100 eggs per parent and the related *Nucula annulata* 1200 eggs per parent (Scheltema, 1972). The reproductive effort of the parent is considerably higher per egg in nonplanktotrophs than planktotrophs. Lower mortality rates are predicted in nonplanktotrophic larvae, if there is a correlation between residence in the plankton and mortality rate (Scheltema, 1972).

Lecithotrophy refers to nonfeeding larvae which undergo a short pelagic phase. Nutrition is entirely sourced from the egg and the pelagic phase rarely exceeds a few days whilst still enabling a degree of dispersal (Thorson, 1950). The suggestion that lecithotrophy is absent in gastropods (Thorson, 1950) has been refuted by numerous studies and it has in fact now been recorded in the Patellidae, Acmaeidae, Trochidae, Olividae, Muricidae and Conidae (e.g. Natarajan, 1957; Marcus & Marcus, 1959; Kohn, 1961; Fretter & Graham, 1962; Anderson, 1962, 1966; Gohar & Eisawy, 1967; Eisawy, 1970; Underwood, 1972, 1979; Spight, 1977; Gallardo, 1981; Heslinga, 1981; Perron, 1981a, b; Rex and Warén, 1982; Ellingson & Krug, 2006). This type of development is thought to be the dominant larval strategy in deep sea bivalves (Knudsen, 1979; Schein, 1989) and in asterinid starfish (Byrne, 2006) but is also common in other molluscs and echinoderms.

Direct development occurs when full development to the juvenile stage takes places within the egg mass (Thorson, 1946, 1950; Mileikovsky, 1971, 1974; Webber, 1977; Jablonski & Lutz, 1983). The egg mass or egg case is often attached to the substrate and protects the larvae until metamorphosis is complete. True direct development has only been observed in a relatively small number of marine invertebrates including most cephalopods (Boletzky, 1974; Arnold and Williams-Arnold, 1977; Wells and Wells, 1977), some echinoderms (Chia, 1974), a number of opisthobranchs (Bonar, 1978) and some authors also report direct development in the Polyplacophora (Pearse, 1979). Oviparous development occurs where the parent organism provides nurse eggs as an extra food source for the viable eggs, e.g. the gastropod *Buccinum undatum* (Portman, 1925). The ratio of viable eggs to nurse eggs can be variable but often nurse eggs considerably outnumber eggs that produce offspring (Jablonski & Lutz, 1983).

Brooded development occurs in species where the larvae are retained within the parent organism until metamorphosis is complete and they can emerge as juveniles. It is worth noting that this strategy offers the greatest protection to the offspring but fewer eggs can be developed and the reproductive effort required of the parent organism is distinctly greater than in any other strategy (Hughes & Roberts, 1980). It has been noted that some species developing embryos within their eggs attach those eggs to the shell or the body of the parent until full development is complete (Lindberg & Dobberteen, 1981). Brooded development is the dominant larval strategy in Antarctic echinoids (e.g. Poulin, 1996) with over 95% of Antarctic species displaying brooded development (Magniez, 1983).

Mixed development (seen in a number of benthic marine groups including gastropods) occurs where early development is encapsulated but larvae are still hatched as free-swimming and premetamorphic, e.g. the gastropod *Conus pennaceus* (Perron, 1981c). This strategy may reduce the risk of predation which is very high at early stages of development (Pechenik, 1979).

In summary, three main divisions of nonplanktotrophic development can be recognised. The first refers to species whose development is nonfeeding and pelagic and is termed lecithotrophy. The second refers to nonpelagic, nonfeeding larvae and is termed direct development. The final category occurs where the parent organism retains the eggs until full development has occurred within its protection and is known as brooded development.

### **1.1.3** CLASSIFICATION SCHEMES

Species of marine invertebrate show a wide range of different larval types as outlined in the previous sections. However, the great diversity of larval form has hindered the creation of a universally accepted classification scheme. Many researchers have attempted to produce classification schemes that can be used either for specific groups or which aim to encompass all groups of marine invertebrates or which highlight specific dichotomies (e.g. feeding vs. nonfeeding, pelagic vs. nonpelagic, direct vs. indirect development).

Classification schemes of larval strategies in marine invertebrates commonly follow the scheme outlined by Thorson (1950) who recognised pelagic and nonpelagic development in molluscs (e.g. Ocklemann, (1965); Thompson, (1967). Pelagic strategies included planktotrophy and lecithotrophy whilst nonpelagic strategies included direct and viviparous development, where viviparous refers to giving birth to live young (Thorson, 1950). Studies on echinoids often show a modification of this scheme, replacing direct development with brooded development (e.g. Strathmann, 1974a; Emlet, 1990, 1995; Jeffery & Emlet, 2003). Studies on neogastropods have often further modified Thorson's scheme when examining larval ecology. Scheltema (1977, 1978, 1979) refers to larvae as either pelagic and nonpelagic, or feeding and nonfeeding, thereby concentrating on the time spent within the water column and, as a result, their differing dispersal patterns. A planktic vs. nonplanktic dichotomous scheme was employed by Hansen (1980a) where planktic species are those with planktotrophic larvae and those with nonplanktic larvae include lecithotrophic and direct development.

Creating a universally accepted classification scheme is difficult for a number of reasons. Firstly, the scheme used needs to suit the purpose of the study. For example, palaeobiogeography studies are likely to be interested in feeding capabilities of different types of larvae which can affect their dispersal patterns and may therefore employ a scheme which recognises only planktotrophic and nonplanktotrophic development. On the other hand, an embryology study might be more concerned with the presence or absence of a true larval stage and so may adopt a direct vs. indirect classification scheme. The second issue arises in studies which focus on fossil species. As it is not possible to make direct observations of early development in extinct species it is often hard to define the subtle differences in larval development from fossil species. As a result a simple dichotomous scheme (e.g. planktotrophic vs. nonplanktotrophic) is often used when examining species with no living representatives.

This study will follow a trichotomous scheme where planktotrophic, lecithotrophic and direct developing larvae are recognised. This is a practical approach as inference of these larval types is relatively straightforward from examination of fossil gastropods. As dispersal of larvae is considered to be a major controlling factor in the macroevolution of benthic marine invertebrates, including gastropods, this is the most appropriate scheme to use. A summary of different classification schemes including the one used in this study can be seen in Table 1.1.

| This thesis | Thorson (1950) | | Ocklemann (1965) | Shuto (1974); Hansen (1978, 1980, 1982, 1983) | Scheltema (1978) | Jablonski & Lutz (1980, 1983) | Jeffery & Emlet (2003) | |
|---|---|---|---|---|---|---|---|---|
| Planktotrophic | Pelagic | Planktotrophic | Planktotrophic | Planktotrophic | Pelagic | Planktotrophic | Planktotrophic | |
| Lecithotrophic | | Lecithotrophic | Lecithotrophic | Lecithotrophic | | Non-planktotrophic | Non-planktotrophic | Lecithotrophic |
| Direct Development | Non-pelagic | Direct Development<br>Viviparous | Direct Development | | Non-pelagic | | | Brooded Development |

**Table 1.1** Summary table of various classification schemes for larval strategies in the literature. This thesis uses a trichotomous scheme but it should be noted that in reality these form members of a wider spectrum of possible larval strategies.

## 1.2 MACROEVOLUTIONARY CONSEQUENCES OF LARVAL STRATEGIES

The link between macroevolutionary trends and larval strategy is often debated within the literature (see Jablonski & Lutz, 1983 for review). It has been proposed that species with planktotrophic larvae have greater dispersal abilities than nonplanktotrophic species due to their longer pelagic phase and that this will result in wider geographic ranges (e.g. Shuto, 1974; Scheltema, 1977, 1978, 1979; Ó Foighil, 1989; Emlet, 1995). It is often argued that wide geographic range is linked to long species duration because widely distributed species are less vulnerable to local catastrophes. If this is the case then it is also logical to assume that planktotrophic species will exhibit lower speciation rates than nonplanktotrophs due to their reduced vulnerability to localised extinction events. These predictions are summarised in Table 1.2. Despite much discussion of the possible consequences of different larval strategies in the literature, the topic remains relatively untested. Testing these hypotheses is particularly difficulty when examining changes through geological time due to preservation biases in the fossil record and the paucity of well resolved phylogenies of certain groups, such as gastropods.

| | Geographic distribution | Species longevity | Speciation Rate |
|---|---|---|---|
| **Planktotrophic** | Wide | Long | Low |
| **Nonplanktotrophic** | Narrow | Short | High |

**Table 1.2** Summary table of predicted macroevolutionary consequences for species with planktotrophic and nonplanktotrophic larvae.

### 1.2.1 GEOGRAPHIC DISTRIBUTION

Both living and fossil species of marine invertebrates have been used to examine the correlation between larval mode, dispersal ability and geographic distribution. Much of the literature has focused on species of benthic marine invertebrates in the mollusc classes Gastropoda and Bivalvia and the phylum Echinodermata.

Studies on living gastropods from the Indo-Pacific region have shown that species with planktotrophic larvae have greater dispersal abilities and as a result wider geographic distributions (e.g. species from the genera *Batillaria, Cerithium, Clypeomorus, Strombus, Tibia, Drupa, Lambis, Apollon, Bursa, Cassis, Tonna, Thais, Nassarius* and from the families Triphoridae and Terebridae (Shuto, 1974)). By contrast, nonplanktotrophic species from the same region have more limited dispersal and therefore narrower distributions (e.g. species from the genera *Olivella*, *Fulgoraria, Granulifusus, Siphonalia, Babylonia, Hindsia, Cantharus, Murex, Ocenebra, Latiaxis, Caecum* and *Margarites* (Shuto, 1974)). A similar pattern is seen in species of the slipper limpet *Crepidula* in the waters of the Atlantic and Gulf Coast of USA where direct developers are seen to form geographically distinct monophyletic clades (Collin, 2001). Comparison of gastropod families in Polynesia and the Western Pacific show that teleplanic larvae have considerably wider geographic distributions when compared to those species without a planktic phase (Scheltema and Williams, 1983). Data from southeastern Australia suggests that species of prosobranch gastropods with direct developing offspring inhabit relatively closed local populations which evolve independently from one another (Hoskin, 1997).

These patterns can also be seen in fossil gastropods from various regions. Planktic species of the family Volutidae from the Neogene of the Gulf Coast of USA have wide geographic distributions even during periods of regression when delta building is taking place, indicating that oceanic barriers of this type do not affect planktic larvae dispersal patterns (Hansen, 1980). The median geographic range of planktic species of various neogastropod families equalled 5.5 geographic units compared with the median geographic range of nonplanktic species of only 1.0 unit. This difference was found to be statistically significant using a Mann-Whitney *U*-test ($P<0.05$). Late Cretaceous gastropods from the Atlantic Coast Plain show a statistically significant difference ($P<0.01$, Kolmogorov-Smirnov test) in geographic range between planktotrophs (median = 1,860km) and nonplanktotrophs (median = 380km) (Jablonski, 1986; Jablonski and Hunt, 2006).

A small number of studies on gastropods have contradicted these results. Poor correlation between planktonic period and geographic range is seen in species from the family Cypraeidae in insular, dispersal-limited settings of the Indo-West Pacific (Paulay and Meyer, 2006) but this is likely the result of estimation error, intraspecific variation and inappropriate taxonomic scale which can obscure macroecological patterns (Paulay and Meyer, 2006). Similarly, the brooding species *Littorina saxtilis* has been shown to be more widespread than the closely related planktonic species *Littorina littorea* in the northern

Atlantic but it is noted that the observations are scattered and more data are required to corroborate these results (Johannesson, 1988).

Studies on the geographic range of different larval types in marine bivalves have shown much more variable results than those seen in gastropods. The deep-sea mussel "*Bathymodiolus*" *childressi* is considered to have teleplanic planktotrophic larvae, perhaps spending more than one year within the plankton, and is shown to have wide distribution patterns across the Gulf of Mexico and the amphi-Atlantic which supports the hypothesis of wide geographic range in planktotrophic larvae (Arellano and Young, 2009). Similar results are seen in species of the family Pinnidae in the western Pacific and Polynesia (Scheltema and Williams, 1983). However, many studies on bivalves show that planktotrophic larvae are often less widespread than nonplanktotrophic species. Species of *Lasaea* with planktotrophic development appear to be confined to the Western Pacific whilst species without a pelagic larval phase are found on all continents (with the exception of Antarctica) and on numerous oceanic islands (Ó Foighil, 1989). Ó Foighil (1989) suggests that the greater *collective* geographic range of *Lasaea* species which release crawl-away juveniles implies that a pelagic phase is not always necessary for long distance dispersal within this genus although by treating the data collectively the author loses resolution within his data. He further suggests that rafting of juveniles and small adults promotes the evolutionary success of brooding species. Similarly, Martel and Chia (1991) propose that if species have no pelagic larval phase then dispersal opportunities may arise during juvenile and early adult stages by drifting in currents using mucus threads. Frequent drifting excursions in the brooding species *Musculus* sp., *Lasaea* sp. and *Transenella tantilla* are thought to favour long distance dispersal during post-metamorphic stages resulting in wider geographic distributions (Martel and Chia, 1991). Research on fossil bivalves from the Late Cretaceous have also shown that geographic range in planktotrophs is not significantly greater than in nonplanktotrophs (Jablonski and Hunt, 2006) but the authors caution that low numbers of nonplanktotrophs in the dataset may skew the results.

A study on fossil temnopleurid echinoids from the Cenozoic of southern Australia (Jeffery & Emlet, 2003) shows that when a non-phylogenetic approach is employed a Mann-Whitney *U*-test reveals that planktotrophic species have a significantly greater geographic distribution than species with nonplanktotrophic larvae (P=0.02). However, phylogenetic analysis from the same study shows that analysis by independent contrasts reveals no significant difference in the geographic distribution of species with different larval strategies although it should be taken into account that low numbers of contrasts will impact the results. The study demonstrates that geographic ranges of fossil temnopleurid echinoids are relatively small compared to extant taxa and other fossil taxa with median geographic ranges of 460km and only 36km in planktotrophs and nonplanktotrophs respectively (Jeffery and Emlet, 2003). The low values of geographic range seen in this study may be a result of the distribution of echinoid bearing outcrops in southeastern Australia. The quality of the fossil record, in terms of both taphonomic and sampling biases, is likely to be a major influence on our understanding of evolutionary trends and has been the focus of a number of recent studies, e.g. Cherns et al, 2011; Vilhena & Smith, 2013; Smith & Benson, 2013. Evidence from living temnopleurid and cidarid echinoids has shown that developmental mode only affects geographic range in species occurring in depths of less than 100m and planktic residence time does not appear to be correlated to distribution patterns (Emlet, 1995). The same study suggests that rafting of adults seen in molluscs is not seen in temnopleurid and cidarid echinoids with brooded larvae but geographic ranges of both planktotrophic and brooded larvae are significantly larger than those seen in other living benthic marine invertebrates (Emlet, 1995).

### **1.2.2** SPECIES LONGEVITY

A number of studies have shown that the species longevity of planktotrophic species is longer than that seen in nonplanktotrophic species (e.g. Hansen, 1978, 1980; Jablonski, 1982, 1986; Gili & Martinell, 1994). These findings provide support for theoretical models (Shuto, 1974; Scheltema, 1977; Jablonski & Lutz, 1983) which predict that a greater ability to disperse will increase geographical and stratigraphical range reducing vulnerability to local catastrophes. There is a severe paucity of data for species longevity of marine invertebrates which may be the result of gaps in the fossil record. Species longevity is often correlated with geographic distribution rather than larval mode based on the presumed relationship between larval dispersal and geographic range (e.g. Jablonski & Hunt, 2006; Powell, 2007). This may be the result of poorly constrained stratigraphy making it difficult to define first and last occurrences of species or may be due to poorly understood taxonomy. Studies need to concentrate of species level larval data to overcome complications at higher taxonomic levels (e.g. congeneric species can have different larval strategies). It is an area in much need of attention if we are to fully appreciate the macroevolutionary consequences of larval mode in marine invertebrates.

A study of forty species of nassariid fossils from the Neogene strata of the Mediterranean and North East Atlantic coasts (specifically North Africa, Portugal, France, Italy, Turkey, Belgium, Denmark & UK) shows a strong correlation between larval mode and species longevity (Gili and Martinell, 1994). The median duration of planktotrophs was found to be 9.8 million years compared to only 2.8 million years in nonplanktotrophs. Of the forty species, twelve were found to have the greatest coincidence of absolute duration of 2.8 million years which represents the Pliocene period. A Mann-Whitney *U*-test found the difference in species longevity between planktotrophs and nonplanktotrophs to be highly significant (P<0.001). Studies on Tertiary neogastropods from the Gulf Coast of the USA show comparable results (Hansen, 1978, 1980). Tertiary species from the family Volutidae show that planktic species have a mean species duration double that seen in nonplanktic species, 4.4million years and 2.2million years respectively (Hansen, 1978). The median duration was 5 million years in planktic species and 1 million years in nonplanktic. Cretaceous fossil prosobranch and shelled opisthobranch species from the Gulf Coast and Atlantic Coast Plain of North America showed that species with planktotrophic larvae showed significant frequencies of overlapping stratigraphic range whilst species with nonplanktotrophic larvae showed significant frequencies of abutting species durations (Jablonski, 1986). The same study shows that the median duration of planktotrophic species in this region is 6 million years and 2 million years in nonplanktotrophic species. The difference is shown to be statistically significant (P<0.01, Kolmogorov-Smirnov test). These results strongly support the hypothesis that planktotrophic species with greater dispersal abilities show greater species durations through geological time. By contrast, gastropod species from the families Architectonicidae, Cymatiidae, Tonnidae and Volutidae in Polynesia and the western Pacific islands do not strongly support the argument that temporal longevity is related to mode of development (Scheltema and Williams, 1983).

Cenomanian bivalves from the Western Interior of North America show a positive correlation between geographic distribution and species longevity significant at the 5% level, but species duration was not correlated with larval mode (Koch, 1980). Similarly, Late Cretaceous bivalves from the Gulf and Atlantic Coastal Plain of USA show geographic distribution and species longevity to be related but there is no significant correlation between larval mode and species longevity (Jablonski & Hunt, 2006). Tertiary temnopleurid echinoids from southern Australia show median durations of 9 million years for planktotrophic taxa and 3 million years for nonplanktotrophic taxa. A Mann-Whiney *U*-test indicated that the difference is statistically significant, P=0.02 (Jeffery & Emlet, 2003). The same study showed that analysis by independent contrasts does not find the difference in range between modes of development to be significantly different (P=0.10) but all standardised contrasts were shown to be negative, indicating that nonplanktotrophic taxa have shorter species durations than planktotrophic taxa (Jeffery & Emlet, 2003).

### **1.2.3** SPECIATION RATES

It is predicted in the literature that those species with wide geographic distributions are less vulnerable to localised extinction events resulting in longer species duration and consequently low speciation rates. If planktotrophic taxa are able to disperse across wider distances than nonplanktotrophic taxa then low speciation rates would be expected as gene flow would be maintained between populations. Electrophoretic and biochemical studies on living populations of marine invertebrates support this prediction with evidence that planktotrophic species exhibit low levels of genetic differentiation compared to nonplanktotrophic species (e.g. Wium-Andersen, 1970; Gooch et al., 1972; Berger, 1973; Snyder and Gooch, 1973; Gooch, 1975; Campbell, 1978; Crisp, 1978; Grassle & Grassle, 1978; Siebnaller, 1978; Wilkins et al., 1978; Black & Johnson, 1979; Buroker et al., 1979a, b; Ward & Warwick, 1980). Although this theory is often outlined in the literature it is yet to be adequately tested. As with species longevity, speciation rates are often correlated to geographic range rather than larval mode (e.g. Jablonski & Roy, 2003).

Species with nonfeeding larvae are predicted to be less able to maintain gene flow between geographically isolated populations resulting in increased speciation events (Shuto, 1974). Significant genetic differentiation seen within living populations of nonplanktotrophic *Crepidula* gastropods compared with limited variation in planktotrophic populations of the same genus along the Gulf and Atlantic coasts of North America corroborates this prediction (Collin, 2001). Cretaceous gastropods from the Gulf Coast and Atlantic Coastal Plain show a significant inverse relationship between geographic range and speciation rate (N=90 genera, Spearman's Rank-Order Correlation, R=-0.68, P<0.00001) but show a weak inverse relation between geographic range and total number of species originating within a genus (R=-0.17, P=0.10) (Jablonski & Roy, 2003). Neither the total number of species produced through time nor the number of species within a single time interval is found to be a positively correlated with the geographic range of species in a clade (Jablonski & Roy, 2003).

Jeffery & Emlet (2003) show that speciation rates of planktotrophic larvae of temnopleurid echinoids are significantly higher than in nonplanktotrophic taxa (P=0.03, Mann-Whitney U-Test) but also caution that phylogenetic evidence of switches in larval mode is not taken into account in this data. A study on cowries from the Indo-West Pacific examines the potential for diversification and its relationship with planktonic period (Paulay & Meyer, 2006). The study proposes that planktonic period is roughly correlated with "geographic scale of speciation" which in turn is related to the rate of diversification. The authors note that diversification is limited for highly dispersive species due to the reduced opportunities for isolation whilst diversification of poorly dispersive species is limited by the slow build up of sympatric diversity (Paulay & Meyer, 2006). The study notes that those species with intermediate levels of dispersal are likely to have the greatest potential for diversification. Evidence from Tertiary volute gastropods of the Gulf Coast supports the hypothesis that larval ecology influences evolutionary rates (Hansen, 1978). The study shows that species with nonplanktonic, low dispersal larvae are easily isolated by local barriers along continental shelves during periods of regression and that this results in increased extinction and speciation rates (and as a result decreases average species longevity). Research on the acmaeid limpet *Collisella* shows that during periods of warming planktic larvae of warm-water species can successfully settle at higher latitudes resulting in an extension of their geographic range (Murphy, 1978). If a subsequent cooling event occurs geographic ranges will return to more equatorial regions but it is possible that some species may continue to survive at higher latitudes in warmer embayments resulting in isolation and possible increased speciation (Murphy, 1978).

Figure 1.2 shows the locations where studies on the macroevolutionary consequences of larval mode in different phyla have been undertaken. These examples demonstrate that understanding the relationship between larval mode and speciation rates is not simple and requires greater knowledge of the influences on geographic range. Environmental tolerance may also contribute to determination of geographic range and species longevity and as a result speciation rates.

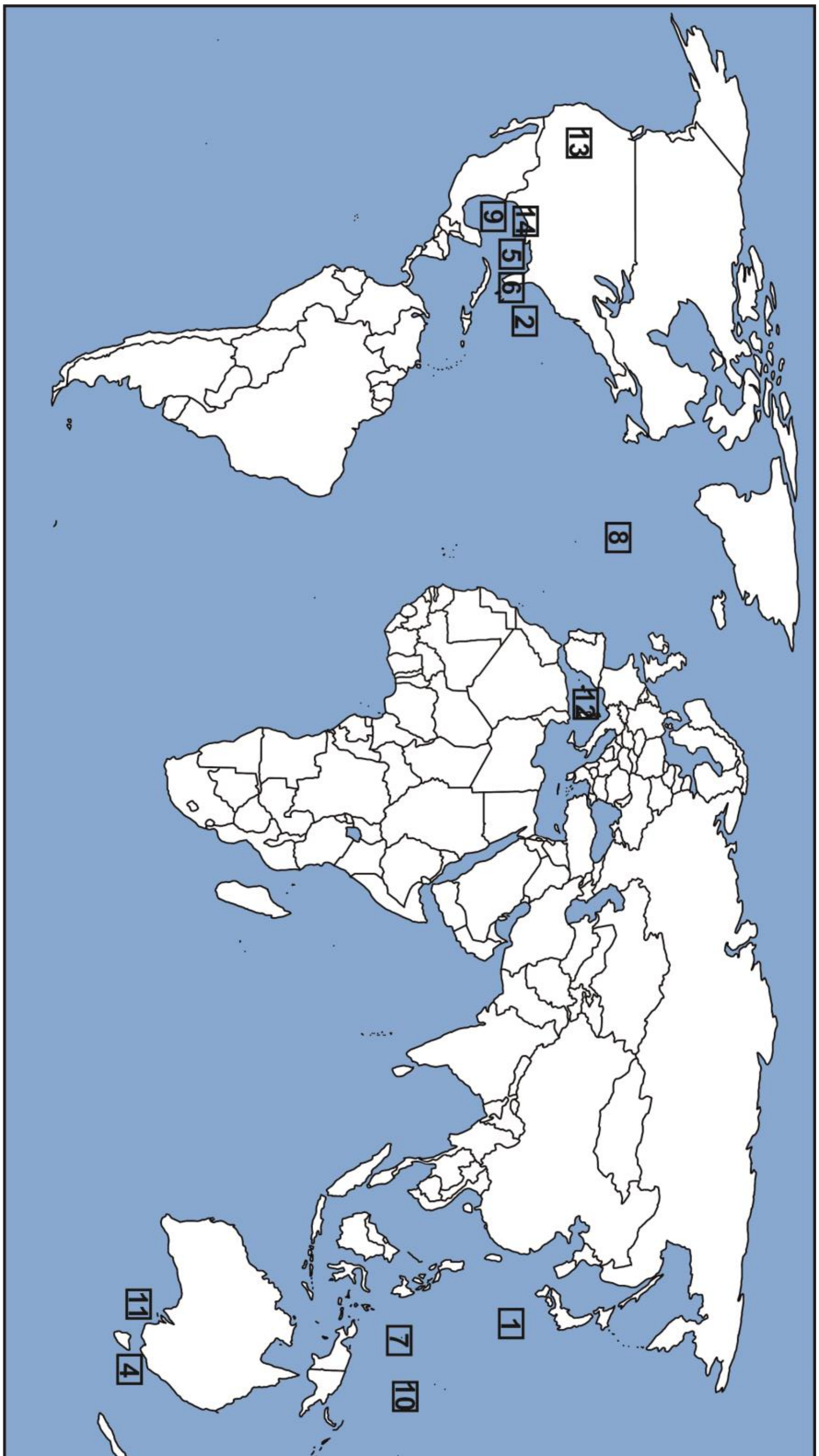


**Figure 1.2** Map summarising localities of studies discussed in this chapter. **Gastropods:** 1. Shuto, 1974; 2. Collin, 2001; 3. Scheltema & Williams, 1983; 4. Hoskin, 1997; 5. Hansen, 1978, 1980, 1982, 1983; 6. Jablonski & Hunt, 2006; 7. Paulay & Meyer, 2006; 8. Johannesson, 1988; 12. Gili & Martinell, 1994; 14. Jablonski & Roy, 2003. **Echinoids:** 11. Jeffery & Emlet, 2003. **Bivalves:** 9. Arellano & Young, 2009; 10. Ó Foighil, 1989; 13. Koch, 1980.

## 1.3 EVOLUTION OF LARVAL MODE

Relatively little research has focused on unravelling the evolutionary history of marine invertebrate larvae through geological time. Preservation biases in the fossil record, due to the extremely patchy preservation of more fragile life stages, means direct observations are often not possible. Well-resolved phylogenies can be difficult to develop, often a result of poorly defined characters and character states, particularly in the molluscs. Consequently our ability to map evolutionary changes in larval mode is severely hampered. This combination of challenges means that questions regarding the plesiomorphic larval condition and the timing and order of switches in larval mode are yet to be adequately answered. The completeness and adequacy of the fossil record have been the focus of a number studies which has shed light on the challenges faced by researchers examining evolutionary patterns and trends (e.g. Donovan & Paul, 1998; Cherns et al, 2011; Vilhena & Smith, 2013; Smith & Benson, 2013).

In order to fully understand the evolutionary patterns of larval strategies both evolutionary and developmental biology must be taken into account (e.g. von Baer, 1828; Haekel, 1866). Evolutionary biology examines the changes of heritable traits of a particular population over successive populations whilst developmental biology examines the changes in morphology of an organism from its early life stages through to its adult body plan. Until relatively recently these two aspects of biological science have been treated separately and the link between them has not been taken into consideration. The integration of these two disciplines has resulted in the creation of evolutionary developmental biology ("evo-devo"). The advancement of new techniques in developmental biology over the past thirty years has played a large part in the establishment of "evo-devo" (e.g. Scott & Weiner, 1984; McGinnis et al, 1984a, b). A significant amount of "evo-devo" research is focused on understanding the relationship between evolutionary and developmental events occurring throughout geological time. Unravelling the evolutionary history of larvae and their subsequent development into adults is just one part of this diverse research area. The term "species selection" is often used within "evo-devo" literature and refers to the evolutionary patterns created by differences in speciation and extinction rates resulting from the interaction of intrinsic biological traits with the environment.

Understanding the relationship between different larval strategies and the timing and order of shifts, often requires well-resolved phylogenies (e.g. Emlet, 1990; Hart, 2000; Collin, 2001). This may account for the limited published data regarding the evolutionary trends of gastropod larvae. Due to the continuous, incremental growth of the gastropod shell and the lack of anatomical or genetic material in fossilised shells it is often difficult to identify useful characters and character states required for phylogenetic analysis. Despite this challenge a number of researchers have examined the evolutionary patterns of gastropod larval strategies using both phylogenetic and non-phylogenetic techniques (e.g. Hansen, 1982; Reid, 1989; Lieberman et al., 1993). Some researchers suggest that whilst planktotrophic species often give rise to nonplanktotrophic species, the opposite is extremely rare, possibly due to the presumed difficulty in reacquiring the specialised feeding and swimming structures associated with planktotrophic development once they are abandoned (e.g. Strathmann, 1974; 1978).

Neogastropods from the Palaeogene of the Gulf Coast of the USA show that there is a high rate of diversification in nonplanktotrophic species and a unidirectional trend in developmental change with nonplanktotrophic species evolving from planktotrophic species but no evidence of the reverse (Hansen, 1982). The same study shows that a planktotrophic species has never been known to result from an entirely nonplanktotrophic genus in the Eocene of this region and that entirely nonplanktotrophic groups remain so even if the pressures initially resulting in this larval mode are removed. These results support the view that planktotrophic species often give rise to nonplanktotrophic species.

Recent advances in molecular phylogenies have proved a useful tool when examining the evolution of larval mode in living gastropods. A molecular study of Recent Turritellidae species has investigated the evolution of larval modes and the role of species selection and development in determining transitions in larval strategies (Lieberman et al., 1993). The study found planktotrophy to be the plesiomorphic condition in the Turritellidae and showed that nonplanktotrophy must have been acquired at least twice based on a molecular phylogenetic analysis. The results also supported the general view that nonplanktotrophic lineages are unlikely to give rise to planktotrophic species but did not rule out the possibility completely. Examination of each of the separate lineages acquiring nonplanktotrophic larval type suggested that species selection may play an important role but the authors argued that developmental processes are also an important factor in transitions between larval modes (e.g. independently acquired nonplanktotrophic larvae are not descended from the same common ancestor (Lieberman et al., 1993)).

Molecular phylogenetic reconstructions of living species of the genus *Conus* from the Indo-West Pacific and Western Atlantic found that the relationship between clades was poorly resolved and attributed this to saturation of the phylogenetic signal due to potential repeated substitutions occurring over time (Duda & Palumbi, 1999). As with other taxa it was determined that planktotrophy is the primitive larval condition and nonplanktotrophy the derived larval condition in species of *Conus*. Shifts from planktotrophy to nonplanktotrophy were shown to occur at least eight times and there was no indication that a nonplanktotrophic lineage could give rise to planktotrophic species. As with other studies (e.g. Lieberman et al., 1993) the authors rejected the hypothesis that species selection alone controls diversification in nonplanktotrophic taxa but instead stated that "developmental shifts and species selection represent two extremes that can be used to explain why there have been increases in the number of nonplanktotrophic species relative to species with planktotrophic larvae in prosobranch gastropods" (Duda & Palumbi, 1999: 10276).

A phylogenetic reconstruction of the family Littorinidae based on morphological characters shows that within a single clade of six genera, the Lacuninae, both planktotrophic and nonplanktotrophic larvae are represented (Reid, 1989). The study used phylogenetic analysis along with shell morphology to determine the possibility of a transition from nonplanktotrophy to planktotrophy within the clade. The results show that the shells of the planktotrophic species more closely resemble the shells of their nonplanktotrophic sister taxa than those of other planktotrophic littorinids and other gastropods. Reid (1989) suggests that the similarity in shell morphology and the phylogenetic analysis imply a recent reversal from nonplanktotrophy to planktotrophy among the Lacuninae.

The question of the reacquisition of the specialised structures used for mobility and feeding in planktotrophic taxa is yet to be explored in detail in the Gastropoda. There is a general bias in interpretations towards the loss of feeding larvae due to the presumed difficulty in reacquiring the complex morphology required for an extended planktonic period. However, there is some evidence that gastropods can retain specialised larval structures in nonplanktotrophic taxa, such as those required for feeding and swimming (e.g. opposed-band ciliary mechanism required for feeding), making a transition from nonfeeding to feeding development possible (Collin, 2004; Collin et al., 2007).

Echinoderms present an excellent opportunity to investigate evolutionary patterns in marine invertebrate larvae using a phylogenetic approach. Echinoids are often used as a model organism due to their morphological complexity which makes them relatively straightforward to classify both taxonomically and phylogenetically (Jeffery et al., 2003). A number of studies show that planktotrophy is the primitive larval mode within various groups of echinoderms (e.g. Jägersten, 1972; Strathmann, 1978, 1993; Wray 1992, 1995, 1996; McEdward & Janies, 1997; Jeffery & Emlet, 2003; Jeffery et al., 2003; Cunningham & Jeffery Abt, 2009) and that in many lineages it has been lost entirely due to the increased speciation of nonplanktotrophs (Strathmann, 1985; Wray, 1996). There is no evidence to suggest that nonplanktotrophic echinoid larvae existed until the end-Cretaceous (Jeffery, 1997) although it is estimated that it has independently arisen a minimum of twenty times since that point through the loss or reduction of complex larval structures (Wray, 1995; Jeffery, 1997). Phylogenetic analysis of Recent temnopleurid echinoids from southern Australia using both parsimony and maximum likelihood analyses supports the hypothesis that planktotrophy is the primitive larval condition in this group if the transition from planktotrophy to lecithotrophy is irreversible (Jeffery et al., 2003). The same study showed a single transformation to lecithotrophy in this group with the lecithotrophs forming a single monophyletic group suggesting that reversal to planktotrophy had not occurred. Similarly, Tertiary temnopleurid echinoids showed that nonplanktotrophy had independently arisen in three clades (Jeffery & Emlet, 2003). Because the nonplanktotrophic taxa in this study are found in clades which contain no planktotrophic taxa, the authors suggest that the transition is both unidirectional and irreversible. Research on Cretaceous spatangoid echinoids showed that nonplanktotrophy arose independently five times within this group (Cunningham & Jeffery Abt, 2009). Switches were shown to be concentrated at a discrete geological time interval suggesting that external factors, such as predation or nutrition, were influencing shifts to nonplanktotrophy. Some species of echinoid are thought to represent intermediary forms between planktotrophy and nonplanktotrophy due to evidence of reduced larval structures (Emlet, 1986) suggesting that it is possible to reacquire planktotrophy from nonplanktotrophic taxa within this group (e.g. the echinoid *Clypeaster rosaceus*).

Molecular phylogenetic analysis of the asterinid starfish genera *Patiriella* and *Asterina* suggests that the manner in which characters and character states are treated can greatly alter our understanding of the evolutionary history of larval strategies (Hart et al., 1997). The authors reconstructed ancestral larval strategies under three differing assumptions of four differing character states: feeding, planktonic development; nonfeeding, planktonic development; development in benthic egg masses; viviparous brooding (see Figure 1.3). If these larval traits are treated as unordered and reversible then there is no conclusion regarding ancestral mode of development. If the characters are treated as ordered but reversible (feeding planktonic ↔ nonfeeding planktonic ↔ benthic egg masses ↔ viviparous brooding) either planktonic, nonfeeding or benthic egg mass development is found to be ancestral with parallel evolution of feeding larvae and viviparous brooding occurring. Where shifts in mode of development were treated as ordered and irreversible (feeding planktonic → nonfeeding planktonic → benthic egg masses → viviparous brooding) it was shown that the loss of ancestral feeding larvae increased the number of inferred switches in larval strategy (from six to nine steps). These results do not wholly support the widely held assumption that planktotrophy is the ancestral larval strategy in the genera *Patiriella* and *Asterina* (Hart et al., 1997) but show that the way in which we analyse data can greatly alter our conclusions regarding larval strategy evolution.

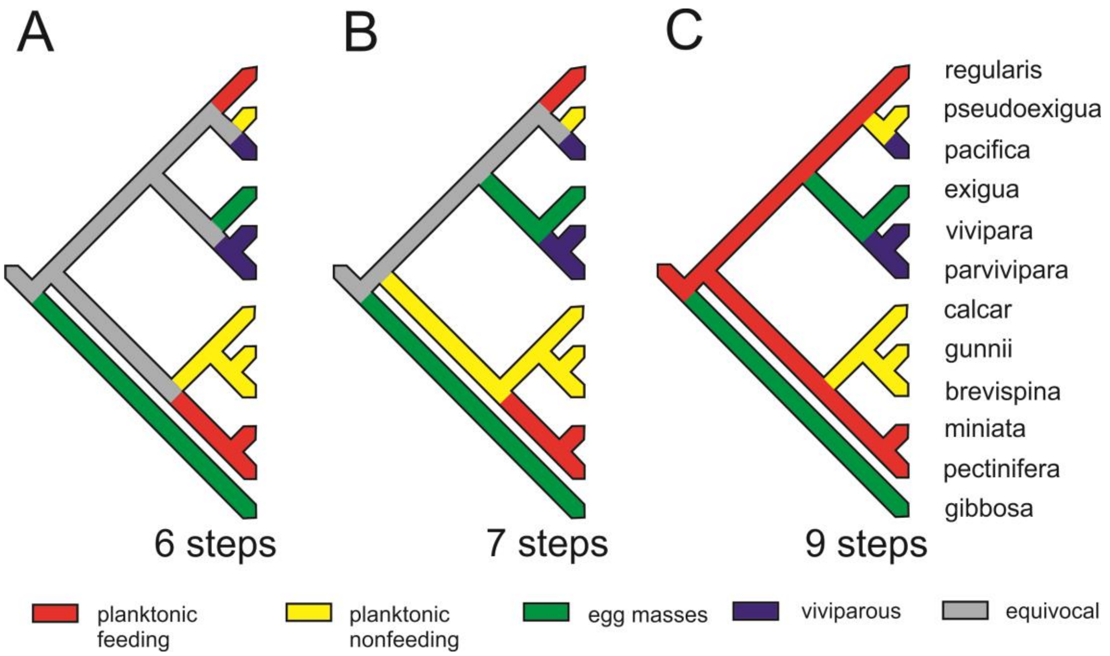


**Figure 1.3** Phylogenetic trees showing the number and order of changes in type of developmental mode of asterinid starfish from the genera *Patiriella* and *Asterina* (redrawn from Hart et al. (1997: 1854)). **A** Unordered: mode of development can evolve between character states in any order or direction. **B** Ordered: developmental mode can evolve in one order but any direction (feeding planktonic ↔ nonfeeding planktonic ↔ benthic egg masses ↔ viviparous brooding). **C** Irreversible: developmental mode can evolve in one order and one direction only (feeding planktonic → nonfeeding planktonic → benthic egg masses → viviparous brooding).

Although a great deal of research supports the hypothesis that planktotrophy is ancestral in marine invertebrates there is some evidence to suggest that this may not be the case (e.g. von Salvini-Plawen, 1985; Chaffee & Lindberg, 1986; Peterson, 2005; Nielsen, 2009). Examination of fossilised eggs and embryos from the Precambrian and Cambrian suggests that planktotrophic larvae did not exist in many marine invertebrate groups at this time (see discussion in Nielsen, 2009). However, the apparent absence of planktotrophy at this time does not necessarily prove the plesiomorphic character of direct development and such evidence should be treated with caution. Molecular clock analysis has provided evidence that nonfeeding is the ancestral larval strategy in a number of marine invertebrate groups with between four and eight instances of planktotrophy independently evolving between the Late Cambrian and Middle Ordovician (Peterson, 2005).

From the literature, it is clear that a number of factors influence our understanding of the evolution of larval strategies in marine invertebrates. Species from different geological time periods may not produce the same conclusions even if they are from the same group and it is worth comparing fossils of the same time period to draw conclusions about the bigger picture. Similarly, the ancestral state and timing and order of switches in larval mode may alter depending on the taxonomic level of the taxa being examined. The results for the phylum might not mirror the results for individual genera, families or classes. When using phylogenetic analysis it is important to understand the limitations of the technique and to examine the data in a way that reduces the need for assumptions based on limited evidence e.g. assumptions regarding the order or reversibility of different characters.

## 1.4 FACTORS DRIVING SWITCHES IN LARVAL STRATEGY

Despite research showing that switches in larval strategy are both possible and evident in the fossil record, very little research has focused on examining the factors that influence such shifts. Coordinated shifts in larval strategies have been shown to occur in echinoids as well as other marine invertebrate groups (Jeffery, 1997; Peterson, 2005; Cunningham & Jeffery Abt, 2009) suggesting that environmental changes may be responsible for switches in developmental mode, although increased numbers of predatory organisms have also been considered (Wray, 1995; Peterson, 2005).

Peterson (2005) discusses the role of predation in determining shifts in larval strategies. He suggests that the exploitation of the pelagic realm by nonfeeding larvae at the end of the Cambrian was likely driven by the onset of benthic predation. Peterson argues that limited predation in the pelagic realm at this time created a safe environment in which larvae could undergo their early development. He further suggests that the radiation of epifaunal suspension feeders from the Upper Cambrian to the Middle Ordovician resulted in coordinated shifts to planktotrophy, increasing the numbers of offspring, whilst later switches to nonplanktotrophy, increasing parental protection, were driven by increased benthic predation. Wray (1995) argues that increased time to metamorphosis into the benthic adult body plan can be disadvantageous during periods of high predation therefore forcing species to reduce the transition time from planktic larvae to benthic juvenile. The role of predation is considered in studies on echinoids where coordinated shifts to nonplanktotrophy at the end of the Cretaceous occur (Cunningham & Jeffery Abt, 2009). The authors suggest that a major radiation of benthic predators occurred earlier in the Cretaceous than the shift to nonplanktotrophy indicating that there is no correlation between high predation levels and shifts in developmental mode.

Since the 1950s there has been a great deal of research examining the distribution of developmental mode in marine invertebrates across a variety of habitats and environmental conditions (e.g. Thorson, 1950; Mileikovsky, 1971; Vance, 1973; Strathmann, 1985; Pearse et al. 1991; Tyler & Young, 1992), mostly associated with latitude and depth. “Thorson’s Rule” (coined by Mileikovsky, 1971) suggests that low latitudes favour planktotrophic larvae whilst high latitudes favour nonplanktotrophic larvae (Thorson, 1950). Similarly, at greater depths Thorson (1950) notes that nonplanktotrophic development is more prevalent. He attributes this global trend in benthic marine invertebrates to restricted nutrient availability and colder temperatures at high latitudes and greater depths. A number of authors have found similar results in a variety of benthic marine invertebrates (e.g. Vance, 1973; Christiansen & Fenchel, 1979; Picken, 1980; Strathmann, 1985; Roughgarden, 1989). However, a number of studies have revealed the many exceptions to this general rule (e.g. Pearse et al. 1991; Tyler and Young 1992; Clarke, 1992; Pearse 1994). Many of the most prevalent marine invertebrates in Antarctica, such as asteroids and bivalves, produce planktotrophic larvae. In gastropods, there are exceptions within the nudibranch and ascoglossan opisthobranchs, where direct developing larvae are most often seen in the tropics (Clark & Goetzfried, 1978) and within the stenoglossa which are predominantly nonplanktotrophic at all latitudes (Radwin & Chamberlain, 1973).

Studies on fossil echinoids in southern Australia have shown some interesting patterns. Cold water temperature was thought to be responsible for the large numbers of brooding taxa occurring in southern Australia during the Eocene following the opening of Drakes Passage (Foster, 1974). However, more recent studies in the same region have shown that there is no positive correlation between cold palaeotemperatures and the high numbers of brooding echinoids in this region (McNamara, 1994). Instead, it is suggested that the northward migration of Australia during the Cenozoic towards lower latitudes resulted in greater environmental instability and consequently reduced diversity of brooding echinoids. Present day brooding echinoids dominate the environmentally stable Antarctic region whilst southern Australia is dominated by lecithotrophic taxa. Evidence from the end Maastrichtian shows that coordinated switches to nonplanktotrophy in many independent echinoid lineages is confined to a relatively short period of time (Jeffery, 1997; Cunningham & Jeffery Abt, 2009). These studies suggest that increasing seasonality at the end of the Cretaceous resulted in less stable nutrient supply. As nonplanktotrophs gain all their nutrition from the egg from which they hatch, it is likely that it is the more favourable developmental mode in environmentally unstable regions and as a result a switch from planktotrophy might occur. Recent echinoderms living in areas of unstable nutrient supply (e.g. Pearse & Cameron, 1991) either synchronise their reproductive cycles to coincide with nutrient blooms, or acquire nonplanktotrophic development in order to be independent of nutrient supply.

Very little of the research on developmental mode in marine invertebrates concentrates on correlating shifts in larval strategy with possible environmental factors and it is an area still in need of much work. It is possible that different groups respond in very different ways to changes in environment and therefore one rule may not apply to all marine invertebrates (Table 1.3).

| **Geological Period** | **Direction of switch** | **Possible external cause** |
|---|---|---|
| **Campanian/Maastrichtian** | Feeding<br>→<br>Nonfeeding | Environmental instability |
| **P/T Mass Extinction** | | |
| **Ordovician** | Nonfeeding<br>→<br>Feeding | Suspension feeder predation |
| **Cambrian** | Larvae absent<br>→<br>Nonfeeding | Benthic predation |

**Table 1.3** Examples of possible external factors causing switches in larval strategy.

## 1.5 AIMS AND OBJECTIVES

Despite the vast amount of research examining larval strategies from a biological perspective, such as “evo-devo” (discussed previously), there is a real paucity of knowledge of historical patterns that can be gleaned from the fossil record. Studies using fossil material could shed light on the causes and consequences of different larval modes. As gastropods are one of a few groups where larval mode can be determined from fossil specimens (discussed fully in Chapter 5), they provide an excellent opportunity to test whether predications on the evolution of larval mode from living taxa are evident throughout geological time.

Examination of the published literature on larval strategies and their evolutionary trends suggests that a number of general “rules” have been established. It is predicted that planktotrophic larvae will exhibit wider geographic distributions than nonplanktotrophic species as a result of greater dispersal ability. This is thought to result in increased species longevity in planktotrophs, due to their decreased vulnerability to local catastrophes, and low speciation rates when compared to nonplanktotrophs.  These predictions are generally accepted in the literature despite a lack of supporting data. The literature reveals a large gap in published data to establish whether these predictions are true patterns in the fossil record or simply a logical assumption based on suggested trends seen in living species. This research seeks to increase the global dataset examining the macroevolutionary consequences of larval strategies in fossil marine invertebrates using Cenozoic gastropods from southeastern Australia as an example (Table 1.4).

| Southeastern Australia | Gulf Coast, USA | |
|---|---|---|
| ? ★ | √<br>(e.g. Hansen, 1978, 1980) | Gastropods |
| √<br>(e.g. Jeffery & Emlet, 2003) | ? | Echinoids |

**Table 1.4** Table to show where research has been carried out on gastropods and echinoids in the main research regions of southeastern Australia and the Gulf Coast of USA. The star indicates the research to be carried out in this study.

The first three chapters of this thesis provide the foundations for the analyses carried out in later chapters. Chapter 1 has ascertained what is already known about the evolution of larval strategies by examining the key literature, identifies the general rules that are to be tested and provides the justification for this research. Chapter 2 examines the geology of the area from which both collected and museum specimens have come from. This provides some insight into the possible taphonomic and sampling biases whilst also aiding our understanding of palaeoenvironments, which may be important in trying to unravel whether external factors cause shifts in larval mode. Chapter 3 is a taxonomic revision of all the taxa used in this research. Close examination of type material provides the justification for distinguishing between individual species.

Most published research suggests that planktotrophy is the ancestral larval strategy in marine invertebrates, with nonplanktotrophy being acquired independently in a variety of groups (e.g. echinoids, gastropods) although there are examples of the opposite having occurred. However, due to the difficulties in creating well resolved phylogenies of gastropods (similar to those based on echinoids) there is a paucity of phylogenetically tested data. In order to increase our understanding of the plesiomorphic larval strategy and the subsequent switches in developmental mode, attempts must be made to increase our confidence in phylogenetic data. As part of this study phylogenetic analyses will be carried out (Chapter 4) in order to show the relationships between taxa and to map switches in larval strategy throughout the Cenozoic in marine gastropods (Chapter 5). Whilst our understanding of evolutionary trends in developmental mode of marine invertebrates is slowly increasing, the external factors which control switches are still yet to be fully explored. Suggestions to date include increased predation and environmental instability but this has only been tested on limited taxa and with limited temporal and spatial constraints. By establishing well resolved phylogenies and it may be possible to show if switches in larval mode correlate to environmental and ecological disturbances.

It is predicted that taxa with planktotrophic larvae will exhibit wider geographic distributions, longer species durations and lower speciation rates than taxa with nonplanktotrophic larvae. Chapter 6 uses nonphylogenetic and phylogenetic analyses to test these assumptions and compares the results to studies on gastropods from the Gulf Coast of USA and on echinoids from southeastern Australia.

In summary, this study aims to 1) identify larval strategies of Cenozoic marine gastropods from southeastern Australia, 2) establish the macroevolutionary consequences of different developmental modes to test widely held predictions, 3) build phylogenies on which larval strategies can be mapped to determine the plesiomorphic larval strategy and any switches occurring in this region during this time period and 4) propose possible factors influencing coordinated switches using geological data, if applicable. The data provided will help to expand the existing global dataset and, as a result aid, our understanding of evolutionary patterns of larval strategies.

# CHAPTER 2

# GEOLOGICAL SETTING

In order to determine the macroevolutionary consequences of different larval strategies and the possible environmental factors influencing switches in developmental mode, the geology of southeastern Australia must be understood. A review of the Cenozoic stratigraphic framework of the region will help to ascertain the temporal distribution of gastropod species.

The majority of specimens used in this thesis come from the extensive collections housed in the Museum Victoria in Melbourne, the South Australian Museum in Adelaide and the Natural History Museum in London. Other specimens have been collected in the field and are used where type material has not been available for examination. Despite the extensive fossil bearing formations in each of the sedimentary basins, gastropod specimens were restricted to particular horizons resulting in significant gaps in the gastropod fossil record of southeastern Australia. Gastropod moulds have been found outside of these fossil-rich horizons but unfortunately they cannot be adequately identified and therefore are excluded from this study. Specimens included in this thesis come from six basins: St Vincent Basin, Murray Basin, Otway Basin, Torquay Basin, Port Phillip Basin, and Gippsland Basin (Figure 2.1). The focus of this chapter is to provide a brief stratigraphic overview of each of these basins. Some of the fossil gastropods from southeastern Australia have wide distributions extending into Western Australia and Tasmania. A brief summary of these Western Australian and Tasmanian formations is also provided.

Full locality descriptions, with longitude and latitude data, are available in Appendix 1 and have been assigned locality codes which are used throughout this thesis. Localities are often found in small clusters (often within metres of one another) and each cluster is usually a considerable distance from the next. As a result a locality map is deemed impractical and is therefore not included.

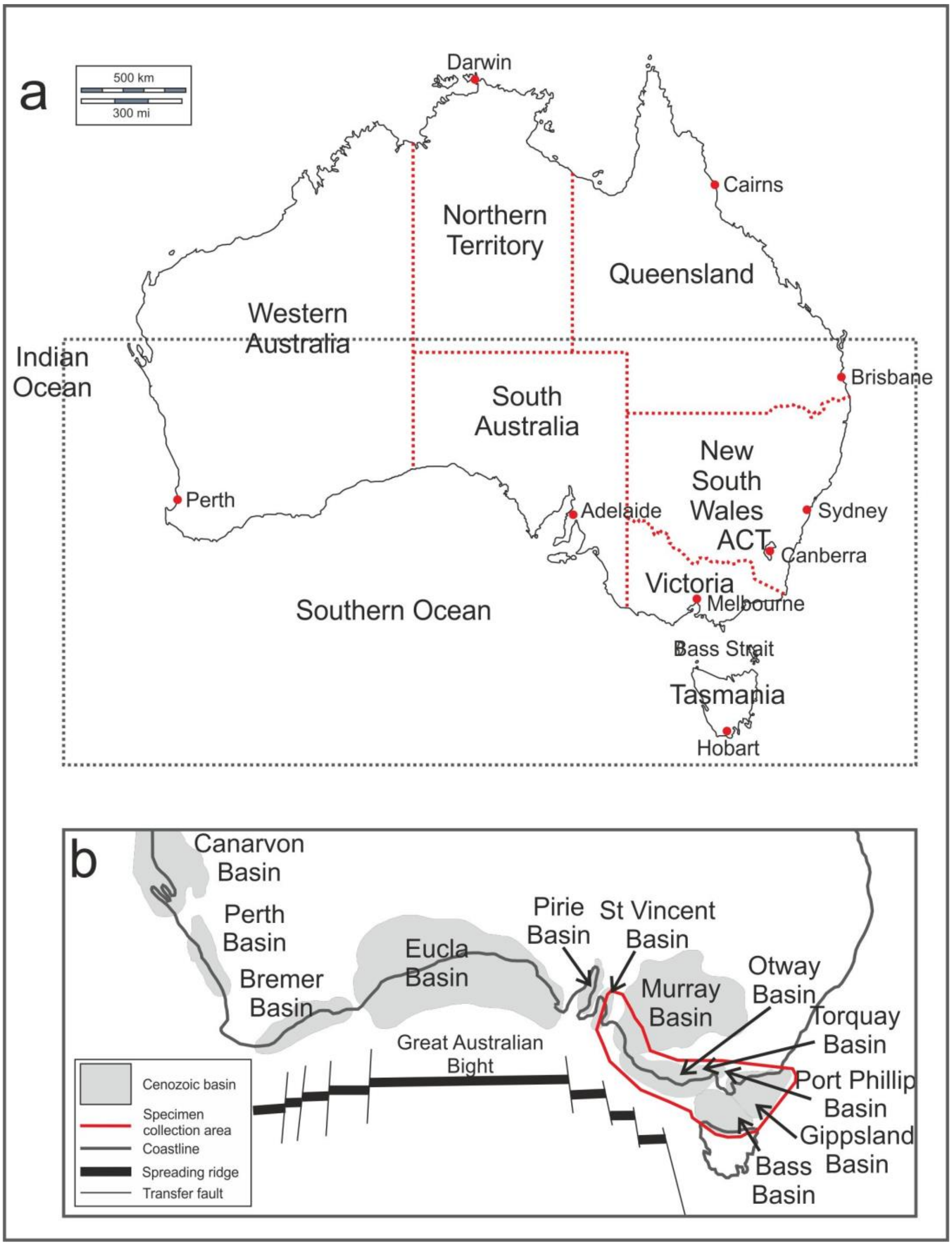


**Figure 2.1** Map of Australia showing state boundaries and all major cities (a); Inset showing major sedimentary basins of southern Australia (redrawn from McGowran et al., 2004: 460, Fig. 1) with outline of specimen collection area in red (b).

## 2.1 SOUTH AUSTRALIA

In South Australia fossil gastropod specimens have been collected from two basins: the St Vincent Basin and the Murray Basin (Figure 2.1b). In each basin three formations contain gastropods relevant to this research.

### **2.1.1** ST VINCENT BASIN

The St Vincent Basin is located in South Australia, covering the Gulf St Vincent and surrounding coastal regions (Figure 2.2). The basin extends to the Mount Lofty Ranges in the east and is separated in the south from the southern continental margin and Eucla Basin by Kangaroo Island (Lindsay & Alley, 1995). Throughout its history, the St Vincent Basin has had restricted marine access to the Southern Ocean through Backstairs Passage and Investigator Strait (Lindsay & Alley, 1995). The St Vincent Basin is subdivided into four sub-basins from north to south: the Adelaide Plains Sub-basin, Golden Grove Embayment, Noarlunga Embayment and Willunga Embayment (Figure 2.2). The majority of specimens from the St Vincent Basin used in this thesis have been recovered from the Willunga Embayment.

The St Vincent Basin is an intracratonic, elongate graben resulting from fault reactivation and sediment deposition initiated by the northerly migration of Australia from Antarctica during the Paleogene and Early Neogene. Older lines of weakness were reactivated approximately 45-42 million years ago resulting in faulting, much of which is still active today (James & Bone, 2000). By 42Ma the St Vincent Basin was a large, open gulf facing the Southern Ocean and basin development continued until the Early Neogene. The eastern margin of the basin (Mount Lofty Ranges) is part of a Neogene fold and thrust belt which has created a series of half-graben embayments. Deposition occurred in these shallow grabens, and strata are up to 700m thick (Lindsay & Alley, 1995). The four sub-basins follow the grain of the underlying Delamerian fold belt (Lindsay & Alley, 1995). Of the four sub-basins, the Adelaide Plains Sub-basin is the largest and has been the subject of much exploration into groundwater supplies resulting in well understood subsurface stratigraphy (e.g. Shepherd, 1975; Sheard & Bowman, 1996). The remaining three sub-basins are all asymmetric tectonic wedges with strata dipping gently south and strata thickness increasing southeasterly towards presumed fault margins (Lindsay & Alley, 1995).

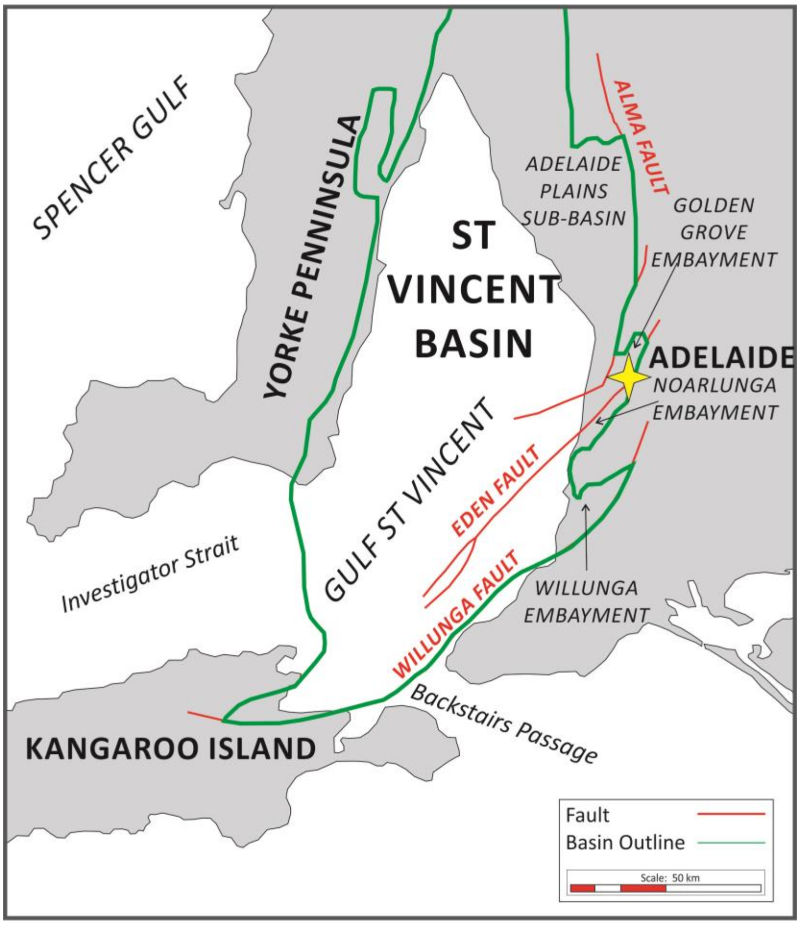


**Figure 2.2** Location map of the St Vincent Basin. Redrawn from James & Bone (2000: 763, Fig. 1).

The geology of the St Vincent Basin has been the focus of numerous studies since the late nineteenth century. Work by Glaessner during the 1950s and 1960s provided the foundations of modern stratigraphic studies in South Australia and included a detailed review of the St Vincent Basin (e.g. Glaessner & Wade, 1958). The first modern stratigraphic review of the basin was compiled by Reynolds (1953) with modifications of this stratigraphy made by Cooper (1979), Jenkins et al. (1982) and Fairburn (1998). More recent studies examining the geology and stratigraphy of the St Vincent Basin have concentrated on particular aspects of formations (e.g. mineralogy, biostratigraphy, palaeoceanography or geological time periods (e.g. Lindsay, 1967; Jenkins, 1974; Jones & Fitzgerald, 1984, 1987; Lindsay & McGowran, 1986; McGowran, 1987; McGowran et al., 1992, 1997, 2004; Boreen & James, 1995; Dyson 1998; James & Bone, 2000)). A brief overview of the geological history of the basin and the formations can be found in Alley & Lindsay (1995) whilst Boreen & James (1995) examined the sedimentology and sedimentary structures of the Willunga Embayment in detail. Correlation of the St Vincent Basin stratigraphy with other southeastern Australian Basins is examined in McGowran et al. (2004).

Specimens used in this thesis have been recovered from the Late Eocene Blanche Point Formation (Figure 2.3a, b, c) and the Pliocene Dry Creek Sand and Hallett Cove Sandstone Formations. The Dry Creek Sand was not observed in the field as access to outcrops is restricted. Details of the localities and species associated with each formation are presented in Table 2.1.

The Blanche Point Formation is Late Eocene in age and is comprised of four members: the Tuketja Member, the Gull Rock Member, the Perkana Member and the Tuit Member (which does not occur in the Willunga or Noarlunga Embayments). The Tuketja Member is approximately 2.3m thick and comprises green/grey, glauconitic, fossiliferous mudstone with limestone lenses (Lindsay & Alley, 1995). The presence of the planktonic foraminifera *Hantkenina alabamensis* has been valuable in regional correlations and is indicative of warm conditions (McGowran, 1989, 1991). The Gull Rock Member is approximately 12.2m thick (Lindsay & Alley, 1995) and consists of interbedded fossiliferous glauconitic, non-fossiliferous glauconitic and burrowed marlstones. The fossil content includes bryozoans, bivalves, gastropods, cephalopods, sponges, corals and brachiopods. The majority of gastropod fossils in this member are turritellids and it is likely that all the specimens from this formation included in this thesis come from this member, although washout on the cliff makes it difficult to be entirely confident in this assessment. The Perkana Member is a massive calcareous mudstone with spiculite beds. It is not found under the city of Adelaide, probably a result of erosion (Lindsay & Alley, 1995). The youngest member, the Tuit Member, is comprised of fossiliferous glauconitic and burrowed marlstones and chert-bearing bands (Lindsay & Alley, 1995; James & Bone, 2000). Specimens from this formation included both collected material and museum types. Material collected in the field was not collected incrementally due to washout on the cliff.

The Dry Creek Sand underlies and interfingers the Hallett Cove Sandstone in the Adelaide Plain Sub-basin. This formation is between 43m and 60m thick and is mostly confined to the Adelaide Plains Sub-Basin. The shelly sand has been dated as Late Pliocene based on the molluscan faunas preserved in it (Ludbrook, 1963, 1973). Towards the base of this unit the sand becomes finer grained and siltier and is often referred to as the “Croydon Facies” (Lindsay, 1969). This basal unit is glauconitic with numerous bryozoans and foraminifera indicating Early Pliocene age (Lindsay & Alley, 1995). The Dry Creek Sand only includes specimens from museum collections.

The Hallett Cove Sandstone varies from 1m to 4m thick and is somewhat variable in its lithology. In the Hallett Cove area it is identified as a transgressive, shallow marine sandstone to sandy limestone whereas near Port Willunga it consists of interbedded sandstone, limestone and sand with thick horizons of fossiliferous shelly sand towards the base of the unit (Lindsay & Alley, 1995). All specimens from this formation are from museum collections.

| Formation | Age | Localities | Species |
|---|---|---|---|
| Hallett Cove Sandstone | Cheltenhamian – Yatalan<br>(Pliocene – Pleistocene)<br>5.0-2.4Ma | SA033 | *Nassarius (Hima) tatei tatei* |
| Dry Creek Sand | Kalimnan – Yatalan<br>(Pliocene)<br>4.4-2.59Ma | SA030<br>SA031<br>SA032 | *Nannamoria strophodon strophodon*<br>*Notovoluta ellipsoidea*<br>*Antiguraleus incisus*<br>*Guraleus adelaidensis*<br>*Guraleus subnitidus*<br>*Nassarius (Zeuxis) spiraliscabrus*<br>*Nassarius (Zeuxis) subcopiosus* |
| Blanche Point Formation | Johannian – Aldingan<br>(Late Eocene)<br>37.8 – 34.0Ma | SA034<br>SA035<br>SA036<br>SA037<br>SA049 | *Notovoluta capitonica*<br>*Alcithoe (Waihaoia) pagodoides pagodoides*<br>*Notopeplum protorhysum*<br>*Guraleus eocenicus*<br>*Alcithoe (Waihaoia) cribrosa* |

**Table 2.1** Table of formations from the St Vincent Basin with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropod species found in these formations include both collected and museum material which will be used in later analyses.

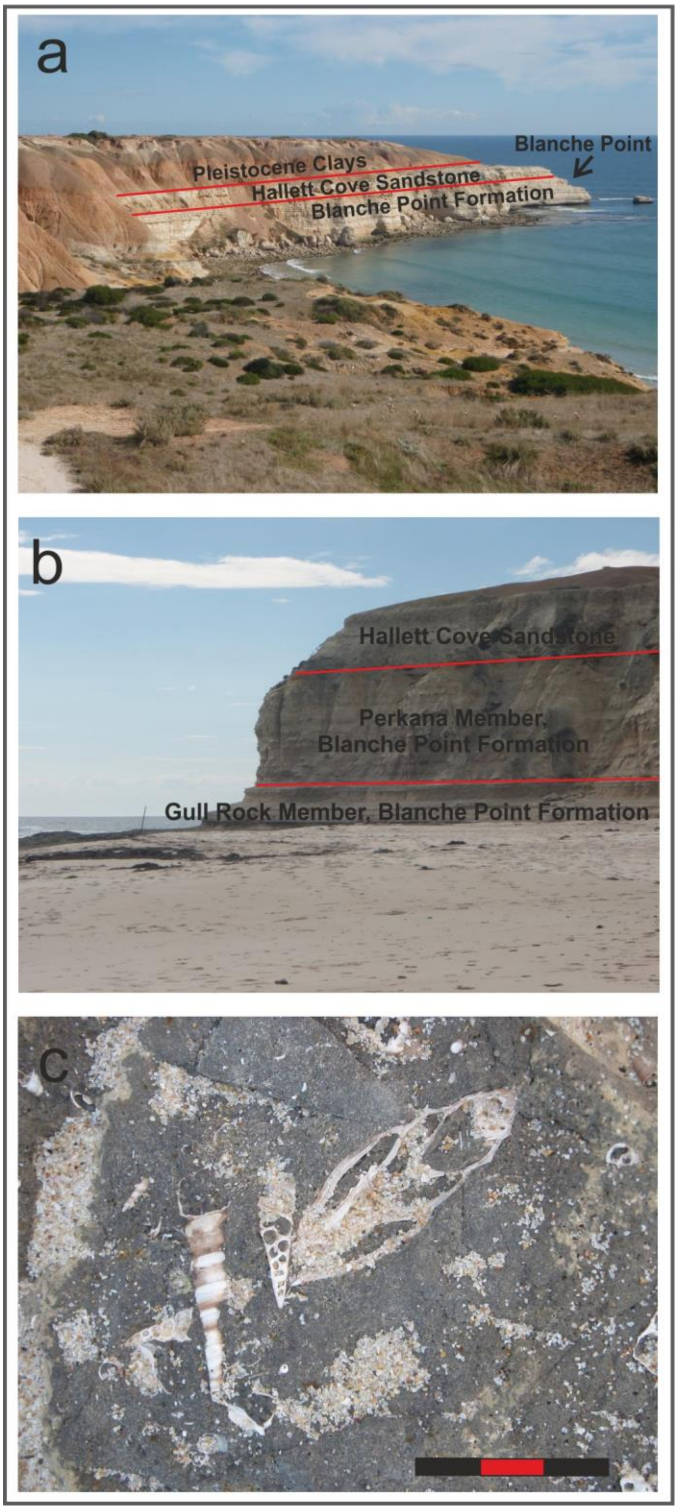


**Figure 2.3** Photos of outcrops of the Blanche Point Formation and the Hallet Cove Sandstone. a) View towards Blanche Point from Maslin Beach showing the contact between the Blanche Point Formation and the Hallet Cove Sandstone; b) Blanche Point viewed from the south at the beach at Port Willunga c) Photo of gastropod fossils in the Gull Rock Member of the Blanche Point Marl (Scale = 3cm).

### **2.1.2** MURRAY BASIN

The Murray Basin covers an area of approximately 300,000 km² across southeastern South Australia, northwestern Victoria and southwestern New South Wales (Cowley & Barnett, 2007), although only the South Australian region is considered in this research (Figure 2.4). The South Australian area of the Murray Basin is bound to the south by the Padthaway Ridge Palaeozoic basement high, to the north and west by uplifted Neoproterozoic and Cambrian metasediments and Cambrian – Ordovician granites (Rogers et al., 1995). The Cenozoic sequence lies unconformably on Neoproterozoic – Early Palaeozoic basement, the Late Palaeozoic Troubridge and Nadda Basins and the Early Cretaceous Monash Formation of the Berri Basin (Rogers et al., 1995). The Cenozoic sedimentary succession can be simplistically divided into four depositional sets: Late Palaeocene to Early Oligocene fluvial, lacustrine and marginal marine sediments including the Renmark Group; Oligocene to Middle Miocene shallow, marine sediments including the Murray Group; Late Miocene to Pliocene marine, estuarine and fluvial sediments; and Pliocene to Pleistocene lacustrine and marginal marine sediments (Rogers et al., 1995; Cowley & Barnett, 2007; McLaren et al., 2011).

The Murray Basin is a shallow, epicratonic Cenozoic basin occurring as a result of the rifting of Australia from Antarctica (Pufahl et al., 2004). The rifting event resulted in a number of normal faults which created a series of northeast-trending grabens that underwent intermittent reactivation throughout the Cenozoic, the most recent of which occurred in the Late Miocene and the Late Pliocene (Dickinson et al., 2002; Pufahl et al., 2004). The Late Miocene event caused the reactivation of the Cretaceous Florieton, Morgan, Hamley and Murrayville faults resulting in localised folding of the Murray Group formations (Benbow et al., 1995; Telfer et al., 2003; Pufahl et al., 2004). It has been noted that this uplift event may have been a major influence on the current course of the River Murray (Twidale et al., 1978; Pufahl et al., 2004). The weaker Late Pliocene uplift event resulted in the upward movement of the Pinnaroo Block leading to reduced outflow from the River Murray and forming a large, tectonically limited lacustrine system referred to as Lake Bungunnia (Stephenson, 1986; Brown & Stephenson, 1991; Pufahl et al,. 2004; McLaren et al., 2011).

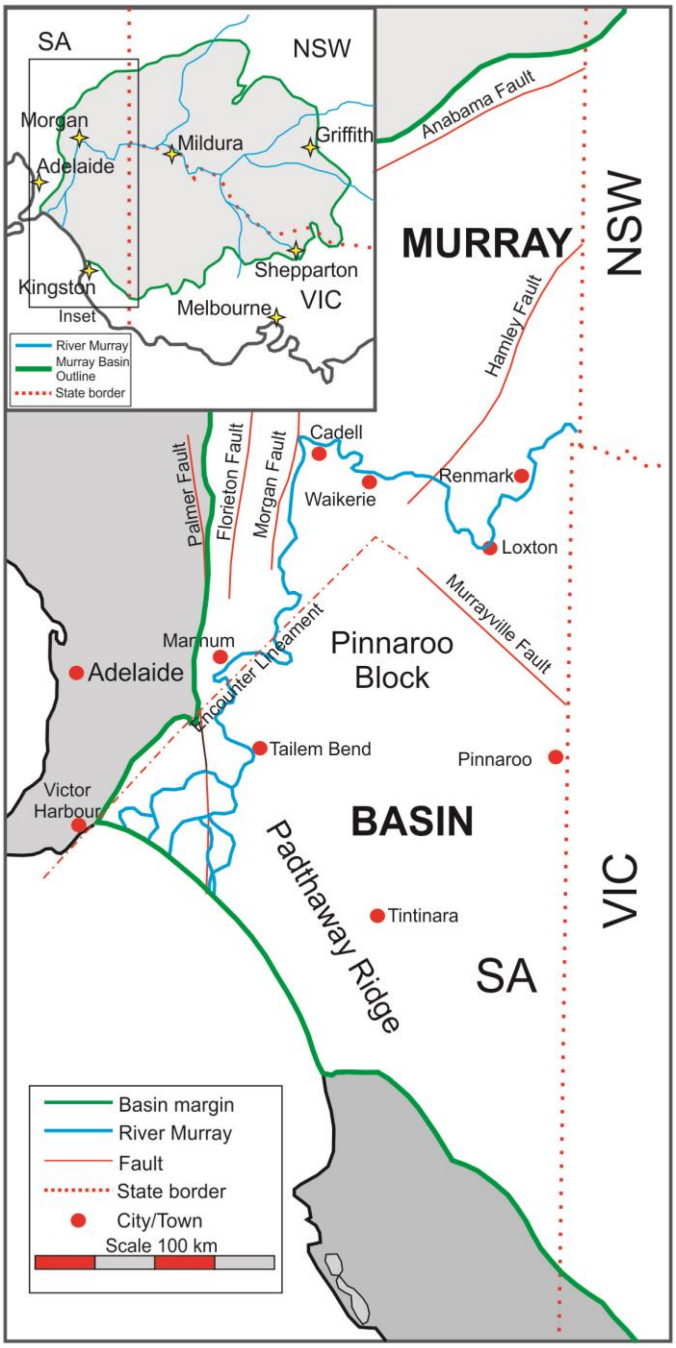


**Figure 2.4** Location map of the Murray Basin. Redrawn from Rogers et al. (1995).

The stratigraphy of the Murray Basin was first reviewed in detail by Ludbrook (1961) and Pels (1969). The most recent comprehensive review of the Murray Basin stratigraphy can be found in Rogers et al (1995) but more concise accounts have also been published (e.g. Drexel & Preiss, 1995; Fabris, 2002). Much of the modern literature examining the geology and stratigraphy of the Murray Basin is restricted to particular geographic areas (e.g. Gill, 1973) or geological time periods (e.g. Lukasik & James, 1998; Gallagher & Gourley, 2007) whilst other authors have examined the stratigraphy in order to characterise particular sediments (e.g. Carter, 1985; Lukasik et al., 2000; Lukasik & James, 2003; Pufahl et al., 2004). Authors whose main concern is examining the palaeontological aspects of the Murray Basin have also contributed to the understanding of the stratigraphy in this region of South Australia (e.g. Beu & Darragh, 2001; Fitzgerald, 2004). The Murray Basin region is rich in mineral resources and is also an important area for groundwater exploration which has resulted in increased efforts to understand the geology (e.g. Lindsay & Barnett, 1989; Brown & Stephenson, 1991; Rogers et al., 1995; Cowley & Barnett, 2007).

Specimens used in this thesis have been recovered from the Eocene – Oligocene Buccleuch Formation, the Miocene Cadell Formation and the Late Miocene Bookpurnong Formation, although only the Cadell Formation has been observed in the field (Figure 2.5). The Buccleuch Formation is Late Eocene – Middle Oligocene in age and consists of three distinct units: a bryozoal limestone and glauconitic limestone with a glauconitic marl base overlain by bryozoal clay sand and black pyritic clay overlain by a thin, ferruginous black clay (Ludbrook, 1961). This series can only be recognised in the northwestern Padthaway Ridge, and is distinguished from the underlying Olney Formation by the absence of quartz sand and mica, and the presence of shelly fossils and bryozoal calarenite (Rogers et al., 1995). All specimens from this formation come from museum collections and, due to logistical restrictions, the formation has not been examined in the field.

The Middle Miocene Cadell Formation, originally the Cadell Marl Lens (Ludbrook, 1958), was promoted to formation status by Lukasik & James (1998) on the basis of its distinctive lithological and palaeontological attributes. This formation is comprised of two members: the Murbko Marl Member and the Overland Corner Clay Member (Lukasik & James, 1998). The Murbko Marl Member is a brown-grey, heavily weathered marl with thin laminated green-grey clay beds. It is extremely fossiliferous, dominated by gastropods (in particular turritellids), bivalves and scaphopods, all of which are exceptionally well preserved (Figure 2.5c). The Overland Corner Clay Member is a grey weathered, unlithified dark green clay with some irregular beds of marlstone and calcarenite. It is much less fossiliferous than the Murbko Marl Member, with only gastropod moulds and the uncommon bryozoans. The two members occur along the River Murray where access to outcrops is often limited due to high water levels. Specimens from this formation are likely to come exclusively from the Murbko Marl Member and include both collected specimens and museum material. Specimens collected from the cliffs of the River Murray were not collected incrementally because of extreme wash out and collapse of the cliff due to the soft nature of the rock and the degree of weathering.

The Late Miocene Bookpurnong Formation is comprised of marl, silty clay and sand (Rogers et al., 1995) and contains numerous shelly fossils, glauconite and mica (Ludbrook, 1961; Carter, 1985). The widest distribution of this formation in South Australia is east of Loxton, although exposures within Loxton itself are limited (Rogers et al., 1995). A review of the molluscs found in this formation has indicated that the sediments were deposited in warm, shallow marine water (Ludbrook, 1973). Specimens from the Bookpurnong Formation used in this study were all museum specimens.

| **Formation** | **Age** | **Localities** | **Species** |
|---|---|---|---|
| Bookpurnong Formation | Mitchellian<br>(L. Miocene)<br>7.2 – 6.5Ma | SA002<br>SA044<br>SA045<br>SA046<br>SA047<br>SA048<br>NSW037 | *Athleta (Ternivoluta) antiscalaris antispinosa*<br>*Nannamoria strophodon strophodon*<br>*Notovoluta tabulate*<br>*Alcithoe (Alcithoe) macrocephala* |
| Cadell Formation | Batesfordian<br>(M. Miocene)<br>15.5 – 15.0Ma | SA001 | *Athleta (Ternivoluta) antiscalaris antiscalaris*<br>*Amoria costellifera*<br>*Nannamoria trionyma*<br>*Nannamoria strophodon strophodon*<br>*Notovoluta cathedralis*<br>*Notovoluta lintea*<br>*Alcithoe (Waihaoia) sarissa*<br>*Ericusa ancilloides*<br>*Livonia heptagonalis*<br>*Notopeplum mccoyi translucidum*<br>*Nassarius (Hima) tatei tatei*<br>*Bathytoma rhomboidalis*<br>*Lophiotoma murrayana* |
| Buccleuch Formation | Johannian – Janjukian<br>(L. Eocene – M. Oligocene)<br>38.0 – 28.0Ma | SA038 | *Alcithoe (Waihaoia) pagodoides pagodoides* |

**Table 2.2** Table of formations from the Murray Basin with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropod species found in these formations include both collected and museum material which will be used in later analyses.

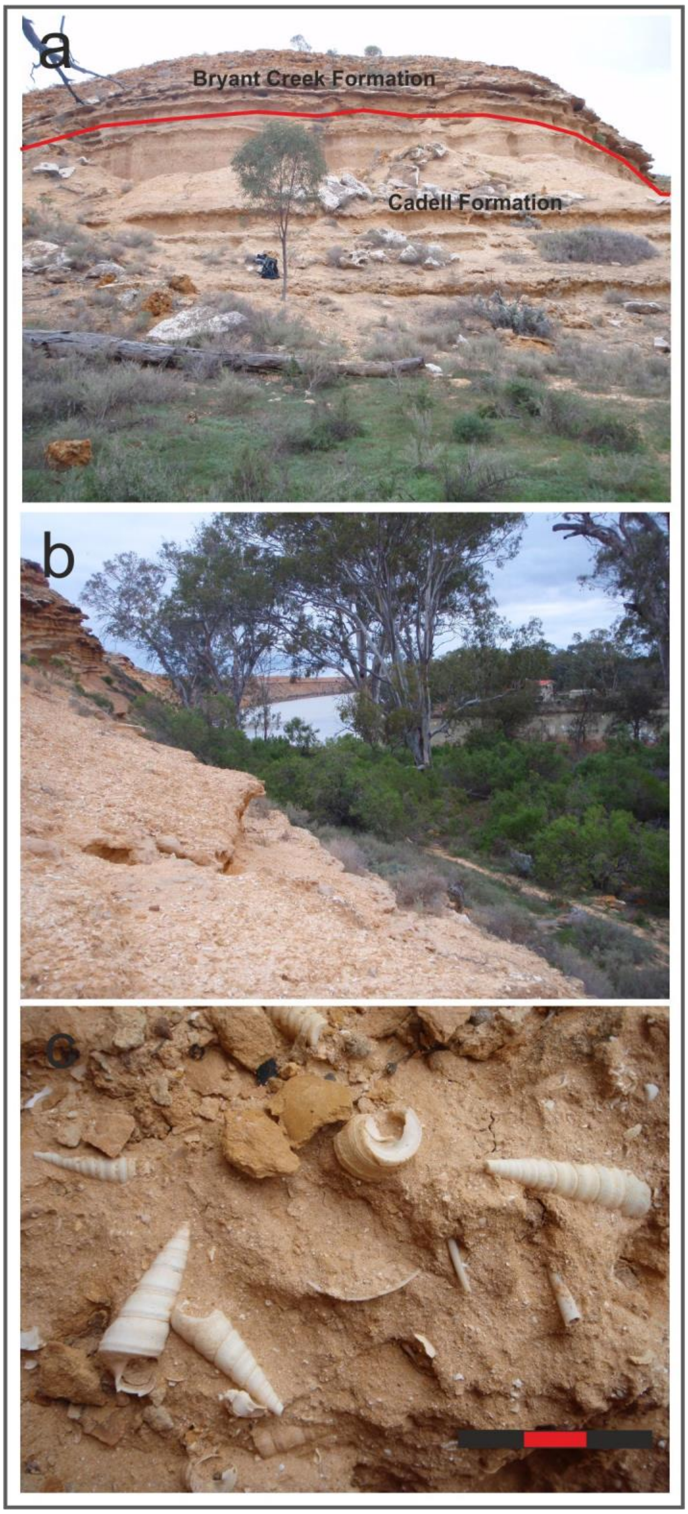


**Figure 2.5** Photos of the outcrop of the Murbko Marl Member of the Cadell Formation on the River Murray Cliffs south of Morgan, South Australia. a) Photo of the contact between the Cadell Formation and the overlying Bryant Creek Formation (day-bags by tree for scale); b) Photo showing the fossiliferous Cadell Formation; c) Magnified view of the exceptionally well preserved gastropod fossils of the Cadell Formation (Scale = 3cm).

## 2.2 VICTORIA

In Victoria, four sedimentary basins contain fossil gastropods used in this research. The Otway Basin contains ten formations that are useful in this study, most of which have been observed in the field. The Torquay, Port Phillip and Gippsland Basins each contain two formations which have yielded fossil gastropods useful to this study. Of these, only the Gippsland Basin has not been visited.

### **2.2.1** OTWAY BASIN

The Otway Basin covers an area of approximately 60,000km² in western Victoria (Figure 2.6) extending from Lacepede Bay in South Australia to the eastern edge of the Otway Ranges in Victoria (Gallagher & Holdgate, 2000; Holdgate & Gallagher, 2003). The basin is bound to the north by Palaeozoic basement and to the south by the edge of the continental slope in the Hunter sub-basin (Holdgate & Gallagher, 2003). A limited seismic study suggests that the basin extends substantially further than this into water depths up to 4500m in the Southern Ocean, although the sedimentary fill is yet to be fully understood (Moore et al., 2000). The onshore portion of the basin comprises approximately half the total area and is subdivided into a number of embayments, troughs and ridges including the Gambier Embayment (which occurs in South Australia), the Portland Trough and the Port Campbell Embayment (Holdgate & Gallagher, 2003). The Otway Basin has the most gastropod fossil bearing formations of any basin included in this thesis and the majority of specimens come from this region.

The Otway Basin is a northwest-striking passive margin rift basin which belongs to a series of sedimentary basins along the southern margin of Australia that formed during the break up of Gondwana and the separation of Antarctica from Australia (Willcox & Stagg, 1990). The sedimentary fill is comprised of Late Jurassic to Recent sedimentary rocks of both marine and terrestrial origin. The basin rift system was initiated in the Late Jurassic as a result of north-south extension, forming a series of asymmetric half-grabens (Williamson et al., 1990; Cooper & Hill, 1997). Throughout the Late Mesozoic the Otway Basin underwent periods of rifting and uplift. A 6.5Ma hiatus during the Late Cretaceous was followed by a new phase of extension and rifting during which syn-rift sedimentation occurred (Partridge, 1997; Lavin, 1997). Thermal subsidence and a paucity of clastic material resulted in the deposition of marine sediments during the Eocene (Jensen-Schmidt et al., 2002). Wrenching and compression, intiated during the Miocene, has proved an important factor to consider in hydrocarbon exploration (Boult et al., 2002). Extensive volcanic activity, perhaps influenced by Miocene – Recent faulting (Perincek & Cockshell, 1995), occurred in two phases during the Late Neogene: the Pliocene-Pleistocene “older volcanics” and the Pleistocene-Holocene “newer volcanics” (Sheard, 1990; Jensen-Schmidt et al., 2002). A concise review of the tectonic history of the basin is available in Jensen-Schmidt et al. (2002).

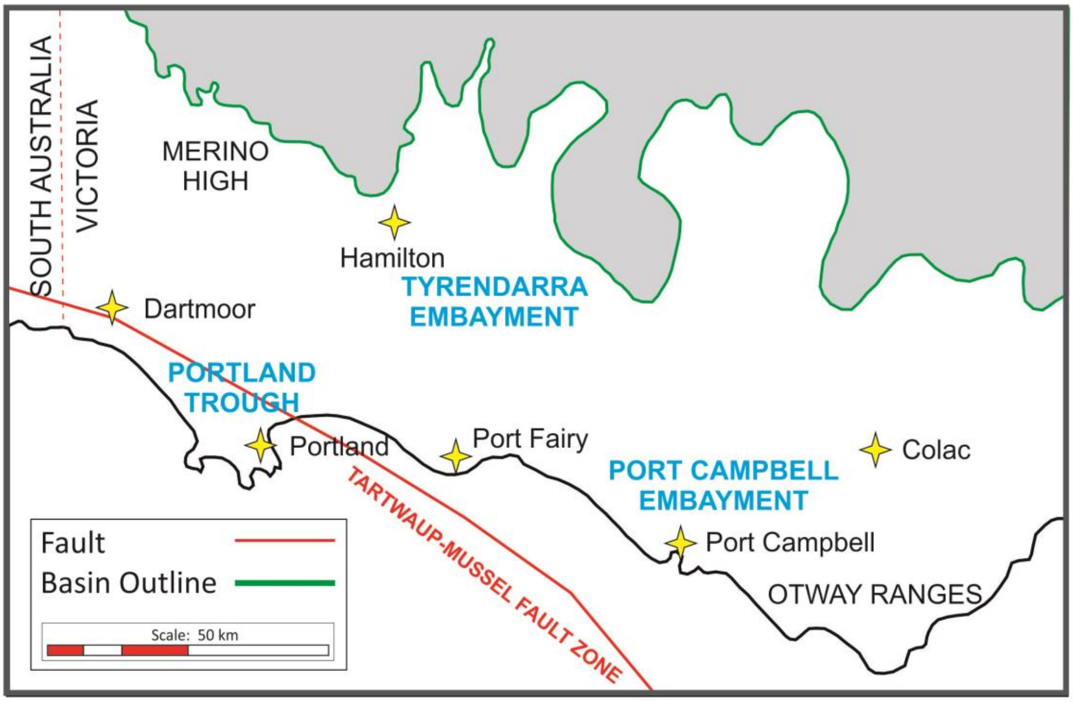


**Figure 2.6** Location map of the Otway Basin. Redrawn from Dickinson et al. (2002: 291, Fig. 4).

Due to both mineral and hydrocarbon resource potential, the Otway Basin has received considerable attention in the published literature, with a strong focus on the stratigraphy which may aid exploration. The stratigraphy of the basin is reviewed as a whole by a number of authors (e.g. Reynolds, 1971; Singleton, 1973; Abele et al., 1976; Douglas, 1977; Douglas & Ferguson, 1988; Birch, 2003; Hall & Keetley, 2009) whilst some authors choose to concentrate their efforts on particular sub-basins or embayments (e.g. Glenie, 1971; Kenley, 1971; Holdgate, 1980). Much of the literature examines the biostratigraphy of the basin, with a strong emphasis on palynology and foraminifera (e.g. Harris, 1971; McGowran, 1970; McGowran et al., 1971; Darragh, 1985; Glenie, 1988; Gallagher et al., 1999; Li et al., 1999, 2000) although the lithostratigraphy has also been examined (e.g.

Morton et al., 1995). The hydrocarbon potential of the basin has significantly improved our understanding of the complex stratigraphic and structural framework (e.g. Felton & Jackson, 1987; Holdgate, 1981; Geological Survey of Victoria, 1995; Morgan et al., 1995). Efforts have also been focused on correlating the various sub-basins and embayments with one another and the basin as a whole with other basins along the southeastern coastline of Australia (e.g. Ludbrook, 1971; McGowran et al., 2004).

Specimens used in this thesis have been recovered from: the Palaeocene Dilwyn and Pebble Point Formations; the Eocene-Oligocene Glen Aire and Browns Creek Clays; the Oligo-Miocene Fishing Point Marl and Gellibrand Marl; the Miocene Muddy Creek Marl and Port Campbell Limestone; and the Pliocene Whalers Bluff and Grange Burn Formations (Table 2.3). A number of these have been briefly observed in the field. Specimens used in this study from formations not observed in the field are from museum collections.

The Pebble Point Formation is the oldest unit of the Wangerrip Group and is Middle to Late Palaeocene in age. The formation is comprised of dark green-grey clayey sandstone, with the occasional gravel bed and carbonaceous sandy claystone (Geological Survey of Victoria, 1995). The formation is bioturbated throughout. Well logs have indicated that a middle sandy unit is sandwiched between clays (Holdgate, 1977). A few horizons contain molluscs, corals and shark teeth (Boult et al., 2002). Foraminifera, pollen and microplankton are also found in this formation (e.g. Harris, 1965; McGowran, 1965; Cookson & Eisenack, 1965). The Pebble Point Formation was deposited in a marginal marine environment. All specimens from this formation are housed in the museum collections in Melbourne and Adelaide.

The Dilwyn Formation is a member of the Wangerrip Group and is Early Eocene in age. The formation is exposed along the southeast coast of the Otway Basin and along the northwestern margin of the Otway Ranges (Geological Survey of Victoria, 1995). The unit conformably overlies the Pember Mudstone (Holdgate & Gallagher, 2003). The lower part of the formation consists of carbonaceous silty clay with ferruginous and pyritic sandstone. The upper portion of the Dilwyn Formation is a carbonaceous sandy claystone interbedded with fine- to medium- grained sandstone (Geological Survey of Victoria, 1995). Close to the margins of the basin are aggregates of thick cyclic sand units. The formation includes a number of different fossils including molluscs, echinoderms, bryozoans, foraminifera and shark teeth (Boult et al., 2002). The Dilwyn Formation has been interpreted as being deposited in a prograding deltaic environment (Geological Survey of Victoria, 1995). All material from this formation are museum specimens.

The Miocene Gellibrand Marl is a member of the Heytesbury Group and is best exposed at the eastern end of the Otway Basin, near Princetown. This formation is comprised of grey calcareous silty claystone to clayey siltstone, with minor calcarenite beds. Bedding is often distinguished by calcareous concretions. Horizons of cemented burrows are found within this unit. The marl of this formation is abundant in fossil material including molluscs, bryozoans, echinoids, brachiopods, corals, crabs and shark teeth (Geological Survey of Victoria, 1995). The Gellibrand Marl was deposited in a low energy, shelf environment. The presence of glauconite suggests that water depths were in excess of 60m (Deacon, 1990). Although this formation has been examined, all specimens included in this study were from museum collections.

The Miocene Muddy Creek Marl is exposed along the banks of Muddy Creek and Grange Burn near Hamilton and includes a diverse array of fossil gastropods (Figure 2.7c). The formation consists of fossiliferous grey silty marlstone with distinct limonite, phosphatised burrows and shell horizons (Dickinson et al., 2002; Fitzgerald, 2004). It conformably overlies the Bochara Limestone (Gill, 1957) and is disconformably overlain by the Grange Burn Formation (Fitzgerald, 2004). This formation has been observed in the field and specimens were collected.

The Miocene Port Campbell Limestone is a member of the Heytesbury Group and is best exposed in coastal cliffs southeast and west of Port Campbell (Baker, 1944). The formation consists of grey to yellow, weakly cemented calcisiltite to fine-grained calcarenite (Figure 2.7b). The base of the formation is characterised by marley and clayey limestone beds. Extensive bioturbation can be seen in the marley units. Fossils found in this formation include abundant molluscs and bryzoans, echinoids and brachiopods, and occasional crab shells. The Port Campbell Limestone was deposited in moderate energy continental shelf environments above fair weather wave base (Geological Survey of Victoria, 1995). Access to this formation is extremely restricted. All specimens from this formation are from museum collections.

The Late Miocene - Pliocene Grange Burn Formation consists of shelly marlstones and sandy to pebbly limestones. It outcrops along the banks of Muddy Creek and Grange Burn near Hamilton (Figure 2.7a). The base of the formation is a phosphate nodule horizon with abundant marine vertebrate fossils, disconformably overlying the Muddy Creek Marl (Turnbull et al., 1965; Dickinson et al., 2002). The formation is interpreted as being deposited during a marine transgression (Macphail, 1996). This formation has been observed in the field and fossil material collected.

The Late Miocene - Pliocene Whalers Bluff Formation is comprised of fossiliferous claystones, oyster beds and sandy limestones overlying a karst surface above the Port Campbell Limestone. This formation outcrops in Portland and is suggested to be the sedimentary infill of submarine canyons formed during the Late Miocene (Leach & Wallace, 2001). This formation has not been observed in the field and all specimens from the Whalers Bluff Formation are from museum collections.

| **Formation** | **Age** | **Localities** | **Species** |
|---|---|---|---|
| Whalers Bluff Formation | Micthellian – Yatalan<br>(L. Miocene - Pliocene)<br>6.0-3.0Ma | VIC020<br>VIC096 | *Amoria undulata undulata*<br>*Ericusa sowerbyi sowerbyi* |
| Grange Burn Formation | Mitchellian – Kalimnan<br>(L. Miocene - Pliocene)<br>6.0-4.0Ma | VIC060<br>VIC061 | *Lyria gemmata*<br>*Amoria undulata masoni*<br>*Ericusa fulgetroides*<br>*Nassarius (Niotha) sublirellus*<br>*Nassarius (Niotha) crassigranosus*<br>*Nassarius (Hima) tatei tatei* |
| Port Campbell Limestone | Batesfordian – Mitchellian<br>(M. – L. Miocene)<br>16.0-6.0Ma | VIC040<br>VIC043<br>VIC110 | *Athleta (Ternivoluta) antiscalaris antispinosa*<br>*Nannamoria limbata*<br>*Nannamoria strophodon strophodon*<br>*Lyria gemmata*<br>*Amoria undulata masoni*<br>*Nannamoria paraboloides*<br>*Alcithoe (Alcithoe) macrocephala*<br>*Nannamoria deplexa* |
| Muddy Creek Marl | Balcombian – Bairnsdalian<br>(M. Miocene)<br>15.0-11.0Ma | VIC038<br>VIC039 | *Athleta (Ternivoluta) antiscalaris antiscalaris*<br>*Athleta (Ternivoluta) antiscalaris levior*<br>*Lyria acuticostulata*<br>*Lyria harpularia*<br>*Leptoscapha crassilabrum*<br>*Amoria costellifera*<br>*Nannamoria ralphi*<br>*Nannamoria limbata*<br>*Nannamoria trionyma*<br>*Nannamoria strophodon strophodon* |

| Formation | Age | Localities | Species |
|---|---|---|---|
| Muddy Creek Marl Continued | Balcombian – Bairnsdalian<br>(M. Miocene)<br>15.0-11.0Ma | VIC038<br>VIC039 | *Notovoluta pseudolirata*<br>*Notovoluta cathedralis*<br>*Notovoluta ellipsoidea*<br>*Alcithoe (Waihaoia) sarissa*<br>*Alcithoe (Waihaoia) pagodoides pagodoides*<br>*Ericusa ancilloides*<br>*Ericusa hamiltonensis*<br>*Livonia mortoni connudata*<br>*Livonia gatliffi*<br>*Livonia hannafordi*<br>*Notopeplum mccoyi translucidum*<br>*Notopeplum politum*<br>*Cymbiola macdonaldi*<br>*Microdrillia steiroides*<br>*Bathytoma rhomboidalis*<br>*Bathytoma fontinalis*<br>*Guraleus volutiformis*<br>*Lophiotoma murndaliana*<br>*Turris septemliratus*<br>*Optoturris optatus* |
| Gellibrand Marl | Longfordian<br>(E. Miocene)<br>23.0-16.5Ma | VIC009<br>VIC016<br>VIC017<br>VIC018<br>VIC019<br>VIC035<br>VIC036<br>VIC037<br>VIC041<br>VIC042<br>VIC081<br>VIC082<br>VIC087<br>VIC100<br>VIC113<br>VIC116 | *Athleta (Ternivoluta) antiscalaris antispinosa*<br>*Athleta (Ternivoluta) antiscalaris antiscalaris*<br>*Athleta (Ternivoluta) anticingulata craticula*<br>*Athleta (Ternivoluta) antiscalaris levior*<br>*Lyria acuticostulata*<br>*Amoria costellifera*<br>*Nannamoria weldii*<br>*Nannamoria deplexa*<br>*Nannamoria limbata*<br>*Nannamoria strophodon strophodon*<br>*Notovoluta pseudolirata*<br>*Notovoluta differta*<br>*Notovoluta ellipsoidea*<br>*Alcithoe (Waihaoia) sarissa*<br>*Ericusa sowerbyi pellita*<br>*Ericusa atkinsoni*<br>*Ericusa ancilloides*<br>*Ericusa hamiltonensis*<br>*Livonia spenceri*<br>*Livonia hannafordi*<br>*Notopeplum mccoyi translucidum*<br>*Cymbiola macdonaldi*<br>*Nassarius (Hima) tatei tatei*<br>*Zemacies procerior*<br>*Bathytoma decomposita*<br>*Gemmula gellibrandensis* |

| Formation | Age | Localities | Species |
|---|---|---|---|
| Dilwyn Formation | Johannian<br>(E. Eocene)<br>53.5-46.5Ma | VIC001 | *Athleta (Ternivoluta) wangerrip* |
| Pebble Point Formation | Wangerripian<br>(L. Palaeocene)<br>61.0-56.0Ma | VIC118 | *Zemacies procerior* |

**Table 2.3** Table of formations from the Otway Basin with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropod species found in these formations include both collected and museum material which will be used in later analyses.

Stratigraphic sequences occurring on the southwestern margin of the Otway Ranges (referred to as the Aire district) are thought to be different from other areas of the Otway Basin (Holdgate & Gallagher, 2003). Within this area three gastropod fossil bearing formations occur: the Browns Creek Clay, the Glen Aire Clay and the Fishing Point Marl (Table 2.4). Compared to other areas of the Otway Basin, this region has received much less attention in terms of its stratigraphy and correlation.

The Browns Creek Clay is Late Eocene in age and consists of clayey calcarenite and banded marlstone with intermittent beds of shelly claystones and occasional sandstone horizons (Holdgate & Gallagher, 2003). The formation is extremely fossiliferous with gastropods dominating both in terms of frequency and diversity although fossils of bivalves, foraminifera, ostracods, bryozoans and corals are also present. The formation is interpreted as being deposited within a marine shelf environment (Holdgate & Gallagher, 2003). All specimens from this formation included in this research are from museum collections.

The Glen Aire Clay is Late Eocene to Early Oligocene in age (Abele, 1994) and outcrops along coastal regions at Cape Otway. The formation is comprised of carbonaceous sandy claystone with interbedded limestone and ironstone. Pyritic bryozoal claystone occur towards the base of the unit. Like other formations from this part of the Otway Basin, detailed descriptions are not available in modern literature. Specimens from the Glen Aire Clay are from museum collections.

The Fishing Point Marl, originally referred to as the Upper Glen Aire Clay, is equivalent to the lower beds of the Gellibrand Marl and considered to be Miocene in age (Holdgate &

Gallagher, 2003). The formation is a grey marlstone interbedded with claystone and calcarenite bands (Darragh, 1985). Molluscs are the most common fossils found in this formation and outcrops from which they can be recovered are confined to the north shore of Lake Craven (Darragh, 1985). Museum specimens have been used to represent this formation.

| Formation | Age | Localities | Species |
|---|---|---|---|
| Fishing Point Marl | Longfordian<br>(E. Miocene)<br>23.0-17.0Ma | VIC011<br>VIC012<br>VIC021 | *Athleta (Ternivoluta) subcrenulifera*<br>*Nannamoria fasciculate*<br>*Nannamoria deplexa*<br>*Notovoluta linigera*<br>*Alcithoe (Waihaoia) sarissa*<br>*Ericusa sowerbyi pellita*<br>*Ericusa atkinsoni*<br>*Notopeplum mccoyi translucidum*<br>*Cymbiola macdonaldi* |
| Glen Aire Clay | Aldingan - Willunhgan<br>(L. Eocene – E. Oligocene)<br>35.0-31.5Ma | VIC002<br>VIC003 | *Athleta (Ternivoluta) curvicostata*<br>*Notovoluta variculifera*<br>*Alcithoe (Waihaoia) cribrosa*<br>*Alcithoe (Waihaoia) pagodoides pagodoides*<br>*Notopeplum primarugatum*<br>*Borsonia protensa*<br>*Borsonia otwayensis*<br>*Borsonia polycesta*<br>*Guraleus eocenicus* |
| Browns Creek Clay | Johannian – Aldingan<br>(L. Eocene)<br>38.5-35.5Ma | VIC091<br>VIC092<br>VIC114 | *Scaphella (Aurinia) johannae*<br>*Notovoluta variculifera*<br>*Notovoluta capitonica*<br>*Alcithoe (Waihaoia) cribrosa*<br>*Alcithoe (Waihaoia) pagodoides pagodoides*<br>*Notopeplum protorhysum*<br>*Cryptocordieria variabilis*<br>*Borsonia tatei*<br>*Guraleus eocenicus*<br>*Macteola eocenica*<br>*Gemmula (Clavogemmula) prima* |

**Table 2.4** Table of formations from the Aire District of the Otway Basin with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropod species found in these formations include both collected and museum material which will be used in later analyses.

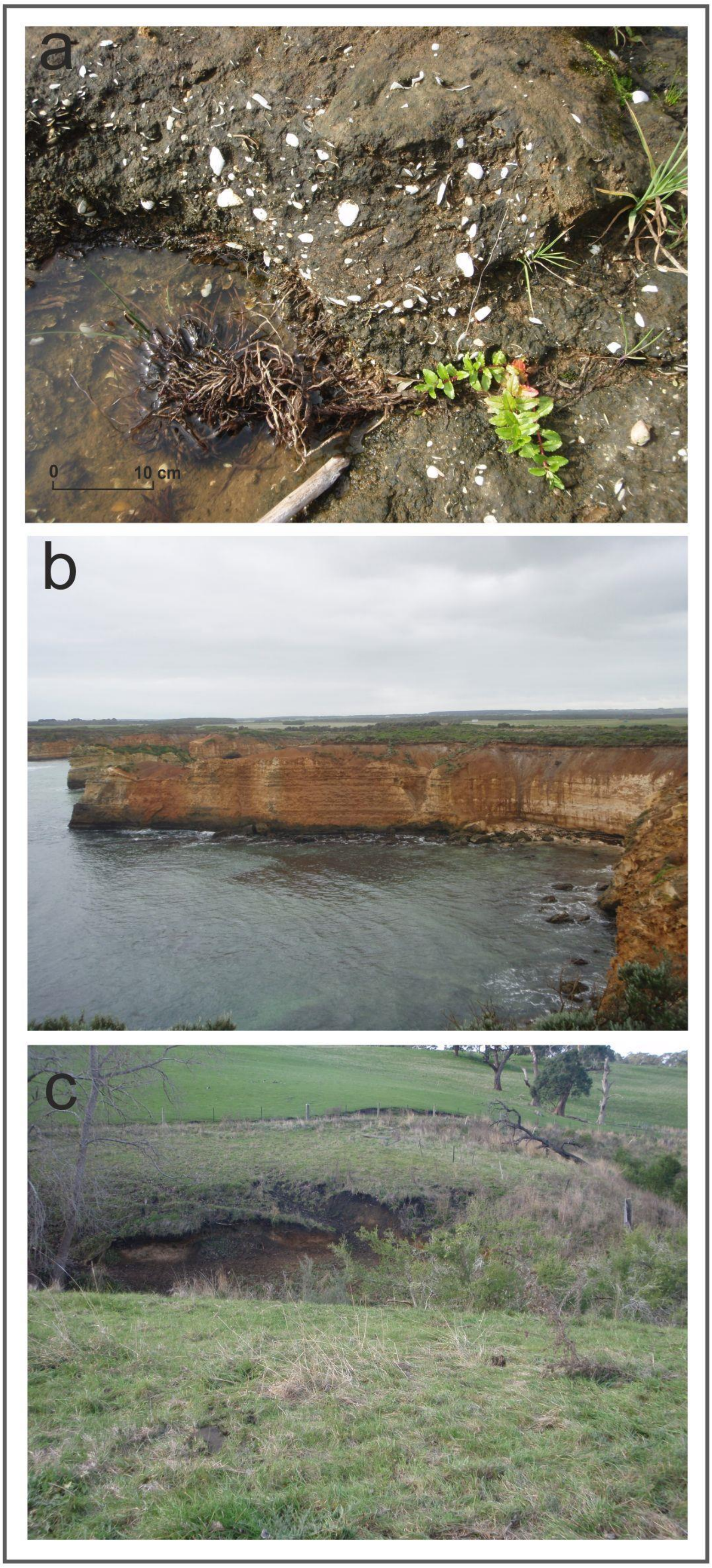


**Figure 2.7** Photos of outcrop of the Grange Burn Formation, Port Campbell Limestone and Muddy Creek Marl in Victoria. a) Grange Burn Formation outcrop on the banks of Muddy Creek, Hamilton, b) Port Campbell Limestone exposed in the cliffs along the Great Ocean Road and c) Clifton Bank, Muddy Creek, Hamilton.

### **2.2.2** TORQUAY BASIN

The Torquay Basin is one of a series of basins referred to as the Central Coastal Basins. The literature often refers to the Torquay Basin as a sub-basin of the Otway Basin (e.g. Dickinson et al., 2002; Holford et al., 2011). The formations of the basin outcrop in the coastal cliffs between Eastern View in the south and Torquay in the north (Holdgate & Gallagher, 2003). The basin is located adjacent to the Otway Ranges (Figure 2.8) which separate it from the Port Campbell Embayment of the Otway Basin, although the majority lies offshore (Holdgate & Gallagher, 2003). It is bound on all sides by Cretaceous rock highs: northerly by the Barrabool High, easterly by the Bellerine High and westerly by the Otway Ranges High (Li et al., 1999). Tectonically, this basin has undergone much of the same evolution as the Otway Basin, forming as a result of the separation of Australia from Antarctica (Holdgate & Gallagher, 2003). Much of the literature examining the geology of this region is a result of exploration of coal measures (e.g. Holdgate & Clarke, 2000; Holdgate et al., 2001) although it has also been the focus for researchers examining particular geological time periods (e.g. Li et al., 1999; Dickinson et al., 2002) and has also been examined as part of a synthesis of the regional geology of Victoria (e.g. Holdgate & Gallagher, 2003).

Two gastropod fossil bearing formations are included in this research from the Torquay Basin: the Jan Juc Marl and the Puebla Clay (Table 2.5). Although both formations have been observed in the field, collecting of fossils is extremely limited along the Torquay coastline due to it being a protected area and therefore all fossils from this basin are museum specimens.

The Jan Juc Marl is Late Oligocene in age and is best exposed along the coast at Bird Rock in Torquay. The exposure of this formation at Jan Juc Beach forms the type section for the Janjukian Australian Stage (Hall & Pritchard, 1902; Singleton, 1941; Holdgate & Gallagher, 2003). The Oligo-Miocene boundary is suggested to correspond to the contact between the Jan Juc Marl and the overlying Puebla Formation (Holdgate & Gallagher, 2003). The formation consists of silty glauconitic marlstone interbedded with clayey glauconitic wackestones. Horizons of thin skeletal grainstone and mollusc packstones also occur (Li et al., 1999). The formation is heavily burrowed and includes a wide diversity of fossil material with turritellid gastropods and bivalves dominating (Li et al., 1999).

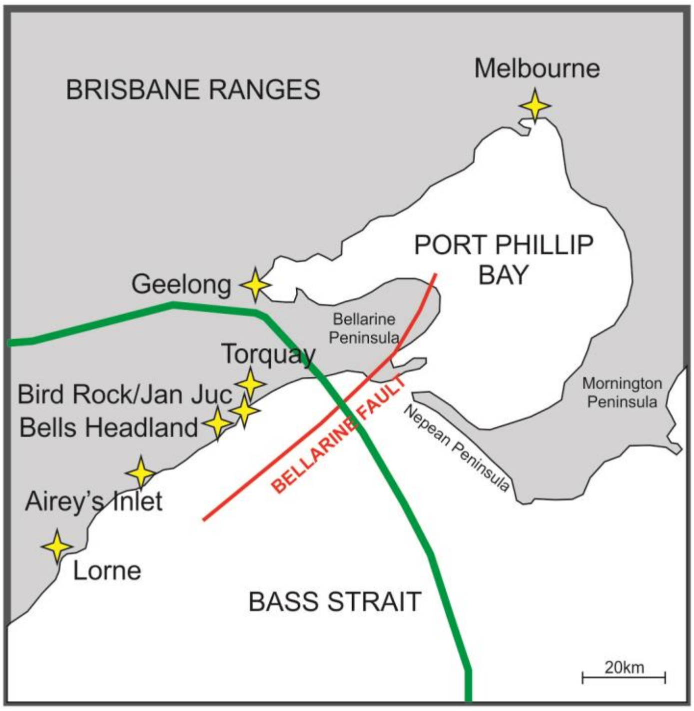


**Figure 2.8** Location map of the Torquay Basin. Modified from Kelly & Webb (1999: 100, Fig 1).

The Puebla Formation is Early – Middle Miocene in age and can be subdivided into four members: the Puebla Clay Members, Cellepora Beds, Zeally Limestone and Yellow Bluff Beds (Boreen & James, 1995). The formation consists of fossiliferous and bioturbated calcareous claystones and siltstones with bryozoal calcarenite at its type section between Bird Rock and Jan Juc Creek (George & Wallace, 1992; Reeckmann, 1994). The Puebla Clay member comprises bioturbated and pyritic shelly calcareous siltstone and claystone whilst the Cellepora Beds are characterised by bryozoal calcarenites interbedded with silty claystone. The Zeally Limestone consists of massive bryozoal calcarenites (Holdgate & Gallagher, 2003). The Yellow Bluff Beds are bioturbated, interbedded packstones and claystones with echinoderms and bryozoan fossils (Cook & O'Brien, 1990). The Puebla Clay member has been interpreted as being deposited in cool, deep water whilst the other members of this formation are likely to have been deposited in shallower, warmer marine conditions (Smith, 1998). All specimens from this formation are from museum collections.

The Jan Juc Marl is Late Oligocene in age and is best exposed along the coast at Bird Rock in Torquay. The exposure of this formation at Jan Juc Beach forms the type section for the Janjukian Australian Stage (Hall & Pritchard, 1902; Singleton, 1941; Holdgate & Gallagher, 2003). The Oligo-Miocene boundary is suggested to correspond to the contact between the Jan Juc Marl and the overlying Puebla Formation (Holdgate & Gallagher, 2003). The formation consists of silty glauconitic marlstone interbedded with clayey glauconitic wackestones. Horizons of thin skeletal grainstone and mollusc packstones also occur (Li et al., 1999). The formation is heavily burrowed and includes a wide diversity of fossil material with turritellid gastropods and bivalves dominating (Li et al., 1999).

| Formation | Age | Localities | Species |
|---|---|---|---|
| Puebla Formation | Longfordian – Balcombian<br>(E. – M. Miocene)<br>23.0-14.0Ma | VIC008 | *Athleta (Ternivoluta) anticingulata craticula*<br>*Nannamoria weldii*<br>*Notovoluta linigera*<br>*Alcithoe (Waihaoia) sarissa*<br>*Ericusa sowerbyi pellita*<br>*Ericusa atkinsoni*<br>*Livonia spenceri* |
| Jan Juc Marl | Janjukian<br>(L. Oligocene)<br>25.0–23.0Ma | VIC004<br>VIC005<br>VIC006<br>VIC007<br>VIC093<br>VIC097 | *Athleta (Ternivoluta) anticingulata anticingulata*<br>*Nannamoria weldii*<br>*Alcithoe (Waihaoia) pagodoides pagodoides*<br>*Alcithoe (Waihaoia) pagodoides sorcula*<br>*Alcithoe (Waihaoia) neglectoides*<br>*Alcithoe (Waihaoia) pueblensis*<br>*Ericusa sowerbyi pellita*<br>*Ericusa macroptera*<br>*Ericusa atkinsoni*<br>*Ericusa ancilloides*<br>*Livonia stephensi*<br>*Borsonia balteata*<br>*Borsonia torquayensis*<br>*Bathytoma fontinalis*<br>*Bathytoma decomposita* |

**Table 2.5** Table of formations from the Torquay Basin with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropod species found in these formations include both collected and museum material which will be used in later analyses.

### **2.2.3** PORT PHILLIP BASIN

The Port Phillip Basin (another of the Central Coastal Basins) lies to the east of Melbourne, covering the area of Port Phillip Bay and the surrounding coast (Figure 2.9). It is considered to be an extension of the Torquay (and therefore Otway) Basin, separated by the Bellarine and Nepean Peninsulas (Abele et al., 1976; Holdgate & Gallagher, 2003). The basin covers an area of approximately 40,000km$^2$ and is bound to the northeast by the Melbourne Monocline, to the northwest by the Rowsley Fault and to the southeast by the Selwyn Fault (Gourley & Gallagher, 2004). Excellent outcrops of gastropod fossil bearing formations occur around Batesford (with particularly good exposure in Batesford Quarry) and around the coast near Beaumaris and Mornington.

Like all other basins along the southern Australian coastline, the sediment fill of the Port Phillip basin coincides with the breakup of Gondwana during the Late Cretaceous and the subsequent opening of the Southern Ocean as Antarctica and Australia separated (Gourley & Gallagher, 2004). The tectonic history of the Port Phillip Basin follows that of the Otway Basin, although a detailed review specific to the basin provides more insight into the regional tectonics (Bowler, 1966).

The geology and stratigraphy of the Port Phillip Basin has received less attention in recent years than other basins in southeastern Australia. Much of the work carried out on the basin relates to the extensive coal seams that occur in the northern parts of the basin (e.g. Anderson & MacKay, 1974; Ripper, 1975; Holdgate & Clarke, 2000; Holdgate et al., 2002). In relation to these coal studies, other researchers have examined the palynology of the formations in this basin which can be a useful tool in producing a stratigraphic framework and palaeoenvironmental analysis of the basin (e.g. Partridge, 1971, 1997a, b, 2001a, b, c). In addition a number of palaeontological studies have proved useful in building up a geological history of the Port Phillip Basin (e.g. Christophel, 1985). As with other basins covered in this chapter a brief overview of the stratigraphy of the basin can be found in Holdgate & Gallagher (2003).

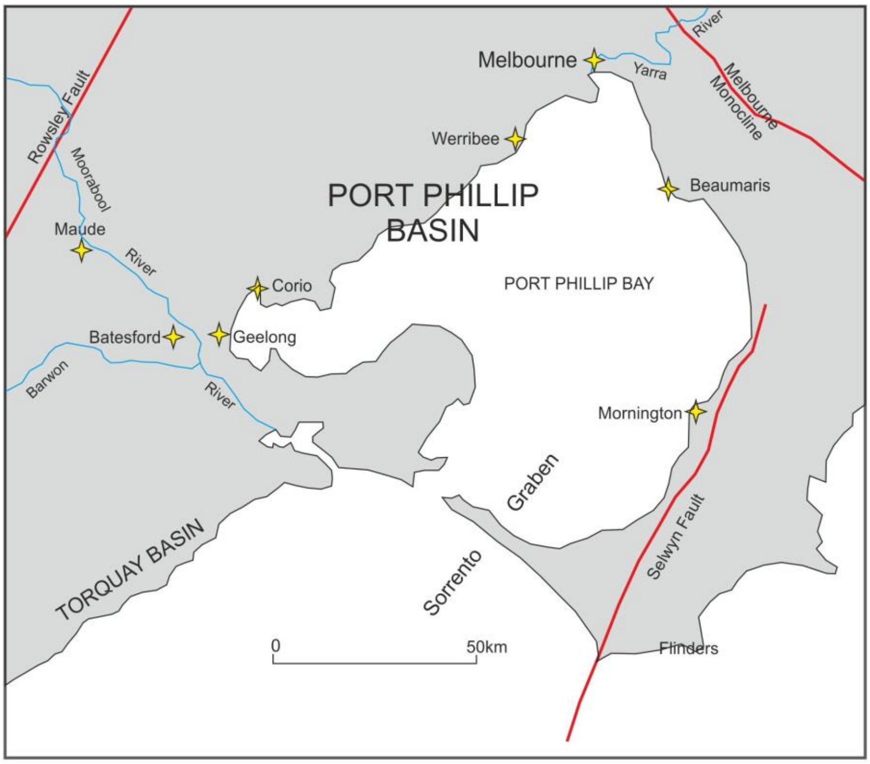


**Figure 2.9** Location map of the Port Phillip Basin. Modified from Gourley & Gallagher (2004: 295, Fig. 1c).

Two formations from the Port Phillip Basin have yielded gastropod fossils used as part of this study: the Miocene Fyansford Formation and the Pliocene Black Rock Sandstone (Table 2.6). Only the Fyansford Formation has been observed in the field.

The Fyansford Formation, originally referred to as the Newport Formation, is Miocene in age. The formation outcrops in the region of the Moorabool and Barwon Rivers near Geelong (Figure 2.10a, b) and in the coastal cliffs surrounding Mornington (Holdgate & Gallagher, 2003). The formation consists of calcareous marlstones, clayey siltstones and sandstone (Holdgate & Gallagher, 2003). The formation is rich in mollusc fossils, particularly well preserved gastropods, although the diverse ostracode and foraminifera fossils have been useful in identifying the palaeoenvironment of the formation and constraining the age of the formation (Gourley & Gallagher, 2004). The Fyansford Formation is considered to have been deposited in marine shelf conditions (Holdgate & Gallagher, 2003). Fossils from this formation included in this research are both collected and museum material.

The Black Rock Sandstone is a member of the Brighton Group (Kenley, 1967) and is Pliocene in age (Holdgate & Gallagher, 2003). Outcrop of this formation at Beaumaris, south of Melbourne, is considered to be the type section for the Cheltenhamian Australian stage

(Singleton, 1941). The basal contact of the formation is distinguished by the presence of ferriginous and phosphatic nodules which include vertebrate fossils (Woodburne, 1969; Wilkinson, 1969; Simpson, 1970; Holdgate & Gallagher, 2003). The formation consists of fine calcareous sandstones and siltstones which coarsen upwards with gravel beds occurring higher in the section (Wallace et al., 2005). Fossils found in this formation include a variety of molluscs and echinoids as well as extensive burrowing (Darragh, 1985; Wallace et al., 2005). The sediments were likely to have been deposited in shoreface conditions (Wallace et al., 2005). All fossils from this formation are museum specimens.

| Formation | Age | Localities | Species |
|---|---|---|---|
| Black Rock Sandstone | Mitchellian - Cheltenhamian<br>(L. Miocene – M. Pliocene)<br>6.0–4.0Ma | VIC103<br>VIC104 | *Amoria undulata undulata* |
| Fyansford Formation | Janjukian - Micthellian<br>(L. Oligocene - L. Miocene)<br>25 - 8Ma | VIC013<br>VIC014<br>VIC015<br>VIC027<br>VIC028<br>VIC029<br>VIC030<br>VIC031<br>VIC032<br>VIC033<br>VIC034<br>VIC079<br>VIC080<br>VIC083<br>VIC084<br>VIC085<br>VIC088<br>VIC089<br>VIC090<br>VIC094<br>VIC098<br>VIC108<br>VIC109<br>VIC111<br>VIC112 | *Athleta (Ternivoluta) antiscalaris antiscalaris*<br>*Athleta (Ternivoluta) antiscalaris levior*<br>*Lyria acuticostulata*<br>*Lyria harpularia*<br>*Amoria costellifera*<br>*Nannamoria ralphi*<br>*Nannamoria deplexa*<br>*Nannamoria limbata*<br>*Nannamoria trionyma*<br>*Nannamoria strophodon strophodon*<br>*Notovoluta pseudolirata*<br>*Notovoluta differta*<br>*Notovoluta cathedralis*<br>*Alcithoe (Waihaoia) sarissa*<br>*Ericusa sowerbyi pellita*<br>*Ericusa ancilloides*<br>*Ericusa hamiltonensis*<br>*Livonia mortoni connudata*<br>*Livonia spenceri*<br>*Livonia hannafordi*<br>*Notopeplum mccoyi translucidum*<br>*Cymbiola macdonaldi*<br>*Nassarius (Hima) tatei tatei*<br>*Daphnella cuspidatus*<br>*Borsonia balteata*<br>*Borsonia tatei*<br>*Bathytoma decomposita*<br>*Lophiotoma murndaliana*<br>*Turris septemliratus* |

**Table 2.6** Table of formations from the Port Phillip Basin with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropod species found in these formations include both collected and museum material which will be used in later analyses.

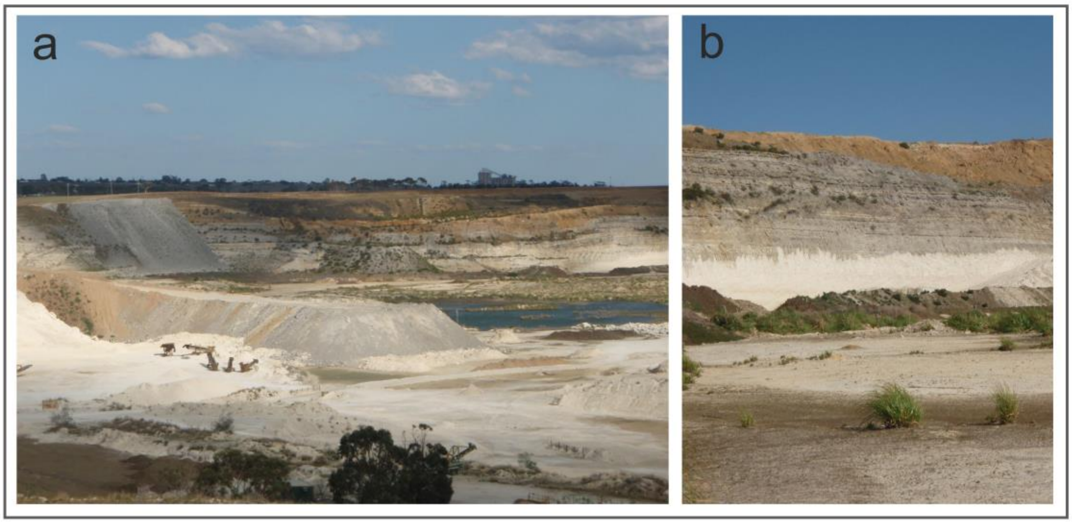


**Figure 2.10** Outcrops of the Fyansford Formation at Batesford Quarry. a) View across the quarry looking northeast, b) View of quarry cliff showing the well-bedded grey strata of the Fyansford Formation.

### **2.2.4** GIPPSLAND BASIN

The Gippsland Basin is located in Victoria, approximately 200km east of Melbourne (Figure 2.11) and covers an area of approximately 56,000km² (Smith, 1982) of which less than 30% occurs onshore (Holdgate & Gallagher, 2003). The basin includes Cretaceous and Cenozoic sediments which represent terrestrial, marginal marine and marine deposition. The basin is bound to the north by the Palaeozoic Eastern Uplands, to the east by the foot of the present day continental slope and to the south and southwest by the Bassian Rise which separates it from the Bass Basin (Holdgate & Gallagher, 2003). The Gippsland Basin is one of the most prolific hydrocarbon regions in Australia and as a result a great deal of research concentrates on hydrocarbon exploration in this area (e.g. Burns et al., 1984; Bernecker et al., 2001; Moore & Wong, 2001; Norvick & Smith, 2001; Volk et al., 2001; Wong & Bernecker, 2001; O'Brien et al., 2008).

During the Late Mesozoic the Gippsland Basin was part of a rift system that occurred between the Australian and Antarctic Plates (Rahmanian et al., 1990). The Late Cretaceous saw regional extension and the development of syn-rift troughs and volcanism, separating the Gippsland Basin from the Otway and Bass Basins (Mehin & Bock, 1998). Compression, occurring during the Late Eocene, resulted in a series of northeast to east-northeast trending anticlines (Smith, 1988). Major fold structures associated with the occurrence of hydrocarbons formed as a result of compression during the Middle Miocene whilst younger sediments are characterised by monoclonal folding and topographic uplift resulting from onshore faulting initiated during the Pliocene (Dickinson et al., 2002; Holdgate & Gallagher, 2003).

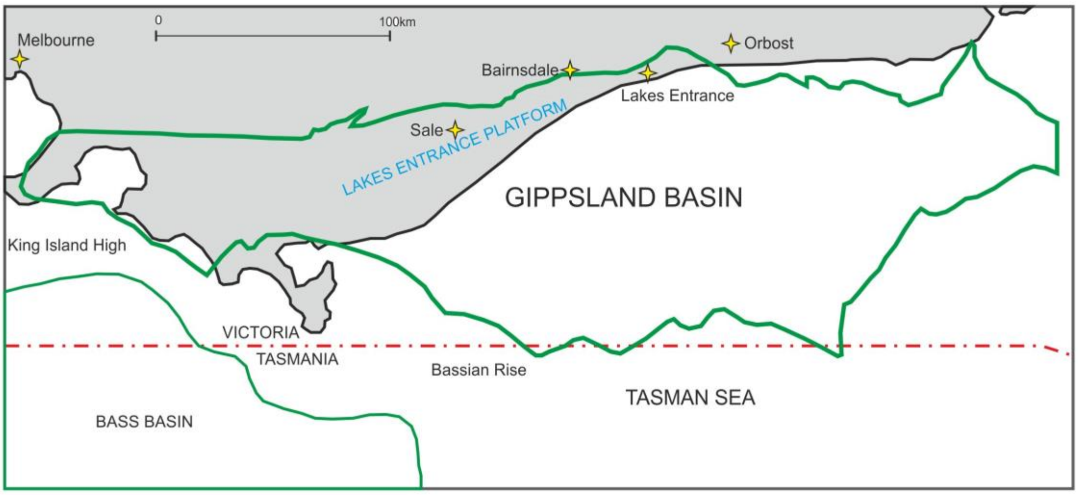


**Figure 2.11** Location map of the Gippsland Basin. Modified from Holdgate & Gallagher (2003: 325, Fig. 10.31).

The geology and stratigraphy of the Gippsland Basin is often examined in studies whose focus is hydrocarbon exploration (e.g. Weeks & Hopkins, 1967; Shibaoka et al, 1978; Rahmanian et al., 1990; Holdgate et al, 1995, 2009). Many of these studies focus on the coal seams that characterise the stratigraphy of the basin. The tectonics of the basin, including research into major unconformities, has been the focus of a number of recent studies (e.g. Dickinson et al., 2001, 2002; Holdgate et al., 2003). Sedimentological studies and facies analysis has provided useful insights into the geological history of the Gippsland Basin (e.g. Tosolini et al., 1999; Wallace et al., 2002; Mitchell et al., 2007). The palaeoenvironment and palaeoceanography of the basin has also been considered (e.g. Gallagher et al., 2001). A review of the tectonic history and stratigraphy of this basin can be found in Holdgate and Gallagher (2003).

Specimens used in this thesis from the Gippsland Basin have been recovered from the Late Miocene Tambo River Formation and the Pliocene Jemmys Point Formation (Table 2.7). The basin was not visited as part of field work in southeastern Australia due to logistical constraints.

The Tambo River Formation is a member of the Seaspray group and is Late Miocene in age (Holdgate & Gallagher, 2003). The best exposures are seen in the Bairnsdale area, just inland from the coast around Lakes Entrance. The formation consists of marlstones and marly limestones with glauconitic sandy conquinas and lenses of sandstone and siltstone (Darragh, 1985). It conformably overlies the Bairnsdale Limestone Member of the Gippsland Limestone (Holdgate & Gallagher, 2003; Fitzgerald, 2004). The dominant invertebrate fossils found in the Tambo River Formation are echinoids, brachiopods and bivalves although the sandstone and siltstone lenses are rich in gastropod and bivalve shells (Darragh, 1985). The formation is interpreted as being deposited in cool-water carbonate shelf conditions (Holdgate & Gallagher, 2003). All gastropod material from this formation used in this research are museum specimens.

The Jemmys Point Formation is Pliocene in age and overlies the closely related Tambo River Formation (Dickinson, 2002; Holdgate & Gallagher, 2003). The formation is the youngest member of the Seaspray Group (Crespin, 1943; Holdgate & Gallagher, 2003) and is best exposed around Lakes Entrance and nearby North Arm and Jemmys Point. The formation is comprised of sandy claystone beds with intermittent shell beds (e.g. Abele et al., 1988). Isolated bones, skulls and vertebrae from vertebrates such as sharks have been found in this formation (Fitzgerald, 2004) but the dominant fossils are molluscs and other marine invertebrates (Darragh, 1985). The formation has been interpreted as being deposited in shoreface to offshore marine environments (Wallace et al., 2005). All gastropod material from this formation used in this research are museum specimens.

| **Formation** | **Age** | **Localities** | **Species** |
|---|---|---|---|
| Jemmys Point Formation | Mitchellian - Kalimnan<br>(Pliocene)<br>5.5–4.0Ma | VIC045<br>VIC046<br>VIC047<br>VIC048<br>VIC049<br>VIC050<br>VIC051<br>VIC062<br>VIC095<br>VIC102<br>VIC106<br>VIC107 | *Athleta (Ternivoluta) antiscalaris antispinosa*<br>*Athleta (Ternivoluta) bungae*<br>*Amoria undulata undulata*<br>*Nannamoria paraboloides*<br>*Nannamoria amplexa*<br>*Ericusa sowerbyi sowerbyi*<br>*Nassarius (Niotha) crassigranosus*<br>*Nassarius (Zeuxis) pyrrhus* |
| Tambo River Formation | Micthellian<br>(L. Miocene)<br>10.0–5.5Ma | VIC044 | *Athleta (Ternivoluta) antiscalaris antispinosa*<br>*Amoria undulata undulate*<br>*Nannamoria paraboloides* |

**Table 2.7** Table of formations from the Gippsland Basin with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropods species include both collected and museum material.

## 2.3 STRATIGRAPHIC CORRELATION

A stratigraphic correlation chart is shown in Figure 2.12. The chart shows the formations from which gastropod fossil specimens have been collected as well as outlining the major gaps in the gastropod fossil record in southeastern Australia. Within these gaps, gastropod moulds have been found but it is not possible to use moulds as part of this study. This suggests that the stratigraphic range of the specimens used in this research may be longer than predicted by this study. It is not within the scope of this study to examine the cause of lack of original shell material in those formations only containing moulds but is an area in need of attention. Major gaps in the Cenozoic fossil record of gastropods from southeastern Australia occur in the Palaeocene, Eocene (except in the Otway Basin) and the Late Oligocene.

## 2.4 OTHER FORMATIONS

A number of species used within this research have wide geographic distributions which extend beyond the southeastern coast of Australia and into Tasmania and/or Western Australia. The age of these formations and the species associated with them are shown in Tables 2.8, 2.9 and 2.10.

In Tasmania, four formations contain gastropod fossils used in this research. The Cameron Inlet and Memana Formations occur on Flinders Island, on the Bassian Rise between the Bass and Gippsland Basins in the Bass Strait (Table 2.8). The Fossil Bluff and Freestone Cove Sandstones occur in Wynyard on the northern coast of Tasmania, just off the southern margin of the Bass Basin (Table 2.9). Six species are found exclusively in Tasmania with no occurrences along the southeastern coast of Australia but are included in this research to aid completeness of familial taxonomy in the region. These species are: *Nannamoria stolida*, *Notovoluta saginata*, *Alcithoe (Waihaoia) tateana*, *Livonia mortoni mortoni*, *Livonia voluminosa* and *Teleochilus gracillima*.

In Western Australia, two formations contain fossil gastropods useful to this study (Table 2.10). The Ascot Formation occurs in the Perth Basin and the Roe Calcarenite occurs in the Nullarbor Plains within the Eucla Basin. Species occurring in this region also have occurrences along the southeastern coast of Australia.

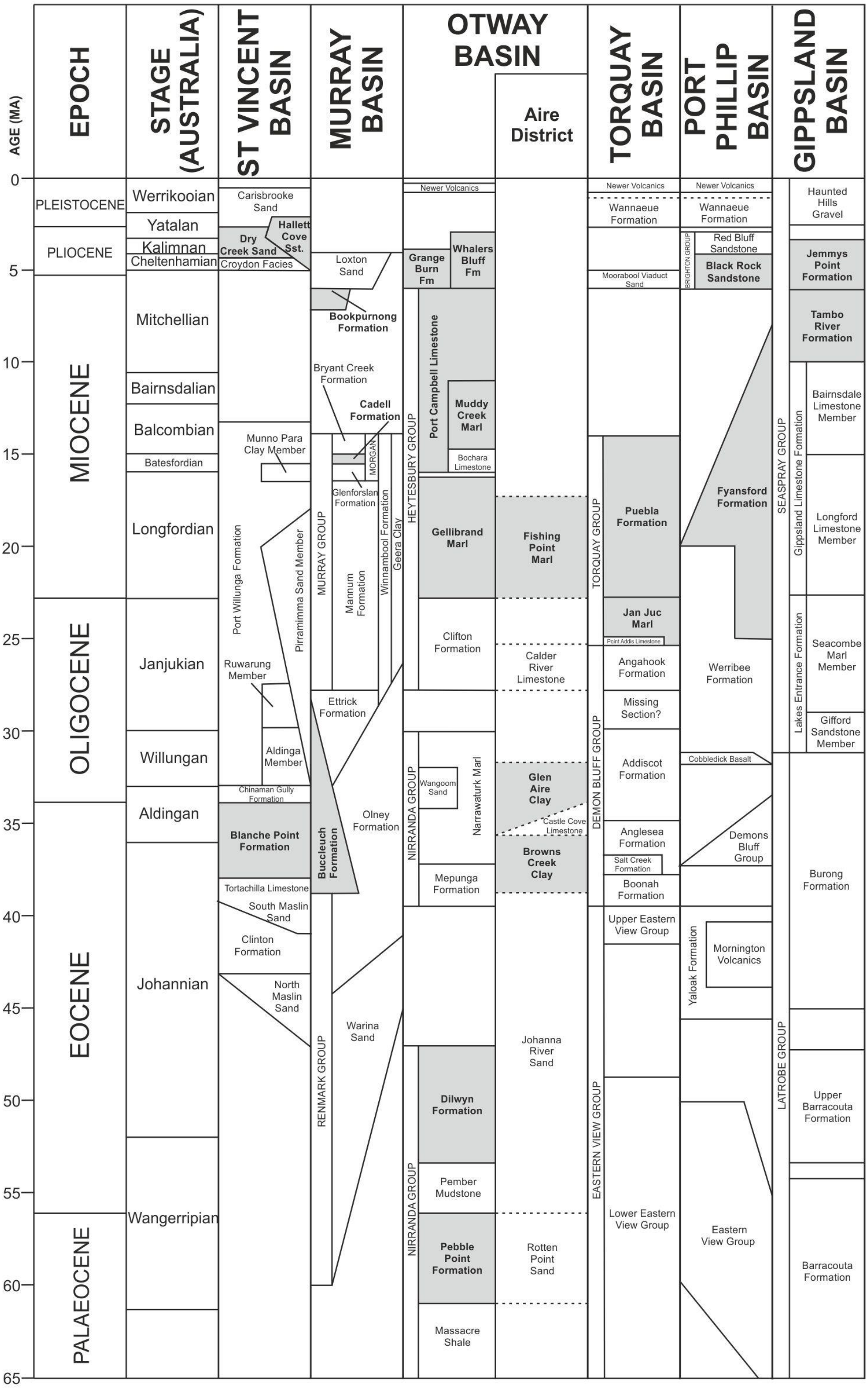


**Figure 2.12** Stratigraphic correlation chart of formations occurring in basins along the southeastern coast of Australia. Formations in bold and highlighted in grey are those from which specimens have been collected. Data from Rogers et al. (1995), Lukasik & James (1998), Holdgate & Gallagher (2003), Fitzgerald (2004). Wallace et al. (2005), Mantle et al. (2009) and McLaren et al. (2011).

| Formation | Lithology | Age | Localities | Species |
|---|---|---|---|---|
| Memana Formation | Shelly sands and limestones, horizons of gravel and clay (Beu & Darragh, 2001). | Yatalan – Werrikooian<br>(E. Pleistocene)<br>2.5 – 1.5Ma | TAS038<br>TAS039 | *Amoria undulata undulata* |
| Cameron Inlet Formation | Fine, silty, coquina limestones and sands (Fitzgerald, 2004). | Kalimnan – Yatalan<br>(L. Pliocene)<br>3.5 – 2.5Ma | TAS034<br>TAS035<br>TAS036<br>TAS037 | *Amoria undulata undulata*<br>*Nannamoria cinctuta*<br>*Nannamoria paraboloides*<br>*Alcithoe (Alcithoe) orphanata*<br>*Ericusa sowerbyi sowerbyi* |

**Table 2.8** Table of formations from Flinders Island, Tasmania with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropods species include both collected and museum material.

| Formation | Lithology | Age | Localities | Species |
|---|---|---|---|---|
| Fossil Bluff Sandstone | Coarse ferriginous shelly sandstone (Sutherland et al., 2004). | Longfordian<br>(E. Miocene)<br>23.0–21.0Ma | TAS002 | *Athleta (Ternivoluta) anticingulata anticingulata*<br>*Nannamoria weldii*<br>*Notovoluta saginata*<br>*Alcithoe (Waihaoia) tateana*<br>*Ericusa sowerbyi pellita*<br>*Livonia mortoni mortoni*<br>*Livonia voluminosa*<br>*Notopeplum mccoyi mccoyi*<br>*Teleochilus gracillima* |
| Freestone Cove Sandstone | Fine siltstonesm shales, and glauconitic calcareous sandstone rich in vertebrate, invertebrate and plant fossils (Kemp, 1991; Fitzgerald, 2004). | Longfordian<br>(E. Miocene)<br>23.9 – 23Ma | TAS001 | *Athleta (Ternivoluta) anticingulata anticingulata*<br>*Lyria semiacuticostata*<br>*Nannamoria stolida*<br>*Nannamoria weldii*<br>*Notovoluta saginata*<br>*Alcithoe (Waihaoia) tateana*<br>*Ericusa sowerbyi pellita*<br>*Ericusa atkinsoni*<br>*Ericusa ancilloides*<br>*Livonia mortoni mortoni*<br>*Livonia voluminosa*<br>*Livonia stephensi*<br>*Livonia spenceri*<br>*Notopeplum mccoyi mccoyi*<br>*Teleochilus gracillima* |

**Table 2.9** Table of formations from Wynyard, Tasmania with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropods species include both collected and museum material.

| Formation | Lithology | Age | Localities | Species |
|---|---|---|---|---|
| Ascot Formation | Shelly calcarenites , silty and glauconitic clay and abundant molluscs (Gozzard, 2007). | Kalimnan - Yatalan<br>(L. Pliocene - E. Pleistocene)<br>2.59–1.8Ma | WA027 | *Nassarius (Zeuxis) spiraliscabrus* |
| Roe Calcarenite | Unlithified, friable sandy limestone, rich in large macrofossils, particularly molluscs (James et al., 2006). | Kalimnan – Yatalan<br>(L. Pliocene)<br>4.4 – 2.59Ma | WA026<br>WA028<br>WA029<br>WA031<br>WA032 | *Nassarius (Zeuxis) subcopiosus*<br>*Nassarius (Hima) tatei tatei*<br>*Amoria undulata undulata* |

**Table 2.10** Table of formations from Western Australia with details of associated gastropod fossils and localities. Localities presented as codes. Full locality descriptions can be found in Appendix 1. Gastropods species include both collected and museum material.

## CHAPTER 3

# TAXONOMY OF CENOZOIC GASTROPODS FROM SOUTHEASTERN AUSTRALIA

The Cenozoic gastropod fauna of southeastern Australia is extremely diverse and abundant and includes a variety of families, many of which are assigned to the order Neogastropoda. Despite the numerous published taxonomic descriptions, very few authors have attempted to revise the taxonomy of complete families, resulting in a confusing and disjointed taxonomic record of many Cenozoic families in this region. Some publications have sought to resolve this issue by dealing with the taxonomy of single families, often restricted to a particular time period (e.g. Darragh, 1971, 1988; Cernohorsky, 1984) and this has resolved many issues regarding taxonomic assignment of species.

The taxonomy that follows is based on both direct observations and reviews of the literature. Material collected in the field, as well as type and non-type specimens from the museum collections at the South Australian Museum in Adelaide and the Museum Victoria in Melbourne were examined. The families Volutidae, Nassariidae, Raphitomidae, Mangeliidae, Borsoniidae and Turridae were selected for this study. These families provide an abundance of material which is representative of the Cenozoic gastropod fauna of southeastern Australia. In addition they include many of the most commonly found species, can be found across all sedimentary basins in the field area and cover the whole of the Cenozoic. Most importantly they include both planktotrophic and nonplanktotrophic taxa. The taxonomy presented here includes only those species that can be confidently assigned to a particular genus and family and as a result some families are more complete than others.

Diagnoses are provided for all species in this study, as well as associated genera and families. Dichotomous keys for genera and species aid navigation through the chapter and outline diagnostic features of genera and species. For brevity, synonymy lists are often not exhaustive (instead including only the first use of any one name). Where this is the case a reference is provided for a full published synonymy list. Distribution data includes the stratigraphic and geographic range of each taxon and for each species description this includes locality codes for specific localities. Full information for localities can be found in

Appendix 1. The abbreviation “TL” refers to the type locality. Type specimen data includes abbreviated institution names (see Table 3.1 for full names). The main morphological features used to distinguish between species are highlighted in Figure 3.1.

| Abbreviation | Insititution name |
|---|---|
| **AIM** | Auckland Institute and Museum, Auckland |
| **AMS** | Australian Museum, Sydney |
| **BMNH** | The Natural History Museum, London |
| **MHN** | Muséum d’Histoire Naturelle, Geneva |
| **MUGD** | Melbourne University Geology Department, Melbourne |
| **NMV** | Museum Victoria, Melbourne |
| **SAM** | South Australian Museum, Adelaide |
| **TM** | Tasmanian Museum, Hobart |
| **ZHMU** | Zoological Museum, Humboldt University, Berlin |

**Table 3.1** Abbreviations for institution names.

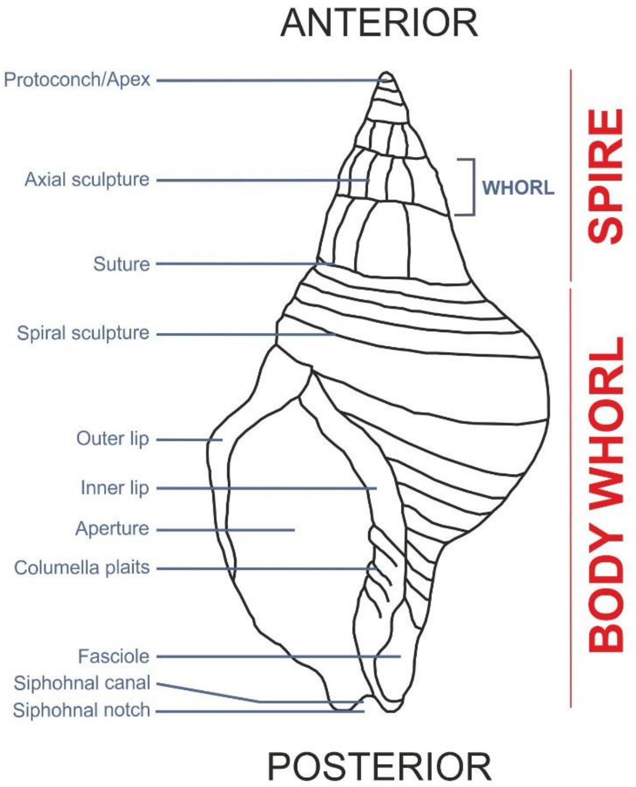


**Figure 3.1** Diagram of the main morphological features of the gastropod shell.

## 3.1 FAMILY VOLUTIDAE

The gastropod family Volutidae are assigned to the superfamily Muricoidea within the Neogastropoda. Darragh (1988) provided the only full revision of Tertiary volute species from southeastern Australia, with the subfamily Athletinae being dealt with separately (Darragh, 1971). The beauty and diversity of this group has resulted in it receiving a great deal of attention but very little work has attempted to evaluate the family as a whole, including both fossil and living species. Most of the published work deals with living species (e.g. Weaver & du Pont, 1970; Wilson, 1972; Bail & Poppe, 2001; Bail et al., 2010) and publications on fossil species tend to be specific to individual genera or geographic regions (e.g. del Río & Martínez, 2006; Landau & da Silva, 2006; Nielsen & Frassinetti, 2007). Subfamilial division is greatly variable between publications with many subfamilies and tribes becoming interchangeable. The size and diversity of this family make a complete taxonomic revision extremely difficult and outside the scope of this thesis.

Many of the species descriptions for fossil representatives of the family Volutidae were published in the nineteenth and early twentieth centuries (e.g. Tate, 1888, 1889b; Pritchard, 1896, 1898, 1913; Johnston, 1880, 1888; McCoy, 1866, 1874, 1876) with many of these taxa assigned to the genus *Voluta* or *Lyria*. The first overview of fossil volutes (Tate, 1898) comprised thirty-two species which were split into two genera, *Volutilithes* and *Voluta*, of which *Voluta* had nine 'sections'. Much of Tate's classification is still valid except for modifications relating to nomenclature (e.g. changes to Latinised species names). Cotton (1949) suggested a classification of both living and fossil species, including all twenty-two genera, forty-eight fossil and seventy-nine living species described up to that point in time. However, the lack of critical appraisal resulted in a vast overestimation of the number of valid species and genera. The current classification of this family accepted by most authors is that of Pilsbry & Olsson (1954).

Australian waters probably account for the greatest diversity of volute genera and one-third of described living species. Fossil species are thought to have lived in similar conditions to extant species (as supported by sedimentological evidence): temperate to warm-temperate waters, between 0 and 250m. Darragh (1971, 1988) provided the basis for the taxonomy of the family Volutidae from the Cenozoic sediments of southeastern Australia. The author recognised five subfamilies (Athletinae, Volutinae, Scaphellinae, Amoriinae and Zidoninae), fifteen genera (*Athleta, Lyria, Lyreneta, Leptoscapha, Mitreola,* *Scaphella, Notovoluta, Amoria, Nannamoria, Alcithoe, Ericusa, Livonia, Notopeplum, Cymbiola, Melo*) and 111 species in this region. Darragh (1988) did not assign the genus *Notovoluta* to a subfamily but instead left it as “subfamily uncertain”.

### **3.1.1** SYSTEMATIC PALAEONTOLOGY

The family Volutidae is a diverse, large family. Examination of the type specimens and comparison with other Australian species (both living and fossil) described in the literature has been used to assign species to genera. The following taxonomic revision closely follows Wilson (1972), Darragh (1971) and Darragh (1988) which provide the most recent comprehensive taxonomic revisions of this family in Australia.

CLASS **GASTROPODA**
ORDER **NEOGASTROPODA**
SUPERFAMILY **MURICOIDEA** Rafinesque, 1815
Family **VOLUTIDAE** Rafinesque, 1815

1815 Volutidae Rafinesque, p.145.

DIAGNOSIS

Shell shape variable, often ovate to fusiform, sometimes biconic. Sculpture variable, axial and radial elements, sometimes cancellate or smooth. Aperture elongate. Short, wide, well developed anterior canal. Siphonal notch and fasciole of varying degrees of development. Outer lip simple, slightly thickened, sometimes winged. Inner lip often with strong, oblique folds, weaker folds at posterior.

DISTRIBUTION

Late Cretaceous - Recent. Cosmopolitan.

REMARKS

The Volutidae have rarely been evaluated as a whole family. There are several reasons for this. Most workers concentrate their efforts either on living representatives or fossil species but rarely make comparisons between the two. The lack of overlap in studies of Recent and fossil species has resulted in excessive splitting and the creation of monotypic genera, poorly resolved relationships between taxa and inflation of species numbers. Some living species, such as those belonging to the genera *Notopeplum*, *Notovoluta* and *Ternivoluta*, have only recently been studied due to their habitation in moderately deep water, beyond the reach of normal collecting techniques. The Volutidae is in need of a complete critical appraisal but this may be difficult due to the large number of species and cosmopolitan distribution (see Darragh (1988)).

## Subfamily **ATHLETINAE** Pilsbry & Olsson, 1954

1954 Athletinae Pilsbry & Olsson, p.15.

### DIAGNOSIS

Shell generally strombiform, high spired, strong cancellate sculpture. Occasional thick callus covering parietal wall and spire. Protoconch small to medium, one or more whorls, elevated, turbinate, sharp apex. Teleoconch with rounded or angled shoulder, smooth, nodular or bearing spines. Sculpture often partly or wholly smooth. Straight anterior canal, shallow siphonal notch, basal fasciole usually absent. One or more columellar plaits, strong or weak. Parietal callus thin or thick with variable extension across ventral shell surface.

### DISTRIBUTION

Upper Cretaceous - Recent. Cosmopolitan.

### REMARKS

In Australia the subfamily Athletinae is represented by nine species from the subgenus *Athleta (Ternivoluta)* during the Cenozoic.

## Genus **ATHLETA** Conrad, 1853

1853 *Athleta* Conrad, pp.448-9.

1890 *Volutocorbis* Dall, p.75

1890 *Neoathleta* Bellardi, p.304.

1890 *Volutopupa* Dall, p.77.

1897 *Ternivoluta* Martens, p.177.

1906 *Volutospina* Newton, pp.102-103.

1926 *Notoplejona* Marwick, pp.262, 270.

1945 *Eoathleta* Gardner, p.227.

1954 *Volutovetus* Pilsbry & Olsson, p.22.

1957 *Bendeluta* Eames, p. 46.

1971 *Athleta* Conrad, Darragh, p. 168.

TYPE SPECIES

*Voluta rarispina* Lamarck, 1811 by subsequent designation (Dall, 1890). Miocene, France.

DIAGNOSIS

Shell small for family, fusiform to biconic, spire gradate in most species. Teleoconch sculpture variable, cancellate with spiral and axial elements equally developed, prominent axial costa and/or peripheral tubercles and weaker spiral elements, or smooth. Columella narrow to strongly padded, sometimes smooth. Variable developed parietal callus. Outer lip often thin but sometimes thickened, variciform or denticulate. Siphonal notch shallow to moderately deep, fasciole weakly to strongly developed.

DISTRIBUTION

Late Cretaceous - Recent. Cosmopolitan.

REMARKS

*Athleta* is taxonomically complex as evident from the large number of synonyms attached to it. The type species *Athleta rarispina* is considered to be atypical of the genus (Cossman, 1906; Darragh, 1971; Maxwell, 2003) and this may be the cause of some confusion. In many cases there appear to be geographically distinct groups placed in this genus (e.g. Maxwell, 2003). Darragh (1971) argued that *Athleta* is a large and diverse genus with great variability in characters whilst Maxwell (2003) suggests that *Athleta* may be a polyphyletic group and that some clades may be better recognised as subgenera or genera in their own right. Many issues regarding the placement of species in this genus may be resolved by a detailed phylogenetic study. *Athleta s.s.* is not found within the Cenozoic sediments of southeastern Australia but *Athleta (Ternivoluta)* is.

## Subgenus **TERNIVOLUTA** Martens 1897

1897 *Voluta (Ternivoluta)* Martens, p.177.
1929 *Volutocorbis (Ternivoluta)* Thiele, p.345.
1949 *Austrovoluta* Cotton, p.185.
1970 *Ternivoluta* Weaver & du Pont, p.13.

### TYPE SPECIES

*Voluta (Ternivoluta) studeri* Martens, 1897 by subsequent designation (Sykes, Smith & Crick, 1898). Recent, Australia.

### DIAGNOSIS

Shell fusiform to subfusiform, often with gradate spire, protoconch deviated. Often prominent axial costae with nodules/spines on shoulder. Spiral threads present on anterior of body whorl. Aperture elongate-elliptical. Shallow siphonal notch, weakly developed plaits. Columella with two to four major plaits. Siphonal fasciole absent.

### DISTRIBUTION

Eocene - Recent. Australia.

### REMARKS

The subgenus *Ternivoluta* is distinguished from others within the subfamily by the deviated protoconch and smooth interior of the outer lip (Darragh, 1971). *Ternivoluta* is comprised of nine fossil species and one living species from Australia. The living species *Athleta (Ternivoluta) studeri* is not included in this study due to its occurrence outside of the field area and lack of fossil record.

### KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:

1. Shell broadly fusiform. ........................ Go to 2
   Shell pyriform. ........................ *antiscalaris antispinosa*

2. Columella with two to three plaits. ........................ Go to 3
   Columella with three to four plaits. ........................ Go to 6

3. Spiral threads over whole shell. .................................... Go to 4
Spiral threads on anterior of body whorl. ........................ Got to 5

4. Sculpture weakly cancellate. ........................................ *subcrenulifera*
Sculpture intersection nodulate. ................................. *antiscalaris antiscalaris*

5. Axial costae nodular at suture. ................................... *wangerrip*
Axial costae rounded at suture. .................................... *curvicostata*

6. Spiral sculpture absent on spire. ................................. Go to 7
Spiral sculpture over whole shell. ................................. *anticingulata craticula*

7. Axial sculpture extending over half of body whorl. .......... Go to 8.
Axial sculpture extending over quarter over body whorl.
........................................................................................ *antiscalaris levior*

8. Whorls shouldered. ...................................................... *anticingulata anticingulata*
Whorls lacking shoulder. .............................................. *bungae*

***Athleta (Ternivoluta) antiscalaris antispinosa*** (Tate, 1899)

1899 *Volutilithes antispinosus* Tate, p.107, pl. 1, figs. 5a, b.
1949 *Austrovoluta antispinosa* Cotton, pl. 15.
1988 *Athleta (Ternivoluta) antiscalaris antispinosa* Darragh, p.181, pl. 16, figs. 29, 34, 37.

DIAGNOSIS

Shell pyriform, squat subconical spire, abruptly tapered anteriorly. Prominent shoulder on body whorl. Axial costae spinose at shoulder, wide, short, extending over up to a third of body whorl. Spiral threads on anterior of body whorl and anterior canal. Columella with three to four plaits.

TYPE SPECIMENS

HOLOTYPE: *Athleta (Ternivoluta) antiscalaris antispinosa*, SAM, T1449.
HYPOTYPES: *Athleta (Ternivoluta) antiscalaris antispinosa*, NMV, P22487, P22488.
DISTRIBUTION

Longfordian – Kalimanan (Early Miocene – Pliocene): South Australia to Victoria (SA002 (TL), VIC040-045).

REMARKS

The very short squat spire characterises this species. Geological younger specimens exhibit a row of subspinose sutural nodules indicating the close relationship with *A. (T.) antiscalaris levior*.

***Athleta (Ternivoluta) subcrenulifera*** Darragh, 1971

1971 *Athleta (Athleta) subcrenulifera* Darragh, p.176, pl. 15, figs. 18-19, 22.

DIAGNOSIS

Shell elongate-fusiform, high gradate spire, gently tapered anteriorly. Axial costae thin, erect, numerous, extending over half body whorl. Spiral threads well developed over whole shell, weakly nodulate at intersection with axial costae. Columella with two to three plaits.

TYPE SPECIMENS

HOLOTYPE: *Athleta (Ternivoluta) subcrenulifera*, NMV, P22481.

PARATYPES: *Athleta (Ternivoluta) subcrenulifera*, NMV, P22482, P22483.

DISTRIBUTION

Longfordian (Early Miocene): Victoria (VIC011 (TL), VIC012).

REMARKS

Species is distinguished by elongate shell and weakly cancellate sculpture. Occurs alongside *A. (T.) antiscalaris antiscalaris* in the Fishing Point Marl of the Aire district but not elsewhere.

***Athleta (Ternivoluta) antiscalaris antiscalaris*** (McCoy, 1866)

Plate 1, figs. 1a, b.

1866 *Voluta antiscalaris* McCoy, p.378.
1897 *Volutilithes antiscalaris* Harris, p.97 partim.

1949 *Austrovoluta antiscalaris* Cotton, p.185, pl. 15.

1971 *Athleta (Ternivoluta) antiscalaris antiscalaris* Darragh, p.177, pl. 15, figs. 17, 20-21, 23; pl. 16, fig. 25; fig. B.

*Refer to Darragh (1971) for full synonymy.*

DIAGNOSIS

Shell broadly fusiform, tapered abruptly at anterior. Axial costae erect, extending over third of body whorl. Spiral threads well developed over whole shell, nodular at intersection with axial costae. Columella with two to three plaits.

TYPE SPECIMENS

LECTOTYPE: *Athleta (Ternivoluta) antiscalaris antiscalaris*, NMV, P12164.

PARALECTOTYPES: *Athleta (Ternivoluta) antiscalaris antiscalaris*, NMV, P12163, P22486.

HYPOTYPE: *Athleta (Ternivoluta) antiscalaris antiscalaris*, NMV, P22484.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): South Australia to Victoria (SA001, VIC022 (TL), VIC023-039).

REMARKS

Darragh (1971) distinguished this subspecies based on the broader fusiform shape and strongly developed spiral sculpture.

***Athleta (Ternivoluta) wangerrip*** (Darragh, 1971)

1971 *Athleta (Athleta) wangerrip* Darragh, p.168, pl. 16, figs. 27-28, 31-32.

DIAGNOSIS

Shell fusiform, tumid, tapered at anterior. Axial costae present, nodular at suture, extended over half of anterior whorl slope, less spinose at shoulder on mature specimens, Spiral sculpture of fine threads on anterior slope of body whorl. Columella with two plaits.

TYPE SPECIMENS

HOLOTYPE: *Athleta (Athleta) wangerrip*, NMV, P28032.

PARATYPES: *Athleta (Athleta) wangerrip*, NMV, P22474, P22475.

DISTRIBUTION

Johannian (Early Eocene): Victoria (VIC001, (TL)).

REMARKS

Darragh (1971) assigned this species to *Athleta* (*sensu stricto*) due to its turbinate protoconch. However, shell morphology seems to be much more similar to *Athleta (Ternivoluta)* species (e.g. *A. (Ternivoluta) curvicostata)*. This revision agrees with Maxwell (2003) in placing this species in the subgenus *Ternivoluta*. The subgeneric division of *Athleta (sensu stricto) and Athleta (Ternivoluta)* is likely in need of some attention.

***Athleta (Ternivoluta) curvivostata*** Darragh, 1971

1971 *Athleta (Ternivoluta) curvicostata* Darragh, p.172, pl. 14, figs. 1, 3, 5-6.

DIAGNOSIS

Shell fusiform, gradate spire, rounded body whorl gently tapered at anterior. Protoconch, large, deviated. Suture deeply grooved. Axial costae thin, elongate, numerous, rounded at suture. Spiral threads only present on anterior third of body whorl. Columella with 2-3 plaits.

TYPE SPECIMENS

HOLOTYPE: *Athleta (Ternivoluta) curvicostata*, NMV, P22476.

PARATYPES: *Athleta (Ternivoluta) curvicostata*, NMV, P22477, P22478.

DISTRIBUTION

Aldingan – Willungan (Late Eocene – Early Oligocene): Victoria (VIC002 (TL), VIC003).

REMARKS

This species is very similar to the Wangerripian species *Athleta (Ternivoluta) wangerrip* but can be distinguished by its lack of spinosity at the shoulder, slender, elongate costae, deep groove at suture and large, deviated, globose protoconch.

***Athleta (Ternivoluta) anticingulata craticula*** Darragh, 1971

1971 *Athleta (Ternivoluta) anticingulata craticula* Darragh, p.174, pl. 14, figs. 2, 4, 7.

DIAGNOSIS

Shell fusiform, tumid, tapered abruptly at anterior. Axial costae numerous, nodulate at shoulder, extending over half of body whorl. Spiral threads over whole shell, subnodular at intersection with axial costae. Columella with four strong plaits.

TYPE SPECIMENS

HOLOTYPE: *Athleta (Ternivoluta) anticingulata craticula*, NMV, P22479.

PARATYPE: *Athleta (Ternivoluta) anticingulata craticula*, NMV, P22480.

DISTRIBUTION

Longfordian - Balcombian (Early - Middle Miocene): Victoria (VIC008 (TL), VIC009-010).

REMARKS

This subspecies is distinguished from *Athleta (Ternivoluta) anticingulata anticingulata* at subspecies level by the presence of spiral threads over the whole shell.

***Athleta (Ternivoluta) antiscalaris levior*** (McCoy, 1866)

1866 *Voluta antiscalaris levior* McCoy, p.379

1897 *Volutilithes antiscalaris* Harris, p.97, pl.4, figs.8a-b.

1971 *Athleta (Ternivoluta) antiscalaris levior* Darragh, p.178, pl. 15, figs. 15-16, pl. 16, figs. 35-36.

DIAGNOSIS

Shell fusiform, narrowly tapered anteriorly. Axial costae short, prominent, extended over quarter of body whorl. Spiral threads absent on spire, weakly developed on body whorl. Columella with three to four plaits.

TYPE SPECIMENS

LECTOTYPE: *Athleta (Ternivoluta) antiscalaris levior*, NMV, P12166.

PARALECTOTYPES: *Athleta (Ternivoluta) antiscalaris levior,* NMV, P12165, P12167, P12168.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC022 (TL), VIC023-039).

REMARKS

This subspecies is distinguished by its narrower body whorl, shorter axial costae and decreased prominence of spiral threads.

***Athleta (Ternivoluta) anticingulata anticingulata*** (McCoy, 1866)

1866 *Voluta anticingulata* McCoy, p.379.
1866 *Voluta anticingulata var.* b *indivisa* McCoy, p.380.
1866 *Voluta anticingulata var.* a *perstriata* McCoy, p.380 (lapsus for *persulcata*).
1874 *Voluta anticingulata var.* a *persulcata* McCoy, p.25.
1888 *Voluta antiscalaris* Johnston, pl. 30, fig. 5, 5a-b. (Non McCoy 1866).
1889 *Voluta anticingulata*, Tate, p.133.
1897 *Volutilithes anticingulatus*, Harris, p.93.
1949 *Austrovoluta anticingulata*, Cotton, p.185, pl. 15.
1971 *Athleta (Ternivoluta) anticingulata anticingulata*, Darragh, p.173, pl. 14, figs. 8-14.
*Refer to Darragh (1971) for full synonymy.*

DIAGNOSIS

Shell fusiform, abruptly tapered at anterior. Axial costae extend over half of body whorl. Narrow sutural groove, sometimes nodular, sometimes shouldered. Spiral threads usually absent on spire whorls, extended over half of body whorl. Columella with three to four plaits.

TYPE SPECIMENS

SYNTYPES: *Athleta (Ternivoluta) anticingulata anticingulata var. persulcata*, NMV, P12159. *Athleta (Ternivoluta) anticingulata anticingulata var. indivisa*, NMV, P12160, P12161, P12162.

LECTOTYPE: *Athleta (Ternivoluta) anticingulata anticingulata*, NMV, P12157.

PARALECTOTYPES: *Athleta (Ternivoluta) anticingulata anticingulata*, NMV, P12156.

DISTRIBUTION

Janjukian - Longfordian (Late Oligocene – Early Miocene): Victoria to Tasmania (VIC004 (TL) VIC005-007, TAS001-002).

REMARKS

This subspecies shows much variation within its morphology. Darragh (1971) attributed this to varying ecological conditions and comments on the different forms found both in Victoria and Tasmania.

***Athleta (Ternivoluta) bungae*** Darragh, 1971

1971 *Athleta (Ternivoluta) bungae* Darragh, p.182

DIAGNOSIS

Shell fusiform-biconic with squat spire. Numerous, thin axial costae extending over half body whorl. Spiral threads present over anterior of body whorl, nodular where intersecting with axial costae, seen as cancellate sculpture. Columella with four well developed plaits.

TYPE SPECIMENS

HOLOTYPE: *Athleta (Ternivoluta) bungae*, NMV, P22485.

DISTRIBUTION

Kalimnan (Pliocene): Victoria (VIC046 (TL), VIC047-051).

REMARKS

This species is distinguished by its shape, lack of spines, lack of shoulder and cancellate sculpture. It bears no obvious similarities with the other Gippsland species *Athleta (Ternivoluta) antiscalaris antispinosa* (Darragh, 1971).

## Subfamily **VOLUTINAE** Rafinesque, 1815

1815 Volutinae Rafinesque, p.145.
1954 Lyriinae Pilsbry & Olsson, p.15.
1954 Volutilithinae Pilsbry & Olsson, p.14.
1954 Calliotectinae Pilsbry & Olsson, p.19.

### DIAGNOSIS

Shell ovate to fusiform, spire elevated or blunt. Sculpture of axial costae, nodular or spiny, sometimes smooth. Columella plaits usually well developed. Siphonal notch often deep, fasciole often well developed. Radula uniserial, rachidian tooth multicuspid or tricuspid.

### DISTRIBUTION

Late Cretaceous - Recent. Cosmopolitan.

### REMARKS

Like other subfamilies in this family, taxonomic position is based on anatomical characters of soft parts and fossil species are compared with shell morphology of living species whose taxonomic position is known.

### KEY TO GENERA FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:

1. Nodulate at posterior suture, outer lip thickened.................*Lyria*
2. Axial sculpture absent, inner lip callused............................*Leptoscapha*

## Genus **LYRIA** Gray, 1847

1853 *Lyria (Lyria)* Adams & Adams, p.166.
1855a *Lyria* Gray, p.16.
1855a *Lyria (Harpella)* Gray, p.17 (non Schrank, 1802 (Lepidoptera)).
1907 *Lyria (Harpeola)* Dall, p.350
1954 *Lyria (Sannalyria)* Pilsbry & Olsson, p.23.
1962 *Lyria (Paralyria)* Shuto, p.69.
1971 ?*Lyria (Cordilyria)* Bayer, p.204.
1988 *Lyria* Darragh, p.207.

*Refer to Darragh (1988) for full synonymy.*

### TYPE SPECIES

*Voluta nucleus* Lamarck, 1811 by original designation. Recent, Eastern Australia.

### DIAGNOSIS

Shell small to medium for family, solid, ovately fusiform, sometimes with channelled sutures. Protoconch smooth, size and shape variable. Spiral sculpture weakly developed. Axial sculpture of close-set costae, nodulate at posterior suture. Aperture elongate-ovate and narrow. Outer lip thickened externally. Columella with two strong anterior plaits. Siphonal notch broad and shallow, fasciole well developed.

### DISTRIBUTION

Late Cretaceous - Recent. Cosmopolitan.

### REMARKS

The genus shows much variation in its sculpture resulting in numerous synonyms (see Darragh, 1988 for discussion). Fossil species of *Lyria* from Australia seem to have many similarities to species from the Paleogene of Europe and southeastern Asia and species from the Neogene and Recent of the Western Indo-Pacific region (Darragh, 1988). Four species are found as fossils in the field area of this study.

### KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:

| | | |
|---|---|---|
| 1. | Shell ovate-fusiform. | Go to 2 |
| | Shell ovate. | Go to 3 |
| 2. | Elevated spire. | *semiacuticostata* |
| | Low spire. | *acuticostulata* |
| 3. | Spiral sculpture of weakly developed threads. | *harpularia* |
| | Spiral sculpture of fine grooves. | *gemmata* |

### ***Lyria semiacuticostata*** Pritchard, 1896

1896 *Lyria semiacuticostata* Pritchard, p. 91, pl. 2, fig. 8.

### DIAGNOSIS

Shell ovate-fusiform, narrow and well-elevated spire, channelled sutures and anteriorly truncate. Protoconch of 2½ small, smooth whorls. Spiral sculpture absent. Axial sculpture of fairly regularly spaced, slender, transverse costae, becoming obsolete on anterior of body whorl. Columella with three well developed plaits. Siphonal notch and fasciole well developed.

TYPE SPECIMENS

HOLOTYPE: *Lyria semiacuticostata*, NMV, P2653.

HYPOTYPES: *Lyria semiacuticostata,* NMV, P2733, P2734.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Tasmania, Victoria (TAS001 (TL), VIC086).

REMARKS

Some resemblance can be seen between this species and *L. harpularia*. *Lyria semiacuticostata* is principally distinguished by its smaller protoconch, more acute spire, acute but gradually fading costae and absence of spiral lirae. Darragh (1988) commented on the poor preservation of the single specimen from the Upper Maude Limestone but strongly indicated that it has been correctly assigned to this species.

***Lyria acuticostulata*** Darragh, 1988

1988 *Lyria acuticostulata* Darragh, p.209, pl. 1, figs. 2-5; Fig. 2.

DIAGNOSIS

Shell thin, ovate-fusiform, low, blunt spire, tumid body whorl, impressed sutures. Spiral sculpture often absent or as faint striae. Axial sculpture of thin, well defined, flexuous costae with wide interspaces. Columella with two well developed anterior plaits. Canal twisted, reflexed dorsally. Siphonal notch shallow, prominent siphonal fasciole.

TYPE SPECIMENS

HOLOTYPE: *Lyria acuticostulata*, NMV, P31145.

PARATYPES: *Lyria acuticostulata*, NMV, P31146, P31147.

HYPOTYPE: *Lyria acuticostulata*, NMV, P31148.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC022 (TL), VIC013-014, VIC025-026, VIC028-029, VIC034, VIC038, VIC082, VIC087-088).

REMARKS

This species shows similarities to *L. acuticostata* but can be distinguished by the thin continuous, erect costae and convex spire whorls. Darragh (1988) noted that Batesfordian and Bairnsdalian specimens appear more flattened and more tumid than Balcombian specimens but that this still falls within the range of variability.

***Lyria harpularia*** Tate, 1888

Plate 1, figs. 2a, b.

1888 *Lyria harpularia* Tate, p.176, pl. 12, fig. 12 (figure only).

DIAGNOSIS

Shell ovate, low gradate spire. Spiral sculpture of weakly developed fine threads. Axial sculpture of thin, erect, flexuous costae separated from posterior suture by narrow channel. Aperture elliptical. Columella with two well developed anterior plaits. Canal twisted, reflexed dorsally. Siphonal notch deep, prominent siphonal fasciole.

TYPE SPECIMENS

HOLOTYPE: *Lyria harpularia,* SAM, T395A.

HYPOTYPE: *Lyria harpularia,* NMV, P31150, P31877, P31878.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC038 (TL), VIC013, VIC022, VIC028-029, VIC088-090).

REMARKS

A single specimen labelled as being found in Curlewis may be erroneous as no other specimens of this age have been found and the matrix suggests that Red Hill is a more likely locality (Darragh, 1988).

### ***Lyria gemmata*** Tate, 1889

1889 *Lyria gemmata* Tate, p.118, pl. 3, fig. 4.

DIAGNOSIS

Shell ovate, subconical spire, sutures weakly channelled. Spiral sculpture of fine grooves. Axial sculpture of closely spaced, slightly flexuous costae terminated by small nodule. Columella with two well developed anterior plaits. Canal reflexed dorsally. Siphonal notch weak, prominent siphonal fasciole.

TYPE SPECIMENS

HOLOTYPE: *Lyria gemmata*, SAM, T631.

HYPOTYPE: *Lyria gemmata*, NMV, P31876.

DISTRIBUTION

Batesfordian – Kalimnan (Middle Miocene – Pliocene): Victoria (VIC060 (TL), VIC043).

REMARKS

The subconical spire, close set costae and anterior spiral grooves separate this species from the very similar *L. acuticostulata*.

## Genus **LEPTOSCAPHA** Fischer, 1883

1883 *Voluta (Leptoscapha)* Fischer, p.608

1899 *Leptoscapha* Cossmann, p.120

TYPE SPECIES

*Voluta variculosa* Lamarck, 1803 by original designation. Eocene, France.

DIAGNOSIS

Shell small for family, fusiform. Spiral threads numerous, close-set. Axial sculpture absent, except apertural varix trace. Outer lip thickened, sometimes with posterior denticle. Inner lip callused. Columella with three plaits anteriorly, weaker plaits at posterior and anterior. Shallow siphonal notch, well developed siphonal fasciole.

DISTRIBUTION

Eocene - Recent: Southeastern Australia, South East Asia.

REMARKS

This genus is characterised by its small size and absence of axial sculpture. It is likely to be most closely related to the genus *Mitreola*. Specimens are rarely found and as a result the evolutionary history and distribution patterns of this genus are poorly understood.

***Leptoscapha crassilabrum*** (Tate, 1889)

Plate 1, figs. 3a, b.

1889 *Voluta crassilabrum* Tate, p.128, p.3, figs. 2a-c.
1949 *Ericusa crassilabrum* Cotton, pl.15.
1988 *Leptoscapha crassilabrum* Darragh, p.213, pl. 1, figs. 1, 8, 9, pl. 27, figs. 2, 3, 5-10.

DIAGNOSIS

Shell small, ovate, convex whorls, tapered anteriorly. Axial sculpture of weakly developed traces of prior apertural varices. Spiral sculpture of thin, closely spaced, undulating threads. Aperture elongate. Outer lip thickened. Inner lip with thick callus. Columella with three well developed plaits. Siphonal canal reflexed dorsally. Well developed fasciole.

TYPE SPECIMENS

HOLOTYPE: *Voluta crassilabrum* SAM, T622A.
HYPOTYPES: *Leptoscapha crassilabrum* NMV, P32207, F53231-4.

DISTRIBUTION

Janjukian – Recent (Late Oligocene – Recent): Victoria, South Australia (SA043, VIC023, VIC025, VIC038 (TL)).

REMARKS

Recent specimens of this species are found in shell sands and as a result have undergone a certain amount of abrasion resulting in damage to sculpture. However, the similarities between Recent and fossil specimens are numerous and therefore they are assigned to the same species (Darragh, 1988).

## Subfamily **SCAPHELLINAE** H. & A. Adams, 1858

1858 Scaphellinae H. & A. Adams, p. 619.
1942 Auriniinae Smith, p. 55.

DIAGNOSIS

Shell ovate-fusiform. Columella smooth or with two plaits. Siphonal canal usually short.

DISTRIBUTION

Cretaceous - Recent: Cosmopolitan.

REMARKS

This subfamily is based on anatomical characters (see Darragh, 1988). Fossil specimens are compared to shells of living species whose taxonomic position is known.

## Genus **SCAPHELLA** Swainson, 1832

1832 *Scaphella* Swainson, p. 84.
1953 *Auriniopsis* Clench, p. 378.
1988 *Scaphella* Darragh, p.216.

TYPE SPECIES

*Voluta junonia* Shaw, 1808 by subsequent designation (Gray, 1847). Recent, Western Atlantic Ocean.

DIAGNOSIS

Shell medium to large, thick, ovate fusiform, short spire. Axial sculpture on initial teleoconch whorls. Columella with four well developed plaits. Siphonal canal short. Siphonal fasciole weakly developed.

DISTRIBUTION

Palaeocene – Recent. Cosmopolitan.

REMARKS

Due to the cosmopolitan distribution of this species there is a relatively large amount of variability in shell sculpture usually associated with specific global regions (see Landau & da Silva, 2006 for discussion of this genus).

### Subgenus **AURINIA** H. & A. Adams, 1853

1853 *Fulguraria (Aurinia)* H. & A. Adams, p.166.
1871 *Voluta (Aurinia)* Crosse, p.309.
1889 *Scaphella (Aurinia)* Dall, p.150.
1890 *Aurinia* Koenan, p. 522.
1946 *Rehderia* Clench, p.45.
1953 *Auriniopsis* Clench, p. 378.

TYPE SPECIES

*Voluta dubia* Broderip, 1827 by monotypy. Recent, southeastern USA.

DIAGNOSIS

Shell fusiform, elongate. Whorls occasionally with weakly developed shoulder. Sculpture very weakly developed if present. Columella with two or three major plaits if present. Siphonal notch and fasciole absent.

DISTRIBUTION

Palaeocene – Recent: North America, Europe, Australia.

REMARKS

This subgenus is characterised by the absent fasciole, absence or paucity of columella plaits and by anatomical features (i.e. radula). Only one species of this subgenus occurs in Australia and it is found in the Late Eocene sediments of Victoria.

***Scaphella (Aurinia) johannae*** (Darragh, 1988)

Plate 1, figs. 4a, b.

1988 *Scaphella (Aurinia) johannae* Darragh, p.216, pl. 2, figs. 9-12. Fig. 5.

DIAGNOSIS

Shell fusiform, slightly turreted spire, large blunt apex, tapered abruptly at anterior. Whorls convex. Sculpture absent. Columella with one well developed plait. Siphonal canal slightly extended.

TYPE SPECIMENS

HOLOTYPE: *Scaphella (Aurinia) johannae* NMV, P41757.

PARATYPE: *Scaphella (Aurinia) johannae* NMV, P41758.

DISTRIBUTION

Johannian - Aldingan (Late Eocene): Victoria (VIC092 (TL)).

REMARKS

See Darragh (1988) for comparison with non-Australian species.

## Subfamily **AMORIINAE** Darragh, 1988

1988 Amoriinae Darragh, p.224.

DIAGNOSIS

Shell glazed, multispiral protoconch. Columella with 4 strong plaits.

DISTRIBUTION

Late Oligocene – Recent. Australia.

REMARKS

This subfamily is defined by soft tissue characters (see Darragh, 1988 for details).

**KEY TO GENERA FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Axial sculpture of weak costae. .......... Go to 2.
   Axial sculpture obsolete. .......... *Amoria*

2. Siphonal fasciole weakly developed. .................................. *Nannamoria*
Siphonal fasciole relatively well developed. ..................... *Notovoluta*

## Genus **AMORIA** Gray, 1855

1855 *Amoria* Gray, p.64.
1882 *Voluta (Amoria)* Tryon, p.92.
1915 *Scaphella* Hedley, p. 721 (non Swainson, 1832).
1929 *Amoria (Amorena)* Iredale, p.180.
1929 *Amoria (Zebramoria)* Iredale, p.180.
1929 *Cymbiola (Cymbiolista)* Iredale, p.181.
1932 *Amorena* Cotton & Godfrey, p.47.
1936 *Relegamoria* Iredale, p.314.
1942 *Amoria* Smith, p.50.
1943 *Amoria (Amoria)* Wenz, p.1339.
1943 *Amoria (Cymbiolista)* Wenz, p.1349.
1960 *Cymbiolista* McMichael, p.11.
1962 *Zebramoria* Macpherson & Gabriel, p. 223.
1970 *Amoria (Regelamoria)* Weaver & du Pont, p.162.
1988 *Amoria* Darragh, p.225.

### TYPE SPECIES

*Voluta turneri* Griffith & Pidgeon, 1834 by subsequent designation (Harris, 1897). Recent, Northern Australia.

### DIAGNOSIS

Shell fusiform to ovate, subconical spire. Body whorls shouldered. Sculpture usually absent, sometimes as weakly developed axial costae or nodules. Columella with 4 well developed plaits, one or two weaker plaits. Deep siphonal notch, well developed siphonal fasciole.

### DISTRIBUTION

Miocene - Recent: Australia, Indonesia.

### REMARKS

Darragh (1988) grouped together the large number of synonyms of this genus based of shell and radular morphology.

### KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:

1. Subconical spire. .................................................. Go to 2
   Conical spire. .................................................. *undulata undulata*

2. Shell fusiform. .................................................. *costellifera*
   Shell ovate-pyriform. .................................................. *undulata masoni*

### ***Amoria undulata undulata*** (Tate, 1889)

1804 *Voluta undulata* Lamarck, p.157. pl.12, fig. 1a, b.
1869 *Voluta sclateri* Cox, p. 358, pl. 26, fig. 3.
1871 *Voluta kingi* Cox, p. 76, pl. 4, fig. 2.
1897 *Voluta (Amoria) undulata* Harris, p. 109.
1953 *Amoria (Amorena) undulata* Ludbrook, p.145, pl.17, figs. 3, 4.
1953 *Amoria (Amorena) sclateri* Ludbrook, p. 147, pl. 16, fig. 7.
1964 *Amoria (Amorena) benthalis* McMichael, p.271, pl. 28.
1988 *Amoria undulata undulata* Darragh, p.228, pl. 6, figs. 1-3, 7.

### DIAGNOSIS

Shell elongate-ovate, conical spire. Body whorl depressed posteriorly, shouldered. Sculpture absent. Columella with four well developed plaits. Siphonal notch deep, siphonal fasciole weakly developed.

### TYPE SPECIMENS

HOLOTYPE: *Voluta undulata* MHN, No. 38.
HYPOTYPES: *Amoria undulata undulata* NMV, P34267, P6593.

DISTRIBUTION

Mitchellian – Recent (Late Miocene – Recent): Victoria, Tasmania, South Australia, Western Australia (VIC020, VIC044, VIC046, VIC048-049, VIC051, VIC095, VIC101-104, TAS035-039, WA031, WA032, AUS001).

REMARKS

This species is commonly found along the coasts of Queensland, New South Wales, Victoria, Tasmania, South Australia and Western Australia although fossil localities are limited to Victoria, Tasmania and Western Australia.

***Amoria costellifera*** (Tate, 1889)

Plate 1, figs. 5a, b.

1889 *Voluta lirata* Tate, p.130, pl. 2, fig. 4 (non Johnston, 1880).
1889 *Voluta costellifera* Tate, p.131, pl. 2, fig. 8.
1897 *Voluta (Aulica) lirata* Harris, p.103, pl. 4, fig. 12.
1949 *Nannamoria absidata* Cotton, p.192, pl. 14.
1949 *Nannamoria costellifera* Cotton, pl. 14.
1988 *Amoria costellifera* Darragh, p. 226, pl. 6, figs. 4, 8, 10-12. Fig. 11.

DIAGNOSIS

Shell fusiform, gradate-subconical spire. Whorls slightly depressed posteriorly with well developed shoulder. Axial sculpture variable of broad, low costae. Spiral sculpture absent. Columella with four well developed plaits. Siphonal notch wide, siphonal fasciole prominent.

TYPE SPECIMENS

HOLOTYPE: *Voluta costellifera* SAM, T603. *Nannamoria absidata* SAM, T597B.
HYPOTYPES: *Amoria costellifera* NMV, P34261, P61286.

DISTRIBUTION

Janjukian - Mitchellian (Late Oligocene – Late Miocene): Victoria, South Australia (VIC022-023, VIC025, VIC034, VIC038 (TL), VIC041, VIC090, SA001).

REMARKS

The axial sculpture of this species can vary in its development, as well as the sutures and the height of the spire.

***Amoria undulata masoni*** (Tate, 1889)

1889 *Voluta masoni* Tate, p.128, pl. 3, fig. 9.
1897 *Voluta (Amoria) masoni* Harris, p.110, pl. 4, fig. 14a, b.
1899 *Amoria masoni* Cossmann, p.120, pl. 5, fig. 10; pl.6, fig. 7.
1988 *Amoria undulata masoni* Darragh, p. 227, pl. 6, figs. 5, 6, 9.

DIAGNOSIS

Shell ovate-pyriform, subconical spire. Whorls flat, slightly depressed posteriorly on body whorl with well developed shoulder. Sculpture absent, smooth, glazed. Columella with four well developed plaits. Siphonal notch wide.

TYPE SPECIMENS

LECTOTYPE: *Voluta masoni* SAM, T385A.
PARALECTOTYPE: *Voluta masoni* SAM T385B-H.
HYPOTYPES: *Amoria undulata masoni* NMV, P34263.

DISTRIBUTION

Batesfordian - Kalimnan (MIddle Miocene – Pliocene): Victoria (VIC043, VIC060 (TL), VIC061).

REMARKS

This subspecies is characterised by its squat conical spire and ventricose body whorl.

### Genus **NANNAMORIA** Iredale, 1929

1929 *Nannamoria* Iredale, p.181.
1943 *Amoria (Nannamoria)* Wenz, p.1339.
1960 *Paramoria* McMichael, p. 12.
1988 *Nannamoria* Darragh, p.229.

TYPE SPECIES

*Nannamoria amicula* Iredale, 1929 by original designation. Recent, New South Wales.

DIAGNOSIS

Shell small to medium sized, subconical-gradate spire, body whorl often concealing spire whorls. Spiral sculpture weakly developed. Axial sculpture of strong costae, spinose or nodular at shoulder. Columella with four well developed plaits, one or two weaker plaits. Weakly developed siphonal notch and siphonal fasciole.

DISTRIBUTION

Oligocene - Recent: Australia.

REMARKS

This genus shares many characters (both shell and anatomy) with *Notovoluta*, *Amoria* and *Cymbiola*. For a detailed discussion see Darragh (1988).

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Three columellar plaits. ........................................ Go to 2
   Four columellar paits. ........................................ Go to 5

2. Whorls shouldered. ........................................ Go to 3
   Whorls lacking shoulder. ........................................ *ralphi*

3. Shell ventriocse. ........................................ Go to 4
   Shell elongate. ........................................ *fasciculata*

4. Blunt spire. ........................................ *stolida*
   Subconical spire. ........................................ *weldii*

5. Spiral sculpture present. ........................................ Go to 6
   Spiral sculpture absent. ........................................ Go to 7

6. Sutures visible. ........................................ *deplexa*
   Suture concealed by lamella extension. .................... *limbata*

7. Whorls shoulded ............ Go to 8

Whorls lacking shoulder. ............ *cinctuta*

8. Siphonal notch shallow. ............ Go to 9

Siphonal notch deep. ............ *paraboloides*

9. Siphonal fasciole lacking ridge. ............ Go to 10

Siphonal fasciole ridged. ............ *amplexa*

10. Gradate spire. ............ *trionyma*

Blunt spire. ............ *strophodon strophodon*

***Nannamoria ralphi*** (Finlay, 1930)

1888 *Voluta (Volutoconus) conoidea* Tate, p. 176, pl. 13, fig. 9 (non Renier, 1804).
1889 *Voluta conoidea* Tate, p.125.
1899 *Volutoconus conoideus* Cossmann, p.131, pl. 7, fig. 3.
1930 *Volutoconus ralphi* Finlay, p.44.
1988 *Nannamoria ralphi* Darragh, p.235, pl. 9, figs. 1, 4, 5, 8; pl. 10, fig. 3.

DIAGNOSIS

Shell biconic-pyriform, low, blunt spire. Whorls convex. Spiral sculpture of close set threads on posterior whorl slope. Sometimes with nodular sculpture, often absent. Columella with three strong plaits. Siphonal notch and fasciole very weakly developed.

TYPE SPECIMENS

HOLOTYPE: *Voluta conoidea* SAM, T588A.
HYPOTYPES: *Nannamoria ralphi* NMV, P33074, P33076.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC028, VIC038 (TL), VIC098).

REMARKS

The reduced nodular sculpture and lack of variability in morphology define this species.

***Nannamoria fasciculata*** Darragh, 1988

1988 *Nannamoria fasciculata* Darragh, p.233, pl. 7, fig. 10; pl. 10, figs. 9, 11.

DIAGNOSIS

Shell elongate, subgradate spire, grooved sutures. Prominent shoulder on teleoconch whorls. Spiral sculpture absent. Axial sculpture of thin costae, nodular at shoulder. Columella with three well developed plaits.

TYPE SPECIMENS

HOLOTYPE: *Nannamoria fasciculata* NMV, P32915.

PARATYPE: *Nannamoria fasciculata* NMV, P32916.

DISTRIBUTION

Longfordian (Early Miocene): Victoria (VIC021 (TL), VIC011-012).

REMARKS

This species differs from others in the genus in its numerous, irregularly spaced axial costae and elevated, subgradate spire.

***Nannamoria stolida*** (Johnston, 1880)

1880 *Voluta stolida* Johnston, p.36.

1896 *Voluta strophodon* var. *stolida* Pritchard, p. 94.

1967 *Paramoria stolida* Ludbrook, p. 68, pl. 3, figs. 9, 10.

1988 *Nannamoria stolida* Darragh, p.230, pl. 7, figs. 12-15; pl. 9, figs. 2, 3.

DIAGNOSIS

Shell ventricose, short, blunt spire. Whorls shouldered, concave. Axial sculpture of costae on later whorls, fading mid-way on body whorl. Columella with three plaits. Siphonal notch wide, shallow, siphonal fasciole moderately developed.

TYPE SPECIMENS

HOLOTYPE: *Voluta stolida* TM, Z186.

HYPOTYPES: *Nannamoria stolida* NMV, P32910, P2534.

DISTRIBUTION

Longfordian (Early Miocene): Tasmania (TAS001 (TL)).

REMARKS

This species is characterised by its ventricose outline and weakly developed siphonal notch and fasciole. It resembles species of *Cymbiola* and is likely to be ancestral to *Nannamoria strophodon* (McCoy).

***Nannamoria weldii*** (Tenison Woods, 1876)

1876 *Voluta weldii* Tenison Woods, p.24, fig. 2.
1897 *Voluta (Aulica) weldi* (sic) Harris, p. 102.
1913 *Voluta weldii* var. *angustior* Pritchard, p.194, pl.20, figs. 4, 5.
1949 *Cymbiola weldii* Cotton, p.189, pl. 14.
1967 *Paramoria weldii* Ludbrook, p. 68, pl.3, figs. 1, 2.
1988 *Nannamoria weldii* Darragh, p.232, pl. 7, figs, 5, 7; pl. 10, figs. 1, 2.

DIAGNOSIS

Shell elongate-ovate/biconic, subconical spire, ventricose. Whorls sometimes with weakly developed shoulder, weakly developed, elongate nodules at anterior suture, stronger on body whorl. Columella with three plaits. Siphonal canal slightly reflexed dorsally. Weakly developed siphonal notch and strong fasciole.

TYPE SPECIMENS

HOLOTYPE: *Voluta weldii* TM, Z191.
HYPOTYPE: *Voluta weldii* MUGD, 1792.
HOLOTYPE: *Voluta weldii* var. *angustior* MUGD, 1794.

DISTRIBUTION

Johannian - Balcombian (Late Oligocene – Middle Miocene): Tasmania, Victoria (TAS001, TAS002 (TL), VIC005, VIC008-009).

REMARKS

This species is distinguished by its biconic outline, narrow spire and elongate nodules. Variation occurs in different regions.

**_Nannamoria deplexa_** Darragh, 1988

1988 *Nannamoria deplexa* Darragh, p.234, pl. 7, figs. 1, 4; pl. 10, figs. 5, 6; pl. 11, figs. 5, 8.

DIAGNOSIS

Shell pyriform, low, blunt spire. Whorls convex, inflated. Body whorl gently tapered anteriorly. Spiral sculpture of numerous, fine, sinuous threads. Columella glazed with four well developed plaits. Siphonal notch and fasciole very weakly developed.

TYPE SPECIMENS

HOLOTYPE: *Nannamoria deplexa* NMV, P32922.

PARATYPES: *Nannamoria deplexa* NMV, P32923, P32924.

DISTRIBUTION

Janjukian - MItchellian (Late Oligocene – Late Miocene): Victoria (VIC012, VIC014-015, VIC018, VIC087, VIC099, VIC108-110).

REMARKS

This species is ventricose with a very blunt spire which separates it from other species in this genus.

**_Nannamoria limbata_** (Tate, 1888)

Plate 1, figs. 6a, b.

1888 *Voluta (Volutoconus) limbata* Tate, p. 176, pl. 13, fig. 8.
1889 *Voluta limbata* Tate, p.125.
1949 *Volutoconus limbata* Cotton, pl. 15.
1988 *Nannamoria limbata* Darragh, p.235, pl. 7, figs. 8, 9, 11; pl. 9, figs. 10, 11. Fig. 12.

DIAGNOSIS

Shell biconic-subcylindrical, spire short or elevated, sometimes concealed. Sutures concealed by lamella extension. Body whorl convex with weak nodules weakening towards aperture. Spiral sculpture of threads on posterior whorl slope. Columella with four strong plaits. Siphonal notch and fasciole weakly developed.

TYPE SPECIMENS

HOLOTYPE: *Voluta limbata* SAM, T590A.

HYPOTYPES: *Nannamoria limbata* NMV, P33086, P33088.

DISTRIBUTION

Janjukian - MItchellian (Late Oligocene – Late Miocene): Victoria (VIC023, VIC025, VIC035-036, VIC039-041, VIC111, VIC112).

REMARKS

This species shows a great deal of variation usually related to geographic location. It is distinguished by lamella extensions concealing the sutures.

***Nannamoria cinctuta*** Darragh, 1988

1988 *Nannamoria cinctuta* Darragh, p.236, pl. 11, figs. 9-12.

DIAGNOSIS

Shell conical with small, pupiform spire. Spire whorls concealed by succeeding whorls. Body whorl convex. Spiral sculpture absent. Axial costae weakly developed on spire, nodular on body whorl. Columella with four strong plaits.

TYPE SPECIMENS

HOLOTYPE: *Nannamoria cinctuta* NMV, P33081.

PARATYPE: *Nannamoria cinctuta* NMV, P33082.

DISTRIBUTION

Kalimnan – Yatalan (Late Pliocene): Tasmania (TAS036 (TL)).

REMARKS

This species is distinguished by the small, pupiform spire.

***Nannamoria paraboloides*** Darragh, 1988

1988 *Nannamoria paraboloides* Darragh, p.234, pl. 9, figs. 6, 7; pl. 10, figs. 7, 8; pl. 11, figs. 2, 3.

DIAGNOSIS

Shell ovate, low, subconical spire. Concave, shouldered whorls. Anterior spire whorl slope absent or reduced. Axial sculpture of low costae or nodules, weakening towards aperture. Columella with four strong plaits. Deep siphonal notch.

TYPE SPECIMENS

HOLOTYPE: *Nannamoria paraboloides* NMV, P33077.

PARATYPES: *Nannamoria paraboloides* NMV, P33079, P52308.

DISTRIBUTION

Batesfordian - Yatalan (MIddle Miocene – Pliocene): Victoria, Tasmania (VIC043 (TL), VIC044, VIC049, VIC062, VIC107, TAS035-037).

REMARKS

The weakly developed sculpture and subconical spire are distinguishing traits of this species.

***Nannamoria amplexa*** Darragh, 1988

1988 *Nannamoria amplexa* Darragh, p. 232, pl. 7, figs. 2, 3, 6; pl. 9, figs, 9, 12; pl. 10, fig. 12.

DIAGNOSIS

Shell biconic, low spire. Body whorls shouldered, convex at suture. Spiral sculpture absent. Axial sculpture of thin, weakly developed costae, nodular at shoulder. Columella with four well developed plaits. Siphonal notch shallow, fasciole weakly developed, ridged.

TYPE SPECIMENS

HOLOTYPE: *Nannamoria amplexa* NMV, P33069.

PARATYPES: *Nannamoria amplexa* NMV, P33071, P33072.

DISTRIBUTION

Mitchellian - Kalimnan (Pliocene): Victoria (VIC051 (TL), VIC050, VIC105-106).

REMARKS

This species is distinguished by its weakly spinose nodules and weak costae covering the whole shell. The fasciole is bound posteriorly by a ridge which is not as well developed in other species.

***Nannamoria trionyma*** Darragh, 1988

1913 *Voluta weldii* var. *intermedia* Pritchard, p.194, pl. 20. Figs. 2, 3 (non Lahille, 1895: 304).

1988 *Nannamoria trionyma* Darragh, p.233, pl. 11, figs. 1, 4, 6, 7.

DIAGNOSIS

Shell ovate-elongate, low, gradate spire. Convex, shouldered whorls. Spiral sculpture absent. Axial sculpture of thin costae on initial teleoconch whorl, appearing as trihedral nodules on later whorls, weakening towards aperture. Siphonal notch shallow, fasciole weakly developed.

TYPE SPECIMENS

HOLOTYPE: *Nannamoria trionyma* NMV, P32920.

PARATYPE: *Nannamoria trionyma* NMV, P32918.

HOLOTYPE: *Voluta weldii* var. *intermedia* MUGD, 1793.

DISTRIBUTION

Janjukian - Mitchellian (Late Oligocene - Late Miocene): Victoria, South Australia (VIC038 (TL), VIC022, VIC028-029, SA001).

REMARKS

The numerous subspinose tubercles and squat spire distinguish this species. The ovate outline distinguishes this species from the more biconic *N. weldii*.

**_Nannamoria strophodon strophodon_** (McCoy, 1876)

1876 *Voluta strophodon* McCoy, p.25, pl. 37, figs. 2, 3, 4, 4a-c.

1897 *Voluta (Aulica) strophodon* Harris, p.101, pl. 4, figs. 11a, b.

1899 *Vespertilio weldi* Cossmann, p. 118, pl. 4, fig. 23; pl. 6, fig. 8.

1913 *Voluta strophodon* var. *brevispina* Pritchard, p. 194 (non Doncieaux, 1908).

1913 *Voluta strophodon* var. *longispira* Pritchard, p. 194.

1949 *Cymbiola strophodon* Cotton, pl. 15.

1949 *Notovoluta tabulata* Cotton, pl.14 (non Tate, 1888).

1958 *Cymbiola (Cymbiola) tabulata* Ludbrook, p. 74, pl. 6, fig. 2 (non Tate, 1888).

1988 *Nannamoria strophodon strophodon* Darragh, p. 230, pl. 8, figs. 1, 4, 5, 6, 9, 11.

DIAGNOSIS

Shell ovate-biconic, low, blunt spire. Body whorl tapered anteriorly. Teleoconch whorls with prominent shoulder, nodular on body whorl. Columella with four well developed plaits. Siphonal notch shallow, fasciole present.

TYPE SPECIMENS

HOLOTYPE: *Nannamoria strophodon strophodon* NMV, P12154.

PARATYPES: *Nannamoria strophodon strophodon* NMV, P26388, P26389, P12153.

DISTRIBUTION

Janjukian - Yatalan (Late Oligocene - Pliocene): Victoria, South Australia (VIC013 (TL), VIC014, VIC018, VIC022-023, VIC025, VIC027-030, VIC033-036, VIC038, VIC040-041, VIC043, VIC082, VIC087, VIC098, SA001-002, SA031-032, SA044-048).

REMARKS

There is a lot of variation between specimens of this subspecies from different localities, generally associated with elevation of the spire.

### Genus **NOTOVOLUTA** Cotton, 1946

1946 *Notovoluta* Cotton, p.15.

1988 *Notovoluta* Darragh, p.217

TYPE SPECIES

*Voluta kreuslerae* Angas, 1865 by original designation. Recent, South Australia.

DIAGNOSIS

Shell fusiform, elongate-ovate. Spire subconical-gradate, shouldered. Domed protoconch. Spiral sculpture of fine threads. Axial sculpture of strong costae, tubercles or absent. Outer lip slightly reflexed dorsally. Columella with four strong plaits. Siphonal notch shallow, wide, fasciole moderately developed.

DISTRIBUTION

Eocene - Recent: Australia.

REMARKS

This genus is characterised by the domed protoconch and fine threads on the first and second spire whorls. See Darragh (1988) for discussion on taxonomic position.

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Spiral sculpture absent. .......... Go to 2
   Spiral sculpture present. .......... Go to 4

2. Whorls shouldered. .......... Go to 3
   Whorls lacking shoulder. .......... *saginata*

3. Axial sculpture nodulose. .......... *pseudolirata*
   Axial sculpture subspinose on shoulder. .......... *tabulata*

4. Columella with three plaits. .......... Go to 5
   Columella with four plaits. .......... Go to 6

5. Axial sculpture present. .......... Go to 6
   Axial sculpture absent. .......... *differta*

6. Axial sculpture nodular. .......... *cathedralis*
   Axial sculpture of thin riblets. .......... *linigera*

| | | |
|---|---|---|
| 7. | Siphonal notch absent. | *variculifera* |
| | Siphonal notch shallow. | Go to 8 |
| 8. | Axial sculpture absent. | *ellipsoidea* |
| | Axial sculpture present. | Go to 9 |
| 9. | Spire gradate. | *capitonica* |
| | Spire elongate and narrow. | *lintea* |

***Notovoluta saginata*** (Finlay, 1880)

1880 *Voluta lirata* Johnston, p.37 (non Brocchi, 1814).
1888 *Voluta allporti* Johnston, pl.30, fig. 10 (non Johnston, 1880).
1896 *Voluta maccoyi* Pritchard, p. 95 (non Tenison Woods, 1877).
1930 *Notopeplum saginatum* Finlay, p.45.
1988 *Notopeplum saginatum* Darragh, p.223, pl.2, fig.2; pl.5, fig. 8.

DIAGNOSIS

Shell fusiform, elongate, conical spire. Spire whorls slightly depressed posteriorly. Axial sculpture of sinuous riblets on spire whorls. Body whorl ventricose, rapidly tapered anteriorly. Columella with four strong plaits. Shallow siphonal notch, prominent fasciole.

TYPE SPECIMENS

HOLOTYPE: *Notopeplum saginatum* TM, Z1072.
HYPOTYPE: *Notopeplum saginatum* MUGD, 1795.
HOLOTYPE: *Voluta lirata* TM, Z185.

DISTRIBUTION

Longfordian (Early Miocene): Tasmania (TAS001, TAS002).

REMARKS

This species is distinguished by the ventricose body whorl, elongate spire and axial riblets.

***Notovoluta pseudolirata*** (Tate, 1888)

1888 *Voluta pseudolirata* Tate, p.176, pl. 13, fig. 6.

1897 *Voluta (Aulica) pseudolirata* Harris, p. 104.

1949 *Notovoluta pseudolirata* Cotton, pl.14.

DIAGNOSIS

Shell fusiform, elongate. Whorls shouldered. Spiral sculpture absent. Axial sculpture variable. Thin costae on initial spire whorls, nodular on later whorls. Siphonal notch deep, siphonal fasciole well developed.

TYPE SPECIMENS

HOLOTYPE: *Voluta pseudolirata* SAM, T608C.

HYPOTYPE: *Notovoluta pseudolirata* NMV, P32211.

DISTRIBUTION

Janjukian - Recent (Late Oligocene – Recent): Victoria, Western Australia (VIC022-023, VIC025, VIC029-030, VIC035, VIC038 (TL), VIC041, VIC088-089, VIC098, WA017, WA020, WA033).

REMARKS

Traces of colour can be seen in specimens from Muddy Creek (VIC038) and Fossil Beach (VIC022). For a full discussion on this species see Wilson (1972).

***Notovoluta tabulata*** (Tate, 1888)

1888 *Voluta tabulata* Tate, p.176, pl. 13, fig. 3.

1988 *Notovoluta tabulata* Darragh, p.220, pl. 4, figs. 1, 6, 8, 10; Fig. 7.

DIAGNOSIS

Shell fusiform, low, gradate spire, shouldered whorls. Spiral sculpture absent. Axial sculpture of sinuous costae, subspinose on shoulder, absent on posterior whorl slope, fading towards middle of anterior whorl slope. Columella with four strong plaits. Siphonal notch wide.

TYPE SPECIMENS

HOLOTYPE: *Voluta tabulata* SAM, T611A.

HYPOTYPE: *Voluta tabulate* SAM, T5740a-b.

DISTRIBUTION

Mitchellian (Late Miocene): New South Wales, South Australia (NSW037 (TL), SA002).

REMARKS

The low spire and subspinose costae define this species.

***Notovoluta differta*** Darragh, 1988

1988 *Notovoluta differta* Darragh, p.223, pl. 4, figs. 11-14.

DIAGNOSIS

Shell ovate, rapidly tapered spire. Whorls depressed posteriorly, convex anteriorly. Axial sculpture absent. Spiral sculpture of closely spaced threads over whole spire and posterior of body whorl. Columella with three strong plaits. Siphonal notch shallow, fasciole present.

TYPE SPECIMENS

HOLOTYPE: *Notovoluta differta* NMV, P32221.

PARATYPE: *Notovoluta differta* NMV, P32222.

DISTRIBUTION

Janjukian - Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC013, VIC016 (TL), VIC087, VIC109).

REMARKS

The ovate shape and lack of elongate nodules separate this species from others in the genus.

***Notovoluta cathedralis*** (Tate, 1888)

1888 *Voluta cathedralis* Tate, p.176, pl. 13, fig. 10.
1897 *Scaphella (Eopsephia) cathedralis* Harris, p. 117.
1949 *Notovoluta cathedralis* Cotton, pl. 15.

DIAGNOSIS

Shell elongate. High, tapered spire. Spiral sculpture of fine threads on spire whorls and on posterior third of whorls. Axial sculpture of elongate nodules on penultimate and body whorls. Siphonal notch wide.

TYPE SPECIMENS

HOLOTYPE: *Voluta cathedralis* SAM, T596B.

HYPOTYPE: *Notovoluta cathedralis* NMV, P32213.

DISTRIBUTION

Janjukian - Mitchellian (Late Oligocene – Late Miocene): Victoria, South Australia (VIC038 (TL), VIC027, SA001).

REMARKS

This species is distinguished by the elongate nodules and the spiral threads present on the posterior whorl slope.

***Notovoluta linigera*** Darragh, 1988

1988 *Notovoluta linigera* Darragh, p.223, pl. 3, figs. 3, 4, 6, 10. Fig. 10.

DIAGNOSIS

Shell ovate-biconic, squat. Spire whorls depressed posteriorly. Body whorls gently convex, depressed posteriorly. Axial sculpture of thin riblets. Spiral sculpture of thin threads over spire whorls and posterior of body whorl. Columella with three strong plaits.

TYPE SPECIMENS

HOLOTYPE: *Notovoluta linigera* NMV, P32216.

PARATYPE: *Notovoluta linigera* NMV, P32218.

DISTRIBUTION

Longfordian - Balcombian (Early – Middle Miocene): Victoria (VIC021 (TL), VIC011, VIC008).

REMARKS

The prominent spiral threads and axial riblets distinguish this species from others in the genus. Spiral sculpture is somewhat variable.

**_Notovoluta variculifera_** Darragh, 1988

Plate 2, figs. 1a, b.

1988 *Notovoluta variculifera* Darragh, p.218, pl.3, figs. 7, 9, 13, 14.

DIAGNOSIS

Shell fusiform, convex whorls. Teleoconch whorls convex. Spiral sculpture of fine threads over whole shell. Weakly developed axial costae on first teleoconch whorl. Outer lip thickened. Columella with four plaits. Siphonal notch and fasciole absent.

TYPE SPECIMENS

HOLOTYPE: *Notovoluta variculifera* NMV, P48599.

PARATYPE: *Notovoluta variculifera* NMV, P48600.

DISTRIBUTION

Johannian – Willungan (Late Eocene – Early Oligocene): Victoria (VIC091 (TL), VIC002).

REMARKS

The narrow, small shell, presence of axial costae and the absence of the siphonal notch and fasciole characterise this species.

**_Notovoluta ellipsoidea_** (Tate, 1888)

1888 *Voluta ellipsoidea* Tate, p.176, pl. 13, fig. 4.
1897 *Voluta (Aulica) ellipsoidea* Harris, p. 105.
1922 *Voluta (Aulica) sexuaplicata* Chapman, p.15, pl. 3, fig. 24.
1949 *Ericusa ellipsoidea* Cotton, pl. 15.
1958 *Ericusa (Ericusa) ellipsoidea* Ludbrook, p.76.
1988 *Notovoluta ellipsoidea* Darragh, p.220, pl.2, fig. 3; pl. 3, fig. 2; pl. 5, figs. 4, 5.

DIAGNOSIS

Shell fusiform, convex whorls. Whorls gently convex, slightly impressed at posterior suture. Axial sculpture absent. Spiral sculpture of fine threads over whole shell. Apertural notch at posterior suture. Columella with four strong plaits. Siphonal notch shallow, wide, fasciole prominent.

TYPE SPECIMENS

HOLOTYPE: *Voluta ellipsoidea* SAM, T601C.

HYPOTYPE: *Voluta ellipsoidea* SAM, T601A.

HOLOTYPE: *Voluta (Aulica) sexuaplicata* NMV, P13250.

DISTRIBUTION

Longfordian – Yatalan (Early Miocene – Pliocene): Victoria, South Australia (VIC038 (TL), VIC113, SA032).

REMARKS

This species is defined by its lack of axial sculpture and the fine, numerous spiral threads that cover the whole shell.

***Notovoluta capitonica*** Darragh, 1988

1988 *Notovoluta capitonica* Darragh, p.218, pl.3, figs. 8, 11, 12, 15; pl. 27, figs. 1, 4.

DIAGNOSIS

Shell elongate, gradate spire. Spire whorls shouldered. Axial costae on initial spire whorls. Spiral sculpture of fine threads over whole shell. Columella with four strong plaits. Siphonal notch unpreserved, fasciole well developed.

TYPE SPECIMENS

HOLOTYPE: *Notovoluta capitonica* NMV, P126803.

PARATYPES: *Notovoluta capitonica* NMV, P32209, P32210.

DISTRIBUTION

Johannian - Aldingan (Late Eocene): Victoria, South Australia (VIC092 (TL), SA034).

REMARKS

This species is distinguished by the axial costae on the early spire whorls and the spiral sculpture which covers the whole shell.

### ***Notovoluta lintea*** (Tate, 1889)

1889 *Voluta lintea* Tate, p.129, pl. 3, figs, 1a, b.
1949 *Notovoluta lintea* Cotton, pl. 15.

DIAGNOSIS

Shell elongate-ovate, tall, narrow spire. Later whorls depressed before posterior suture. Sutures grooved. Spiral sculpture of threads, weakening on body whorl. Axial sculpture of low, elongate nodules on later whorls. Columella with four strong plaits. Shallow siphonal notch.

TYPE SPECIMENS

HOLOTYPE: *Voluta lintea* SAM, T600.
PARATYPE: *Notovoluta lintea* NMV, P32219.

DISTRIBUTION

Batesfordian (Middle Miocene): South Australia (SA001 (TL)).

REMARKS

This species is distinguished by the low, elongate nodules and slender outline.

## Subfamily **ZIDONINAE** H. & A. Adams, 1853

1853 Zidoninae H. & A. Adams, p. 618.
1954 Alcithoninae Pilsbry & Olsson, p.17.
1988 Zidoninae H. & A. Adams, Darragh, p. 237.

DIAGNOSIS

Shell subfusiform, elevated spire. Body whorl often tumid, impressed anteriorly. Axial sculpture of costae, weak or strong, often nodular or spiny at shoulder. Columella with two or more well developed plaits. Siphonal canal short, deep siphonal notch, well developed fasciole. Radular ribbon uniserial, rachidian tooth tricuspid.

DISTRIBUTION

Palaeocene - Recent. Southern Hemisphere.

### REMARKS

Diagnostic characters of this subfamily are based on soft tissue anatomy and radula often making it difficult to assign fossil species correctly. Most fossils are assigned to this subfamily based on similarities with living species whose taxonomic position are confidently known. The subfamily distribution in both Cenozoic and Recent seas is mostly circum-Antarctic with two principal northern extensions into South America and into Australia, New Zealand, Indonesia and the Philippines.

## KEY TO GENERA FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:

| | | |
|---|---|---|
| 1. | Shell broadly fusiform. | Go to 2 |
| | Shell broadly ovate. | Go to 4. |
| 2. | Columella with three plaits. | Go to 3 |
| | Columella with four plaits. | *Alcithoe* |
| 3. | Elongate spire. | *Ericusa* |
| | Gradate spire. | *Livonia* |
| 4. | Columella with three plaits. | *Notopeplum* |
| | Columella with four to five plaits. | *Cymbiola* |

## Genus **ALCITHOE** H. & A. Adams, 1853

1853 *Alcithoe* H. & A. Adams, p.618.

### TYPE SPECIES

*Voluta pacifica* Perry, 1810 by subsequent designation (Cossmann, 1899). New Zealand, Recent.

### DIAGNOSIS

Shell ovate-fusiform, large protoconch. Whorls convex and shouldered. Sculpture absent or axially ribbed. Columella with four plaits.

DISTRIBUTION

?Eocene – Recent: New Zealand, Australia, ?Indo-Pacific.

REMARKS

This genus is in desperate need of a complete revision with a clear genus description, distribution data and confirmation of the type species. There is very little information available regarding the genus itself despite extensive descriptions of species, particularly in New Zealand. As it is not within the scope of this study to revise the complete genus all species that have been assigned to it by Darragh (1988) remain so.

**KEY TO SUBGENERA FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Thickened aperture, deep siphonal notch. ...................................... *Alcithoe*
2. Elongate outline, strong axial sculpture. ....................................... *Waihaoia*

### Subgenus **ALCITHOE** H. & A. Adams, 1853

1853 *Scaphella (Alcithoe)* H. & A. Adams, p. 164.
1858 *Scapha (Alcithoe)* H. & A. Adams, p. 617.
1871 *Voluta (Alcithoe)* Crosse, p. 293.
1899 *Fulguraria (Alcithoe)* Cossmann, p. 132.
1926 *Alcithoe* Marwick, p. 260-270.
1926 *Waihaoia (Palomelon)* Finlay, p.432.
1929 *Alcithoe (Alcithoe)* Thiele, p. 348.
1937 *Alcithoe (Leporemax)* Iredale, p. 105.
1937 *Alcithoe (Carolluta)* Iredale, p. 105.
1937 *Gilvostia* Iredale, p. 105.
1943 *Alcithoe (Carolluta)* Wenz, p. 1345.
1943 *Alcithoe (Gilvostia)* Wenz, p. 1345.
1988 *Alcithoe (Alcithoe)* Darragh, p.242.

TYPE SPECIES

*Voluta pacifica* Perry, 1910 by subsequent designation (Cossman, 1899) = *Voluta arabica* Gmelin, 1791. Recent, New Zealand.

DIAGNOSIS

Medium to large sized shell, elongate, abruptly tapered anteriorly. Axial sculpture of costae of elongate nodules. Spiral sculpture absent. Aperture wide, elongate, thickened and reflexed at outer lip. Columella with four or five well developed plaits. Deep siphonal notch.

DISTRIBUTION

Miocene - Recent: New Zealand, Australia.

REMARKS

Distribution of this subgenus in Australia is limited to only two species and it likely to reflect the outermost distribution of the subgenus extending from New Zealand where the subgenus is much more diverse.

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Convex whorls, very weakly developed sculpture.................... *macrocephala*
2. Very smooth shell.......................................................................... *orphanata*

***Alcithoe (Alcithoe) macrocephala*** (Finley, 1927)

1889 *Voluta capitata* Tate, p.127, pl. 2, figs. 3a, b (non Perry, 1811).
1927 *Scaphella macrocephala* Finlay, p.513.
1988 *Alcithoe (Alcithoe) macrocephala* Darragh, p.243, pl. 13, figs. 6-8. Fig. 18.

DIAGNOSIS

Shell fusiform, abruptly tapered spire. Tumid body whorl. Sculpture absent except for weak spiral threads on initial teleoconch whorl. Whorls convex at anterior. Columella with four plaits, weakest at anterior. Wide, deep siphonal notch. Siphonal fasciole well developed.

TYPE SPECIMENS

HOLOTYPE: *Voluta capitata* SAM, T389.
HYPOTYPE: *Alcithoe (Alcithoe) macrocephala* SAM, P5755.

DISTRIBUTION

Batesfordian – Mitchellian (Middle - Late Miocene): Victoria to New South Wales (VIC043, NSW037 (TL)).

REMARKS

This species is characterised by its convex whorls and paucity of sculpture over the shell.

### ***Alcithoe (Alcithoe) orphanata*** Darragh, 1988

1988 *Alcithoe (Alcithoe) orphanata* Darragh, p.243, pl. 13, figs. 9-12. Fig. 20.

DIAGNOSIS

Shell fusiform, conical spire. Whorls weakly convex anteriorly. Spiral sculpture absent. Axial costae weakly developed on middle whorls. Aperture narrow, inner lip with thick callus. Columella with five plaits. Wide, deep siphonal notch. Siphonal fasciole well developed.

TYPE SPECIMENS

HOLOTYPE: *Alcithoe (Alcithoe) orphanata* NMV, P37635.

PARATYPE: *Alcithoe (Alcithoe) orphanata* NMV, P37636.

DISTRIBUTION

Kalimnan – Yatalan (Late Pliocene): Tasmania (TAS034 (TL), TAS035).

REMARKS

The most remarkable character of this shell is its unique smoothness that is not seen in other taxa.

## Subgenus **WAIHAOIA** Marwick, 1926

1926 *Waihaoia* Marwick, p. 274.

1988 *Waihaoia* Marwick, Darragh, p. 238.

### TYPE SPECIES

*Waihaoia allani* Marwick, 1926 by original designation. Eocene, McCulloughs Bridge, New Zealand.

### DIAGNOSIS

Small to medium sized shell, very elongate, high spired. Well developed axial costae, prominent shoulder on body whorl and often spire whorls. Aperture narrow, elongate with slight reflex on outer lip. Very shallow siphonal notch, siphonal fasciole weakly developed or absent.

### DISTRIBUTION

Eocene - Miocene: Australia, New Zealand.

### REMARKS

This subgenus is characterised by its very elongate outline and well developed axial costae.

### **KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Siphonal fasciole weakly developed. ............ Go to 2
   Siphonal fasciole strong developed. ............ *sarissa*
   Siphonal fasciole absent. ............ *cribrosa*

2. Spiral sculpture well developed. ............ Go to 3
   Spiral sculpture weakly developed/absent. ............ *pagodoides pagodoides*

3. Spiral sculpture over whole shell. ............ Go to 4
   Spiral sculpture on spire and posterior of body whorl. ............ Go to 5

4. Median row of nodules. ............ *pagodoides sorcula*
   Nodules absent on spire. ............ *neglectoides*

5. Axial costae on body whorl only. ............ *pueblensis*
   Axial costae on whole shell. ............ *tateana*

### ***Alcithoe (Waihaoia) sarissa*** (Tate, 1889)

1889 *Voluta sarissa* Tate, p.129, pl. 2, figs. 1a, b.

1897 *Scaphella (Eopsephia) sarissa* Harris, p.116, pl.4, figs. 16a, b.

1949 *Notovoluta sarissa* Cotton, pl. 14.

1988 *Alcithoe (Waihaoia) sarissa* Darragh, p.241, pl. 13, fig. 5. Pl. 14 figs. 5, 11. Fig. 19.

#### DIAGNOSIS

Shell narrowly fusiform, slender, turreted spire. Initial whorls flat, becoming more convex medially. Axial costae over whole shell, extending suture to suture except on anterior of body whorl. Spiral sculpture of thin lirae over spire and posterior of body whorl. Columella of four to five well developed plaits, more poorly developed at anterior. Siphonal canal relfexed dorsally. Wide, shallow siphonal notch, siphonal fasciole strongly developed.

#### TYPE SPECIMENS

LECTOTYPE: *Voluta sarissa* SAM, T578A.

PARALECTOTYPES: *Voluta sarissa* SAM, T578B-G.

HYPOTYPES: *Alcithoe (Waihaoia) pueblensis* NMV, P38303, P38301.

#### DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria, South Australia (VIC008, VIC011, VIC013, VIC015, VIC021-022, VIC025-028, VIC031, VIC034, VIC038 (TL), VIC041, VIC081, VIC094, SA001).

#### REMARKS

This species closely resembles *A. (W.) pueblensis* but is far more elongate and slender. The species' well developed siphonal fasciole is very unusual for this subgenus and some authors may question this species' assignment to *Alcithoe (Waihaoia)*. However, enough of the shell morphology is consistent with other species in this subgenus to merit its inclusion in this subgenus.

### ***Alcithoe (Waihaoia) cribrosa*** (Tate, 1889)

Plate 2, figs. 2a, b.

1889 *Voluta cribrosa* Tate, p.129, pl. 3, fig. 8.

1988 *Alcithoe (Waihaoia) cribrosa* Tate, Darragh, p.238, pl. 13, figs. 1-4.

DIAGNOSIS

Shell fusiform, high spired. Weakly shouldered on body whorls. Thin spiral sculpture over whole shell. Axial costae low, well defined, extending from suture to suture except on body whorl, absent towards aperture. Columella with four plaits, weakest at anterior. Wide, shallow siphonal notch. Siphonal fasciole absent.

TYPE SPECIMENS

LECTOTYPE: *Voluta cribrosa* SAM, T605A (crushed).

PARALECTOTYPES *Voluta cribosa* SAM, T605B-D.

HYPOTYPES: *Alcithoe (Waihaoia) cribrosa* NMV, P348824 (crushed), P34825.

DISTRIBUTION

Johannian - Willungan (Late Eocene – Early Oligocene): Victoria, South Australia (VIC002, VIC091, SA034 (TL)).

REMARKS

The specimens used by Tate (1889b) have been crushed making comparison with undeformed specimens more difficult. Many fossil specimens from the Blanche Point locality have suffered from some degree of deformation resulting in incomplete or flattened specimens making comparisons more difficult.

***Alcithoe (Waihaoia) pagodoides pagodoides*** (Tate, 1888)

1888 *Voluta pagodoides* Tate, p.176, pl. 13, fig. 7.

1897 *Scaphella (Eopsephia) pagodoides* Harris, p.117.

1949 ?*Notovoluta pagodoides* Cotton, pl. 14.

1988 *Alcithoe (Waihaoia) pagodoides pagodoides* Tate, Darragh, p.239, pl. 12, figs. 1, 4, 7, 10, 13. Fig. 17.

DIAGNOSIS

Shell fusiform. Narrow, turreted spire with median nodules. Sculpture of median row of well defined nodules, appearing as thin axial costae on first teleoconch whorl. Spiral sculpture absent or weakly developed on second and third spire whorls. Columella with four well developed and sometimes weaker fifth plaits. Siphonal canal dorsally reflexed with shallow siphonal notch. Siphonal fasciole as weak cord.

TYPE SPECIMENS

HOLOTYPE: *Voluta pagodoides* SAM, T610B.

HYPOTYPES: *Alcithoe (Waihaoia) pagodoides pagodoides* NMV, P34821, P34822.

DISTRIBUTION

Johannian – Janjukian (Late Eocene – Late Oligocene): Victoria, South Australia (VIC002, VIC092-093, SA034 (TL), SA035-038).

REMARKS

The presence of shoulder nodules and the absence/weak development of spiral sculpture separate this subspecies from all others. The subspecies can vary in the elongation of the spire and the development of the nodules between different geographic areas but there is enough common morphology to assign all these variants to one subspecies (Darragh, 1988).

***Alcithoe (Waihaoia) pagodoides sorcula*** Darragh, 1988

1988 *Alcithoe (Waihaoia) pagodoides sorcula* Darragh, p.239, pl. 12, figs. 2, 3, 6, 8.

DIAGNOSIS

Shell small, elongate-fusiform. Nodules as in *A. (W.) pagodoides pagodoides*. Spiral sculpture of closely spaced lirae over whole shell. Columella of four well developed plaits, occasional weaker plaits in between. Very shallow siphonal notch, siphonal fasciole very weakly developed.

TYPE SPECIMENS

HOLOTYPE: *Alcithoe (Waihaoia) pagodoides sorcula* NMV, P37630.

PARATYPE: *Alcithoe (Waihaoia) pagodoides sorcula* NMV, P37631.

DISTRIBUTION

Janjukian (Late Oligocene): Victoria (VIC005 (TL), VIC007).

REMARKS

This subspecies is distinguished from *A. (W.) pagodoides pagodoides* by its smaller size and the presence of strongly developed spiral lirae across the whole shell.

***Alcithoe (Waihaoia) neglectoides*** Darragh, 1988

1988 *Alcithoe (Waihaoia) neglectoides* Darragh, p.240, pl. 12, figs. 5, 9, 11, 12.

DIAGNOSIS

Shell elongate-fusiform, narrowly-turreted spire. Axial nodules on body whorl, sometimes present on penultimate whorl. Spiral sculpture of closely spaced lirae over whole shell. Columella of four well developed plaits, fith denticle weakly developed, occasional weaker plaits in between. Siphonal canal dorsally reflexed with shallow siphonal notch, siphonal fasciole very weakly developed.

TYPE SPECIMENS

HOLOTYPE: *Alcithoe (Waihaoia) neglectoides* NMV, P37628.

PARATYPE: *Alcithoe (Waihaoia) neglectoides* NMV, P37627.

DISTRIBUTION

Janjukian (Late Oligocene): Victoria (VIC005 (TL)).

REMARKS

This species is characterised by the flat whorls of the turreted spire and the absence of nodules on the spire whorls. It shares most characters with *A. (W.) pagodoides pagodoides* but enough variation exists to classify it as a separate species (see Darragh (1988) for discussion).

***Alcithoe (Waihaoia) pueblensis*** (Pritchard, 1898)

1898 *Voluta pueblensis* Pritchard, p.109, pl.8, fig. 7.

1988 *Alcithoe (Waihaoia) pueblensis* Darragh, p.241, pl. 14, figs. 1-3, 8-10. Fig. 15.

DIAGNOSIS

Shell elongate-fusiform, tall, turreted spire, weakly developed shoulder on body whorl. Axial costae on body whorl, extending to approximately midpoint. Spiral sculpture of closely spaced lirae over spire and posterior of body whorl. Columella of four well developed plaits. Wide, shallow siphonal notch, siphonal fasciole very weakly developed.

TYPE SPECIMENS

HOLOTYPE: *Voluta pueblensis* MUGD, 1806.

HYPOTYPES: *Alcithoe (Waihaoia) pueblensis* NMV, P34842, P12773.

DISTRIBUTION

Janjukian (Late Oligocene): Victoria (VIC005 (TL)).

REMARKS

The tall turreted spire distinguishes this species. On the basis of shell morphology *A. (W.) pueblensis* appears to be closely related to *A. (W.) tateana* and *A. (W.) sarissa* (which may succeed it in younger sediments) but differences in shoulder development and shell sculpture are used to define these species.

***Alcithoe (Waihaoia) tateana*** (Johnston, 1880)

| | |
|---|---|
| 1880 | *Voluta tateana* Johnston, p.37. |
| 1949 | *Notovoluta tateana* Cotton, pl. 14. |
| 1988 | *Alcithoe (Waihaoia) tateana* Darragh, p.242, pl. 14, figs. 4, 6, 7, 12. |

DIAGNOSIS

Shell elongate-fusiform, high spired, strongly shouldered body whorl. Axial costae well developed over posterior of spire whorls and to middle of body whorl. Spiral sculpture of thin lirae over posterior of spire whorls and shoulder of body whorl. Columella of four plaits, more poorly developed at anterior. Wide siphonal notch, siphonal fasciole weakly developed.

TYPE SPECIMENS

HOLOTYPE: *Voluta tateana* TM, Z127.

HYPOTYPES: *Voluta tateana* SAM, T388B; *Alcithoe (Waihaoia) tateana* NMV, P2587.

DISTRIBUTION

Longfordian (Early Miocene): Tasmania (TAS001-002).

REMARKS

This species is distinguished by the tapered spire and large body whorl. Specimens are often abraided resulting in a loss of spiral sculpture (Darragh, 1988).

### Genus **ERICUSA** H. & A. Adams, 1858

1858 *Zidona (Ericusa)* H. & A. Adams, p. 619.
1915 *Ericusa* Hedley, p. 724.
1929 *Alcithoe (Ericusa)* Theile, p. 348.
1929 *Mesericusa* Iredale, p. 181.
1943 *Alcithoe (Ericusa)* Wenz, p. 1345.
1943 *Alcithoe (Mesericusa)* Wenz, p. 1347.
1988 *Ericusa* Darragh, p.244.

TYPE SPECIES

*Voluta fulgetrum* G. B. Sowerby, 1825 by subsequent designation (Cotton & Godfrey, 1932) = *Voluta arabica* Gmelin, 1791. Recent, South Australia.

DIAGNOSIS

Medium to large sized shell, fusiform, elongate spire. Axial sculpture often absent, sometimes ribbed or nodular. Spiral sculpture weakly developed. Aperture large, elongate, and thickened at outer lip. Columella with three well developed plaits. Wide siphonal notch, siphonal fasciole absent.

DISTRIBUTION

Eocene - Recent: Australia.

REMARKS

For discussion of generic placement and synonymies see Darragh (1988).

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Shell fusiform. .......... Go to 2
   Shell ovate-fusiform. .......... *fulgetroides*

2. Axial sculpture absent. .......... Go to 3
   Axial sculpture present. .......... Go to 4

3. Spiral sculpture absent. .......... *sowerbyi sowerbyi*
   Spiral sculpture on initial teleoconch whorls. .......... *sowerbyi pellita*

4. Outer lip extended. .......... Go to 5
   Outer lip not extended. .......... Go to 6

5. Axial sculpture on initial teleoconch whorls only. .......... *macroptera*
   Axial sculpture on whole spire. .......... *atkinsoni*

6. Blunt spire. .......... *ancilloides*
   Spire whorls flattened. .......... *hamiltonensis*

***Ericusa fulgetroides*** (Pritchard, 1898)

1898 *Voluta fulgetroides* Pritchard, p.105, pl. 7, fig. 4.
1949 *Ericusa fulgetroides* Cotton, p. 186.
1988 *Ericusa fulgetroides* Darragh, p.249, pl. 16, figs. 6, 8; pl. 18, figs. 1, 6.

DIAGNOSIS

Shell ovate-fusiform, convex whorls, slightly grooved sutures. Spiral sculpture of thin threads on intial teleoconch whorls. Body whorl with growth striae. Columella with three plaits. Wide, deep siphonal canal.

TYPE SPECIMENS

HOLOTYPE: *Voluta fulgetroides* MUGD, 1804.
HYPOTYPE: *Ericusa fulgetorides* NMV, P7843.

DISTRIBUTION

Mitchellian - Kalimnan (Late Miocene - Pliocene): Victoria (VIC060 (TL), VIC061).

REMARKS

The evenly convex whorls and slightly grooved sutures separate this species from related living and fossil taxa.

***Ericusa sowerbyi sowerbyi*** (Kiener, 1839)

| | |
|---|---|
| 1822 | *Voluta fusiformis* Swainson, p.11 (non Brocchi, 1814). |
| 1839 | *Voluta sowerbyi* Kiener, p.47, pl. 50, fig. 2.. |
| 1929 | *Mesericusa sowerbyi perspecta* Iredale, p. 181, pl. 41, fig. 9. |
| 1942 | *Alcithoe fusiformis* Smith, p. 32, pl. 20, fig. 137. |
| 1954 | *Ericusa sowerbyi porcellana* Jackson, p.37. |
| 1960 | *Mesericusa sowerbyi* McMichael, p.5, fig. 1B (radula). |
| 1961 | *Mesericusa stokes* Cotton, (1). |
| 1970 | *Ericusa (Mesericusa) sowerbyi* Weaver & du Pont, p. 53, pl. 20, figs. E-H. |
| 1970 | *Ericusa (Mesericusa) stokesi* Weaver & du Pont, p. 54, pl. 20, figs. A-B. |
| 1988 | *Ericusa sowerbyi sowerbyi* Darragh, p.246, pl. 16, figs. 1-3, 7; pl.17, fig. 3; pl.18, fig. 8. |

DIAGNOSIS

Shell fusiform, flatly convex whorls. Spiral and axial sculpture absent. Body whorl gently tapered at anterior.  Aperture wide. Columella of three plaits. Very wide siphonal canal, siphonal fasciole absent.

TYPE SPECIMENS

HYPOTYPES: *Ericusa sowerbyi sowerbyi* NMV, P 41732. *Mesericusa stokes* SAM, D14625.

DISTRIBUTION

Mitchellian – Recent (Late Miocene – Recent): Queensland, South Australia and Victoria and Tasmania (QLD021, SA009, VIC020, VIC046-049, VIC095-096, TAS033, TAS035).

REMARKS

The exceptionally plain appearance of this species makes identifying diagnostic characteristics particularly difficult. Protoconch size and colour (on living species) are variable and do not provide a useful diagnostic feature.

***Ericusa sowerbyi pellita*** (Johnston, 1880)

| | |
|---|---|
| 1880 | *Voluta pellita* Johnston, p.36. |
| 1880 | ?*Voluta allporti* Johnston, p.35. |
| 1896 | *Voluta halli* Pritchard, p. 101, pl. 30, fig. 2. |
| 1967 | *Ericusa (Mesericusa) pellita* Ludbrook, p. 67, pl. 4, figs. 9, 10.. |
| 1988 | *Ericusa sowerbyi pellita* Darragh, p.244, pl. 15, figs. 7, 8; pl. 16, figs. 4, 5; pl.17, figs. 4, 5; pl.18, figs. 4, 5. Fig. 21. |

DIAGNOSIS

Shell fusiform, convex whorls. Spiral sculpture of thin lirae over first and second teleoconch whorls. Majority of shell smooth, sculpture absent, gently convex whorls. Aperture wide. Columella of three plaits. Wide siphonal canal.

TYPE SPECIMENS

HOLOTYPE: *Voluta pellita* TM, Z156.

HOLOTYPE: *Voluta halli* MUGD, 1789.

HYPOTYPES: *Ericusa sowerbyi pellita* NMV, P41709, P 41710.

DISTRIBUTION

Janjukian - Mitchellian (Late Oligocene – Late Miocene): Victoria, Tasmania (VIC005, VIC008, VIC011, VIC013, VIC016, VIC087, VIC093, TAS001 (TL), TAS002).

REMARKS

Specimens from Tasmania are far rarer than those from Victoria and there is some discussion to be had regarding the inclusion of *V. halli* as a synonym (see Darragh, 1988). The upper stratigraphic limit of this taxon is not well constrained due to the inclusion of fragmented or juvenile specimens higher in the stratigraphic column that cannot be assigned to this species with complete confidence.

***Ericusa macroptera*** (McCoy, 1866)

1866 *Voluta macroptera* McCoy, p.375.

1949 *Pterospira macroptera* Cotton, pl. 15.

1988 *Ericusa macroptera* Darragh, p.247, pl. 15, figs. 1, 2; pl.17, figs. 1, 2; pl.18, fig. 3. Fig. 23.

DIAGNOSIS

Shell fusiform, tumid body whorl and extended outer lip. Axial sculpture of weakly developed costae on intial teleoconch whorls. Spiral sculpture of thin threads on spire whorls. Outer lip extended into wing-like structure. Siphonal notch wide, triangular. Siphonal fasciole absent.

TYPE SPECIMENS

LECTOTYPE: *Ericusa macroptera* NMV, P 12379.

PARALECTOTYPES: *Ericusa macroptera* NMV, P 12378, P12381, P12380.

HYPOTYPES: *Ericusa macroptera* NMV, P 48588, P61287.

DISTRIBUTION

Janjukian (Late Oligocene): Victoria (VIC004 (TL)).

REMARKS

The wing-like extension of the outer lip is the most unique feature of this species.

***Ericusa atkinsoni*** (Pritchard, 1896)

1896 *Voluta atkinsoni* Pritchard, p.100, pl.3, fig. 1.

1913 *Voluta macroptera* Pritchard, p. 199, pl. 20, fig. 6 (non McCoy, 1866)

1988 *Ericusa atkinsoni* Darragh, p.247, pl. 19, figs. 3, 5; pl.20, figs. 1, 3. Fig. 22.

DIAGNOSIS

Shell fusiform, rapidly tapering spire, tumid body whorl. Axial sculpture of low, wide costae on spire. Spiral sculpture of thin threads on spire whorls. Columella of three well developed plaits. Outer lip reverted and extended posteriorly. Siphonal fasciole absent.

TYPE SPECIMENS

HOLOTYPE: *Ericusa atkinsoni* NMV, P2985.

HYPOTYPE: *Ericusa atkinsoni* NMV, P41723.

DISTRIBUTION

Janjukian – Balcombian (Late Oligocene - Middle Miocene): Victoria, Tasmania, South Australia (TAS001 (TL), VIC008-009, VIC011, VIC021, VIC097, SA039).

REMARKS

This species is very similar to *E. macroptera* except that it lacks the wing-like extension of the outer lip and differs in development of shell sculpture.

***Ericusa ancilloides*** (Tate, 1889)

Plate 2, figs. 3a, b.

| | |
|---|---|
| 1889 | *Voluta ancilloides* Tate, p.126, pl.3, fig. 7. |
| 1897 | *Scaphella ancilloides* Harris, p. 112. |
| 1899 | *Alcithoe ancilloides* Cossmann, p. 133, pl. 7, fig. 6. Fig. 21. |
| 1949 | *Ericusa ancilloides* Cotton, pl.14. |
| 1958 | *Ericusa (Ericusa) ancilloides* Ludbrook, p. 77, pl. 4, fig. 2. |
| 1988 | *Ericusa ancilloides* Darragh, p.248, pl. 15, figs. 3-5. Fig. 25. |

DIAGNOSIS

Shell small, fusiform, blunt spire body whorl tapered anteriorly. Sculpture of growth striae and fine spiral lirae, weakening on body whorl. Inner lip extended. Columella of three plaits. Wide, deep siphonal notch. Siphonal fasciole absent.

TYPE SPECIMENS

LECTOTYPE: *Voluta ancilloides* SAM, T396D.

PARALECTOTYPES: *Voluta ancilloides* SAM, T396A, C; T393.

HYPOTYPES: *Ericusa ancilloides* NMV, P41730, P61288.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene - Late Miocene): Victoria, Tasmania, South Australia (TAS001, VIC007, VIC013, VIC016, VIC022 (TL), VIC023, VIC028-029, VIC034, VIC038, VIC041, VIC082, VIC087, VIC098, SA001).

REMARKS

The poorly developed sculpture and extended inner lip are characteristic of this species which is thought to be ancestral to the living species *E. sericata*.

***Ericusa hamiltonensis*** (Pritchard, 1898)

1889 *Voluta hamiltonensis* Pritchard, p.107, pl.8, fig. 5.

1988 *Ericusa hamiltonensis* Darragh, p.248, pl. 15, figs. 6, 9; pl. 18, figs. 2, 7.

DIAGNOSIS

Shell fusiform, flat spired, large globose protoconch. Deeply grooved sutures. Spiral sculpture of a few thin threads. Columella with 3 plaits. Wide, deep siphonal notch. Siphonal fasciole absent.

TYPE SPECIMENS

HOLOTYPE: *Voluta hamiltonensis* MUGD, 1832.

HYPOTYPE: *Ericusa hamiltonensis* NMV, P12566.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene - Late Miocene): Victoria (VIC022, VIC030, VIC038 (TL), VIC081).

REMARKS

This species has a large protoconch and flattened whorls which distinguishes it from *E. ancilloides*.

### Genus **LIVONIA** Gray, 1855

1855 *Scapha (Livonia)* Gray, p.8.

1871 *Voluta (Mamillana)* Crosse, p.308.

1897 *Voluta (Pterospira)* Harris, p. 100.

1899 *Mamillana* Cossmann, p. 107.

1899 *Pterospira* Cossmann, p. 134.

1915 *Livonia* Hedley, p. 723.

1934 *Cottonia* Iredale, p. 57.

1943 *Cymbium (Mamillana)* Wenz, p. 1338.

1943 *Alcithoe (Cottonia)* Wenz, p. 1344.

1988 *Livonia* Darragh, p. 250.

TYPE SPECIES

*Voluta mamilla* G. B. Sowerby I, 1844 by subsequent designation (Hedley, 1915). Recent, southeastern Australia.

DIAGNOSIS

Large, thick shell, ovate-fusiform, well developed shouler, gradate spire. Axial sculpture of strong costae, nodular at shoulder, when present. Spiral sculpture of threads on spire, often absent on body whorl. Outer lip reflexed laterally, sometimes as wing-like extension. Columella with three well developed plaits. Shallow, wide siphonal notch. Siphonal fasciole absent.

DISTRIBUTION

Oligocene - Recent: Australia.

REMARKS

This genus is characterised by having the mostly strongly developed nodular sculpture on the shell within this family. Anatomical and geographic studies on living and fossil species of this genus find it to be most closely related to *Ericusa* (Darragh, 1988).

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Outer lip extended.............................................................Go to 2
   Outer lip reflexed...............................................................Go to 4

2. Axial sculpture absent.......................................................*mortoni connudata*

Axial sculpture nodular on shoulder. .................................. Go to 3

3. Spiral sculpture absent. .................................................... *mortoni mortoni*
Spiral sculpture on spire whorls. ........................................ *voluminosa*

4. Shell ovate-fusiform. ........................................................ *gatliffi*
Shell fusiform. ..................................................................... Go to 5

5. Spiral threads on spire only. ................................................ Go to 6
Spiral threads on spire and body whorl. ............................... Go to 7
6. Axial costae strongest towards aperture. ............................. *stephensi*
Axial costae strongest on anterior of body whorl. ................. *spenceri*

7. Axial costae coarse and prominent. ...................................... *heptagonalis*
Axial sculpture weakly developed/absent. ............................ *hannafordi*

### ***Livonia mortoni connudata*** Darragh, 1988

1889 *Voluta mortoni* Tate, p.124, pl. 9, fig. 2.
1899 *Pterospira mortoni* Cossmann, p. 134, pl. 6, fig. 4.
1988 *Livonia mortoni connudata* Darragh, p.253, pl. 22, figs. 6-7.

#### DIAGNOSIS

Shell ovate, regularly convex whorls. Spire with very weakly developed spiral threads. Body whorl somewhat depressed at posterior suture. Axial sculpture absent. Columella with 3 plaits. Outer lip laterally extended into small wing. Siphonal notch wide, shallow.

#### TYPE SPECIMENS

HOLOTYPE: *Livonia mortoni connudata* NMV, P41558.
PARATYPE: *Voluta mortoni* SAM, T384.

#### DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene - Late Miocene): Victoria (VIC038 (TL), VIC027).

REMARKS

This subspecies is differentiated from *L. mortoni mortoni* by its well developed columella plaits, regularly convex whorls and lack of axial nodules.

***Livonia mortoni mortoni*** (Tate, 1889)

1889 *Voluta mortoni* Tate, p.124, pl. 9, fig. 1.
1967 *Pterospira mortoni* Ludbrook, p. 67, pl. 3, figs. 6, 8.
1988 *Livonia mortoni mortoni* Darragh, p.252, pl. 22, figs. 1-4. Fig. 28.

DIAGNOSIS

Shell small, smooth, outer lip slightly extended into wing-like expansion. Body whorl with well developed shoulder. Spiral sculpture absent. Axial sculptures of nodules on shoulder where present. Columella with two well developed plaits, one weaker denticle. Wide siphonal notch.

TYPE SPECIMENS

LECTOTYPE: *Voluta mortoni* TM, Z208.
HYPOTYPES: *Livonia mortoni mortoni* NMV, P2571, P61289.

DISTRIBUTION

Longfordian (Early Miocene): Tasmania, (TAS001 (TL), TAS002).

REMARKS

This subspecies is characterised by its smooth appearance, small shell size and angular whorls.

***Livonia voluminosa*** Darragh, 1988

1896 *Voluta alticostata* Pritchard, p.103 (non Tate, 1889).
1913 *Voluta stephensi* Pritchard, p. 195, pl. 21, figs.3- 4 (non Johnston, 1880).
1988 *Livonia voluminosa* Darragh, p.253, pl. 19, figs. 1, 2, 4, 6.

DIAGNOSIS

Shell fusiform, gradate spire, tumid body whorl. Initial teleoconch whorl convex, others with prominent shoulder. Spiral threads on spire whorls. Axial sculpture of large, well defined costae on anterior slope of whorls, appearing nodular at shoulder. Outer lip slightly extended into short wing.

TYPE SPECIMENS

HOLOTYPE: *Livonia voluminosa* NMV, P41368.

PARATYPES: *Livonia voluminosa* NMV, P2986; MUGD, 1796.

DISTRIBUTION

Longfordian (Early Miocene): Tasmania (TAS001 (TL), TAS002).

REMARKS

This species closely resembles *L. heptagonalis* but has more numerous nodules along the shoulder of the whorls and is more abruptly tapered anteriorly.

***Livonia gatliffi*** (Pritchard, 1898)

1898 *Voluta gatliffi* Pritchard, p.108, pl. 8, fig. 6.
1988 *Livonia gatliffi* Darragh, p.255, pl. 20, figs. 2, 4; pl. 21, figs. 1, 3. Fig. 27.

DIAGNOSIS

Shell small for genus, ovate-fusiform, gradate spire. Well developed shoulders with well developed axial costae on anterior whorl slope, nodular at shoulder. Spiral sculpture of fine threads on spire whorl shoulder. Outer lip slightly reflexed. Wide siphonal notch.

TYPE SPECIMENS

HOLOTYPE: *Voluta gatliffi* MUGD, 1805

HYPOTYPE: *Livonia gatliffi* NMV, P41472.

DISTRIBUTION

Balcombian - Bairnsdalian (Middle Miocene): Victoria (VIC038 (TL)).

REMARKS

This species most closely resembles *L. hannafordi* but is far smaller with narrower axial costae.

***Livonia stephensi*** (Johnston, 1880)

1896 *Voluta stephensi* Johnston, p.35.
1913 *Voluta wynyardensis* Pritchard, p.200, pl. 21, figs. 1, 2.
1967 *Alcithoe (Cottonia) stephensi* Ludbrook, p. 67, pl. 3, figs. 3, 4.
1988 *Livonia stephensi* Darragh, p.251, pl. 23, figs. 1, 3-6; pl. 30, figs. 8, 9. Fig. 26.

DIAGNOSIS

Shell fusiform, gradate spire, body whorl with well developed shoulder. Spiral threads on spire, obsolete on body whorl. Axial costae becoming more developed towards aperture, nodulate at shoulder. Columella with three plaits. Outer lip slightly reflexed.

TYPE SPECIMENS

HOLOTYPE: *Voluta stephensi* MUGD, Z183.
HOLOTYPE: *Voluta wynyardensis* AIM, TM839.
HYPOTYPES: *Livonia stephensi* NMV, P41366, P41367, P61290.

DISTRIBUTION

Janjukian (Late Oligocene): Tasmania, Victoria (TAS001 (TL), VIC005).

REMARKS

The lack of a prominent outer lip extension separates this species from others within the genus. The overall shell morphology places this species in *Livonia* despite a protoconch more like those seen in the genus *Ericusa*. The type specimen for this species has been subject to weathering and abrasion resulting in some taxonomic confusion in the past.

***Livonia spenceri*** (Pritchard, 1896)

1896 *Voluta spenceri* Pritchard, p.98, pl. 4, figs. 1, 2.
1988 *Livonia spenceri* Darragh, p.251, pl. 23, fig. 2; pl. 24, fig. 5.

DIAGNOSIS

Shell fusiform, gradate spire, body whorl with well developed shoulder. Spiral threads on spire whorls. Nodular at shoulder, extending anteriorly on body whorl into broad, low costae. Outer lip reflexed.

TYPE SPECIMENS

HOLOTYPE: *Livonia spenceri* NMW, P2990.

PARATYPE: *Livonia spenceri* MUGD, 1813.

DISTRIBUTION

Janjukian - Mitchellian (Late Oligocene – Late Miocene): Tasmania, Victoria (TAS001 (TL), VIC008, VIC013, ?VIC022, VIC087, VIC099).

REMARKS

This species if rarely found and as a result the amount of variation is difficult to calculate. However, the specimens from Fossil Beach (VIC022) are narrower, more elongate and more nodular (Darragh, 1988) than specimens found in other areas and may therefore be another species or subspecies. More specimens would be required in order to examine this fully.

***Livonia heptagonalis*** (Tate, 1889)

Plate 2, figs. 4a, b.

| | |
|---|---|
| 1896 | *Voluta heptagonalis* Tate, p.121, pl.4, figs. 1, 7. |
| 1949 | *Cottonia heptagonalis* Cotton, pl. 14. |
| 1988 | *Livonia heptagonalis* Darragh, p.254, pl. 21, figs. 2, 5; pl. 24, figs. 1, 2. |

DIAGNOSIS

Shell fusiform, gradate spire, gently tapering towards anterior. Whorls with well developed shoulder, flat shoulder slope. Spiral threads on spire, weakly developed on body whorl. Axial costae well developed from shoulder to anterior suture, prominently nodular at shoulder. Columella callus thickened. Outer lip slightly reflexed.

TYPE SPECIMENS

LECTOTYPE: *Voluta heptagonalis* SAM, T397A.

PARALECTOTYPE: *Voluta heptagonalis* SAM, T397C.

HYPOTYPE: *Livonia heptagonalis* NMV, P13895.

DISTRIBUTION

Batesfordian (Middle Miocene): South Australia (SA001 (TL)).

REMARKS

This species is distinguished by the very prominent nodules at the shoulder and the gently tapering body whorl.

***Livonia hannafordi*** (McCoy, 1866)

| | |
|---|---|
| 1866 | *Voluta hannafordi* McCoy, p.376. |
| 1889 | *Voluta alticostata* Tate, p.122, pl. 5, fig. 7. |
| 1897 | *Voluta (Pterospira) hannafordi* Harris, p. 100, pl. 4, figs, 10a, b. |
| 1899 | *Pterospira hannafordi* Cossmann, p.134, pl. 6, fig. 6. |
| 1903 | *Voluta validicostata* Dennant & Kitson, p. 100, nom. non. For *V. alticostata* Tate. |
| 1949 | *Cottonia alticostata* Cotton, pl. 14. |
| 1988 | *Livonia hannafordi* Darragh, p.254, pl. 20, figs. 5, 6; pl. 21, figs. 4, 6; pl. 22, fig. 5. |

DIAGNOSIS

Shell fusiform, gradate spire. Whorls convex, well developed shoulder. Spiral sculpture of fine threads and lirae on posterior of spire whorls and shoulder of body whorl. Axial sculpture variable, nodular at shoulder. Columella with three plaits. Wide siphonal notch. Weakly developed siphonal fasciole.

TYPE SPECIMENS

HOLOTYPE: *Voluta alticostata* SAM, T392

LECTOTYPE: *Voluta hannafordi* NMV, P12155.

PARALECTOTYPE: *Livonia hannafordi* NMV, P6646.

HYPOTYPE: *Livonia hannafordi* NMV, P12972.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC022, VIC023 (TL), VIC025, VIC027, VIC029-031, VIC034, VIC038, VIC041, VIC082, VIC088-089, VIC098).

REMARKS

This species is extremely variable in its sculpture but due to the gradual changes between specimens they are all included in this one species. Some specimens have an outer lip extended into a wing.

### Genus **NOTOPEPLUM** Finlay, 1927

1927 *Notopeplum* Finlay, p. 514.

1988 *Notopeplum* Darragh, p.256.

TYPE SPECIES

*Scaphella victoriensis* Cossmann, 1899 by original designation = *Voluta polita* Tate, 1887. Miocene, Victoria.

DIAGNOSIS

Small shell, ovate-elongate, smooth, glazed. Teleoconch whorls smooth except for growth striae. Aperture lens-shaped, elongate, thickened and reflexed at outer lip. Columella with three well developed plaits. Wide, shallow siphonal notch. Siphonal fasciole weakly developed.

DISTRIBUTION

Eocene - Recent: Australia.

REMARKS

This genus is characterised by its smooth, glazed shell, callused, blunt protoconch and lenticular aperture. The taxonomic position of this genus is somewhat debated (see Darragh (1988) for discussion).

## KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:

1. Whorls convex. ............................................................ Go to 2
   Whorls tumid. ............................................................ Got to 3
   Whorls flattened. ........................................................ *mccoyi mccoyi*

2. Whorls depressed at posterior suture. .................................... *mccoyi translucidum*
   Relatively deep suture. .................................................. *primarugatum*

3. Axial costae strongly developed. ......................................... *protorhysum*
   Axial sculpture of growth lines only. .................................... *politum*

### ***Notopeplum mccoyi mccoyi*** (Tenison-Woods, 1877)

1877 *Voluta m'coyi* Tenison-Woods, p.95.
1888 *Voluta agnewi* Johnston, pl. 30, fig. 9 (non Johnston, 1880)
1913 *Voluta maccoyii* Pritchard, p. 196 (partim.).
1988 *Notopeplum mccoyi mccoyi* Darragh, p.257, pl. 26, figs. 1, 6, 11, 12.

#### DIAGNOSIS

Shell ovate, elongate, grooved sutures, tapered anteriorly. Sculpture of growth striae. Columella with two well developed plaits. Wide deep siphonal notch.

#### TYPE SPECIMENS

HYPOTYPES: *Notopeplum mccoyi mccoyi* NMV, P31161, P31162.

#### DISTRIBUTION

Longfordian (Early Miocene): Tasmania (TAS001 (TL), TAS002).

#### REMARKS

Holotype for this subspecies is presumed missing. The flattened whorls and lack of sculpture are characteristic of this species.

### ***Notopeplum mccoyi translucidum*** (Verco, 1896)

1896 *Voluta translucida* Verco, p. 217 pl. 6, figs. 4a, b.

1898 *Voluta maccoyii* Tate, p.126, pl. 2, fig. 2 (non Tenison-Woods, 1877).

1897 *Scaphella maccoyi* Harris, p. 111.

1930 *Notopeplum balcombensis* Finlay, p.46.

1932 *Notopeplum translucidum* Cotton & Godfrey, p.47, pl. 2, fig. 10.

1988 *Notopeplum mccoyi translucidum* Darragh, p.258, pl. 26, figs. 2-5, 7-9, 13.

DIAGNOSIS

Shell ovate, elongate, convex whorls, slightly turreted spire. Whorls slightly depressed at posterior suture. Shell glazed with growth striae, zigzag axial lines in living species. Deep wide siphonal canal.

TYPE SPECIMENS

HOLOTYPE: *Voluta translucida* SAM, D13614.

HYPOTYPES: *Voluta translucida* SAM, D15013, T382B.

HOLOTYPE: *Notopeplum balcombensis* TM, 1071.

HYPOTYPE: *Notopeplum balcombensis* NMV, P31163.

DISTRIBUTION

Janjukian - Recent (Late Oligocene – Recent): Victoria, South Australia, Western Australia (VIC012-013, VIC015-016, VIC018, VIC022-023, VIC025, VIC034, VIC038, VIC041, VIC087, VIC089, VIC099-100, SA001, SA040 (TL), SA041-042, WA030).

REMARKS

Of all the species in this genus this is the most widely distributed subspecies both spatially and temporally. Shell shape can be variable and shell length rarely exceeds 50mm.

***Notopeplum primarugatum*** Darragh, 1988

1988 *Notopeplum primarugatum* Darragh, p.257, pl. 25, figs. 1-4, 6. Fig. 30.

DIAGNOSIS

Shell ovate, elongate, convex whorls, fairly deep suture. Axial sculpture of thin costae on second and third teleoconch whorls. Growth striae present on penultimate and body whorl. Thickened outer lip.

TYPE SPECIMENS

HOLOTYPE: *Notopeplum primarugatum* NMV, P31158.

PARATYPES: *Notopeplum primarugatum* NMV, P31159, P31160, P61291.

DISTRIBUTION

Aldingan - Willungan (Late Eocene - Early Oligocene): Victoria (VIC002 (TL)).

REMARKS

It is suggested this species is the predecessor to *N. protorhysum*. They differ in that *N. Primarugatum* has more numerous and more closely spaced costae on the intial spire whorls and lacks a well developed shoulder.

***Notopeplum protorhysum*** (Tate, 1889)

Plate 2, figs. 5a, b.

1889 *Voluta protorhysa* Tate, p.126, pl. 2, figs. 6a, b.
1927 *Notopeplum protorhysum* Finlay, p.514
1988 *Notopeplum protorhysum* Darragh, p.256, pl. 25, figs. 7, 10-11. Fig. 31.

DIAGNOSIS

Shell ovate, elongate, well developed shoulder on whorls. Axial sculpture of thin, well developed costae on initial teleoconch whorls. Growth striae present.

TYPE SPECIMENS

LECTOTYPE: *Voluta protorhysa* SAM, T589A.

PARALECTOTYPES: *Voluta protorhysa* SAM, T589B-D (juveniles).

HYPOTYPES: *Notopeplum protorhysum* NMV, P31155, P31156.

DISTRIBUTION

Johannian - Aldingan (Late Eocene): Victoria, South Australia (SA034 (TL), SA036, VIC091-092).

REMARKS

The variation in this species is mostly in shell shape. Elongation of the shell varies between species from South Australia (less elongate) and Victoria (more elongate). The distinguishing feature of this species is the numerous, well defined costae.

***Notopeplum politum*** (Tate, 1889)

1889 *Voluta polita* Tate, p. 127 pl. 2, fig. 7.
1897 *Scaphella polita* Harris, p. 112, pl.4, figs. 15a, b (protoconch).
1899 *Scaphella victoriensis* Cossmann, p.127, nom. nov. For *Voluta polita* Tate non Conrad (invalid name change).
1927 *Notopeplum victoriensis* Finlay, p.513.
1972 *Notopeplum politum* Wilson, p.357, fig. C (protoconch of holotype).
1988 *Notopeplum politum* Darragh, p.258, pl. 25, figs. 8, 9, 12. Fig. 29.

DIAGNOSIS

Shell ovate, tumid whorls, blunt, domed spire. Suture slightly impressed. Sculpture of growth striae. Columella with three well developed plaits. Deep wide siphonal canal.

TYPE SPECIMENS

LECTOTYPE: *Voluta polita* SAM, T602A.
PARALECTOTYPES: *Voluta polita* SAM, T602B-F.
HYPOTYPES: *Voluta translucida* SAM, D15013, T382B.
HYPOTYPE: *Notopeplum politum* NMV, P31164.

DISTRIBUTION

Balcombian - Bairnsdalian (Middle Miocene): Victoria (VIC038 (TL)).

REMARKS

This species is distinguished by its regularly convex whorls, impressed sutures and blunt, domed spire.

## Genus **CYMBIOLA** Swainson, 1831

1831 *Cymbiola* Swainson, p.83.
1847 *Aulica* Gray, p.141.
1847 *Scapha* Gray, p. 141.
1852 *Vespertilio* Morch, p. 123.
1853 *Melo (Ausoba)* H. & A. Adams, p. 160.
1882 *Voluta (Vespertilio)* Tryon, p. 86.
1882 *Voluta (Aulica)* Tryon, p.87.
1883 *Voluta (Cymbiola)* Fischer, p.607.
1899 *Voluta (Aulicina)* Roverato, p. 103. (Nom. nov. pro *Vespertilio*).
1899 *Voluta (Eteroaulica)* Roverato, p. 103. (Footnote, nom. nov. Pro *Aulica* Gray. Invalid replacement).
1929 *Aulica (Aulica)* Thiele, p.348.
1929 *Aulica (Ausoba)* Thiele, p. 348
1929 *Aulica (Aulicina)* Thiele, p. 349.
1929 *Cymbiolena* Iredale, p.181.
1929 *Cymbiola (Cymbiolacca)* Iredale, p.181.
1943 *Cymbiola (Cymbiola)* Wenz, p. 1335.
1943 *Cymbiola (Aulicina)* Wenz, p. 1335.
1943 *Cymbiola (Aulica)* Wenz, p. 1335.
1943 *Adelomelon (Cymbiolena)* Wenz, p. 1349.
1954 *Volutocorona* Pilsbry & Olsson, p.25.
1961 *Pseudocymbiola* McMichael, p.54.
1970 *Cymbiola (Cymbiolena)* Weaver & du Pont, p. 90.
1970 *Cymbiolacca* Weaver & du Pont, p.92.
1988 *Cymbiola* Darragh, p.259.

### TYPE SPECIES

*Voluta cymbiola* Gmelin, 1791 by tautonomy. Recent, Moluccas.

### DIAGNOSIS

Shell ovate, gradate to subconical spire. Spiral sculpture absent. Axial sculpture spinose or nodular on shoulder but sometimes as costae or absent. Columella with four to five well developed plaits. Siphonal notch narrow, deep. Siphonal fasciole prominent, sometimes bound at posterior by ridge.

DISTRIBUTION

Oligocene - Recent: Asia, Australia.

REMARKS

For a full discussion on the synonyms of this genus see Darragh (1988).

***Cymbiola macdonaldi*** (Tate, 1888)

Plate 2, figs. 6a, b.

1888 *Voluta macdonaldi* Tate, p. 176 pl. 12, fig. 11.
1897 *Voluta (Aulica) macdonaldi* Harris, p. 106.
1949 *Cymbiola macdonaldi* Cotton, pl.14.
1988 *Cymbiola macdonaldi* Darragh, p.261, pl. 24, figs. 3, 6.

DIAGNOSIS

Shell ovate, gradate spire. Body whorl ventricose. Axial costae paired, merging at prominent shoulder, nodular at suture on body whorl. Columella with four strong plaits. Deep siphonal notch, prominent siphonal fasciole, bound by sharp ridge.

TYPE SPECIMENS

HOLOTYPE: *Voluta macdonaldi* SAM, T381D.
HYPOTYPE: *Voluta macdonaldi* SAM, T381A.

DISTRIBUTION

Janjukian - Mitchellian (Late Oligocene - Late Miocene): Victoria (VIC022 (TL), ?VIC012, VIC030, VIC038, VIC081).

REMARKS

The most distinguishing feature of this species is the merging of the paired costae. Adult specimens of this species are rare and its relationship with other species is poorly understood.

## PLATE 1 – VOLUTIDAE

**Figure 1** *Athleta (Ternivoluta) antiscalaris antiscalaris,* P314096, non-type, Fishing Point Marl of Lake Craven, VIC:

a) Shell (length = 49mm)

b) Protoconch

**Figure 2** *Lyria harpularia,* P121540, non-type, Muddy Creek Marl of Muddy Creek, VIC:

a) Shell (length = 34mm)

b) Protoconch

**Figure 3** *Leptoscapha crassilabrum,* P33084, non-type, Fyansford Formation of Manyung Rocks, VIC:

a) Shell (length = 11mm)

b) Protoconch

**Figure 4** *Scaphella (Aurinia) joahnnae,* P121524, non-type, Browns Creek Clay of Johanna, VIC:

a) Shell (length = 42mm)

b) Protoconch

**Figure 5** *Amoria costellifera,* T603, holotype, Muddy Creek Marl of Muddy Creek, VIC:

a) Shell (length = 61mm)

b) Protoconch

**Figure 6** *Nannamoria limbata,* T590A, holotype, Fyansford Formation of Grices Creek, VIC:

a) Shell (length = 33mm)

b) Protoconch

# PLATE 1 – VOLUTIDAE

1a

1b

2a

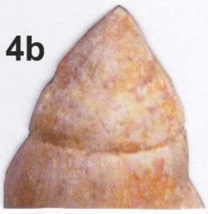
2b

3a

3b

4a

4b



5a

5b

6a

6b

## PLATE 2 – VOLUTIDAE

**Figure 1** *Notovoluta variculifera,* P121663, non-type, Browns Creek Clay of Johanna, VIC:

a) Shell (length = 35mm)

b) Protoconch

**Figure 2** *Alcithoe (Waihaoia) cribrosa,* T605A, lectotype, Blanche Point Marl of Blanche Point, SA:

a) Shell (length = 34mm)

b) Protoconch

**Figure 3** *Ericusa ancilloides,* T396A, paralectotype, Muddy Creek Marl of Muddy Creek, VIC:

a) Shell (length = 76mm)

b) Protoconch

**Figure 4** *Livonia heptagonalis,* T397C, paralectotype, Cadell Formation of the River Murray Cliffs, SA:

a) Shell (length = 41mm)

b) Protoconch

**Figure 5** *Notopeplum protorhysym,* T589A, lectotype, Dry Creek Sand of the Adelaide Bore, SA:

a) Shell (length = 40mm)

b) Protoconch

**Figure 6** *Cymbiola macdonaldi,* T381A, holotype, Muddy Creek Marl of Muddy Creek, VIC:

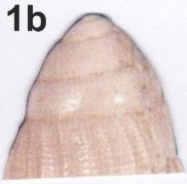
a) Shell (length = 119mm)

b) Protoconch

# PLATE 2 – VOLUTIDAE

1a

1b



2a

2b

3a

3b

4a

4b

5a

5b

6a

6b

## 3.2 FAMILY NASSARIIDAE

The gastropod family Nassariidae is assigned to the superfamily Buccinoidea within the Neogastropoda. Cernohorsky (1984) provided the only full revision of this diverse family, taking into account both fossil and living species, although numerous publications deal with the nassarids in more detail for particular geographical regions (e.g. Mari, 1934; Marche-Marchad, 1955; Tomlin, 1928; Cernohorsky, 1972a; Keen, 1971; Kaicher, 1982). There are approximately 900 species within the Nassariidae (600 of which are thought to be extinct) and these species are organised into 12 genera and 31 subgenera (Cernohorsky, 1984; Haasl, 2000). Subfamilial division varies between publications. Li et al (2010) and Haasl (2000) followed Cernohorsky (1984) in recognising three subfamilies; the Dorsaninae, the Cylleninae and the Nassariinae whilst Bouchet & Rocroi (2005) and Allmon (1990) recognised a fourth subfamily, the Bulliinae.

Taxonomy of the Nassariidae has a long history, spanning approximately 225 years. Numerous similar classification schemes have been proposed with differences mainly concentrated on taxon membership and rank (Haasl, 2000). Until 1799, when Lamarck erected the genus *Nassa*, all early workers assigned Nassariidae species to the genus *Buccinum*. The genus *Nassa* was replaced with *Nassarius* by Duméril in 1806 and the family name Nassariidae was proposed by Iredale in 1916. Cossman (1901) established the foundations of the most commonly used classification of 3 subfamilies (Dorsaninae, Cylleninae and Nassariinae). Cenorhorsky (1984) noted that throughout the taxonomic history of the Nassariidae 2,442 species names have been proposed of which 1,323 belong to living species and 1,119 belong to fossil species. However, these figures are grossly inflated due to a huge number of synonyms and it is likely that only 319 are valid species names for living nassarids and 584 valid species names for fossil nassarids.

Living nassariids have a global distribution in tropical and temperate marine settings, with the majority inhabiting marine or estuarine intertidal mud or sand flats. Others inhabit the muddy-sandy substrate of deeper waters (Yang & Zhang, 2011). Nassariids are active scavengers, mostly feeding on other molluscs, fish and polychaetes (Yang & Zhang, 2011). Cernohorsky (1981) provided the only taxonomic revision of the family Nassariidae in Australia and New Zealand including both fossil and living species. He recognised 25 species of Nassariidae in the region. This represents 7-8% of all living nassarid species. The subfamily Dorsaninae is not represented in the Austral-Zelanic region and there are only three living species of the subfamily Cylleninae confined to temperate Australian waters. The remaining 22 species all belong in the subfamily Nassariinae and are represented by eight subgenera: *Nassarius (Alectrion)*; *Nassarius (Plicarcularia)*; *Nassarius (Niotha)*; *Nassarius (Zeuxis)*; *Nassarius (Gussonea)*; *Nassarius (Hima)*; *Nassarius (Cryptonassarius)*. Twelve of these 22 species are found as fossils or have a fossil record and only seven are found in southeastern Australia.

### **3.2.1** SYSTEMATIC PALAEONTOLOGY

Only seven species of nassarid with a fossil record are found within the field area. Examination of type material and comparison with other Australian species (both living and fossil) described in the literature have been used to assign species to genera. The following taxonomic revision closely follows Cernohorsky (1981) which provided the most recent comprehensive taxonomy of this family.

CLASS **GASTROPODA**
ORDER **NEOGASTROPODA**
SUPERFAMILY **BUCCINACEA** Rafinesque, 1815
Family **NASSARIIDAE** Iredale, 1916

| | |
|---|---|
| 1840 | Nassinae Swainson, pp.63, 69, 299. |
| 1859 | Cyclopsidae Chenu, p.164. |
| 1871 | Cyclonassainae Gill, p.5. |
| 1882 | Cylleninae Bellardi, p.159. |
| 1901 | Dorsaninae Cossman, pp.195, 197. |
| 1908 | Alectrionidae Dall, p.306. |
| 1915 | Arculariidae Iredale, p.345. |
| 1916 | Nassariidae, Iredale, p.182. |

DIAGNOSIS

Shell generally ovate. Fairly high, conical spire. Large body whorl. Sculpture of axial ribbing, nodules/granules, spiral lirae, grooves, striae or spines but occasionally smooth. Sutures distinct or obsolete and occasionally canaliculate. Aperture small. Outer lip often thickened and variced, denticulate or smooth and labrum occasionally with short or long lirae. Columella smooth, or denticulate to varying degrees, with occasional sculpture. Siphonal canal short or long with deep siphonal notch and siphonal fasciole with at least one cord.

DISTRIBUTION

Palaeocene - Recent. Cosmopolitan.

REMARKS

The close relationship between the Nassariidae and Buccinidae makes separation on a familial basis a controversial issue as many morphological and anatomical features overlap. The suite of characters normally used include radular dentition, foot anatomy, operculum morphology and shell sculpture, of which only the latter is useful in fossil specimens. The literature generally supports the taxonomic division of the Nassariidae and Buccinidae at family level despite a large number of similarities (e.g. Bouchet and Rocroi, 2005). It is worth noting that protoconch morphology is not a useful taxonomic character in the case of the Nassariidae due to the highly variable larval development of the family.

## Subfamily **NASSARIINAE** Iredale, 1916

1916 Nassariinae Iredale, p. 82.

DIAGNOSIS

As for Nassariidae, but with shells less inflated and more solid in structure than those of subfamily Dorsaninae and without the sutural groove of subfamily Cylleninae. In recent species visual organs usually present and metapodial tentacles usually found on posterior of foot.

DISTRIBUTION

Miocene - Recent. Cosmopolitan.

REMARKS

This subfamily encompasses approximately 80% of all known nassarid species. The subfamilial taxonomy of the nassarids is in real need of attention with subfamilies currently poorly defined and the diagnostic characters therefore difficult to pin-point. In particular the Nassariinae is usually defined by comparison with other subfamilies but no detailed description or diagnosis for the subfamily itself can be found. Due to the very high species diversity of this subfamily it has not been possible to examine enough species to provide a conclusive definition as part of this study.

### Genus **NASSARIUS** Duméril, 1806

1799 *Nassa* Lamarck, p.71.
1806 *Nassarius* Duméril, p.166.
1807 *Arcularia* Link, p.126.
1828 *Nasa* Fleming, p.340 (invalid emendation).
1888 *Arcularia* Jousseaume, p.184 (invalid emendation – cited twice and included *arcularia* and *deshayesianus*).

TYPE SPECIES

*Buccinum arcularia* Linnaeus, 1758 by subsequent monotypy (Froriep, 1806). Recent, Indo-Pacific.

DIAGNOSIS

Shell size large for family, ovate, often bucciniform, spire moderately high. Whorls convex, often angulate. Sculpture of axial costae, occasionally spiral lirae, nodes along the body whorl suture. Columella callus present, moderately or greatly expanded laterally, denticulate at anterior. Outer lip internally denticulate. Aperture oval, strongly plicate. Siphonal canal very prominent, deeply notched, anteriorly truncated.

DISTRIBUTION

Miocene - Recent. Cosmopolitan.

REMARKS

Cernorhorsky (1984) retained only three species in the genus *Nassarius*, all others being assigned to alternative genera or subgenera.

**KEY TO SUBGENERA FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Spiral sculpture granulose. .................................................... *Niotha*
   Spiral sculpture simple. .................................................... Go to 2.

2. Aperture small. .................................................... Go to 3.
   Aperture wide. .................................................... *Zeuxis*

3. Columellar callus considerably extended. .................................... *Plicarcularia*
   Columella plicate or denticulate. .................................... *Hima*

## Subgenus **NIOTHA** H. & A. Adams, 1853

1853 *Niotha* H. & A. Adams, p.117.
1877 *Niothia* Brazier, p.178 (invalid emend).
1936 *Tavaniotha* Iredale, pp.321, 337.

TYPE SPECIES

*Nassa cumingii* A. Adams, 1852 by subsequent designation (Cossman, 1901) = *Buccinum conoidale* Deshayes in Bélanger, 1832. Recent, Indo-Pacific.

DIAGNOSIS

Shell small for family. Sculpture including axial costae, spiral lirae, granules or spinose nodules. Sutures simple or canaliculate. Aperture oval, interior smooth or lirate. Columellar callus frequently thickened, extended to varying degrees laterally across body whorl. Often anteriorly denticulate, can be smooth or denticulate along entire length. Outer lip denticulate to lirate. Short siphonal canal, fasciole distinct .

DISTRIBUTION

Miocene - Recent. Tropical and temperate Indo-Pacific.

REMARKS

Cernohorsky (1984) suggested that the definition of this subgenus is not well constrained and most of the characters place it between *Nassarius s.str.* and the subgenus *Zeuxis*. Where a species shows overlapping characters, it may be easily placed in *Zeuxis* as an alternative. Although Cernohorsky (1984) suggested a distinction between *Niotha* and *Zeuxis* based on denticulation of the columellar callus, the degree of denticulation is variable in both subgenera, ranging from smooth through anteriorly denticulate to denticulate along the entire length. However, the columellar callus in species of *Niotha* does appear to be wider than in species of *Zeuxis* and narrower than in species of *Nassarius s. str.* and this therefore may be a reasonable character on which to base a distinction between the different subgenera. The presence of a granular or nodular texture is also more prevalent in species of *Niotha* than in species of *Zeuxis*. Only two species of the subgenus *Niotha* are found in the Cenozoic sediments of southeastern Australia.

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Columellar callus with up to five strong denticles.……………………*sublirellus*
2. Columellar callus bordered and smooth.……………………………*crassigranosus*

***Nassarius (Niotha) sublirellus*** (Tate, 1888)

1888 *Nasa (sic) sublirella* Tate, p.171.
1889 *Nassa sublirella* Tate, p.118, pl. 4, fig. 2.
1981 *Nassarius (Niotha) sublirellus* Cernohorsky, p.161, fig. 40.

DIAGNOSIS

Shell generally ovate. Sutures distinct, nodular, separated from main sculpture by a slight concave trough. Axial costae present, spiral sculpture in the form of row of nodules. Siphonal fasciole with a strong oblique cord. Aperture ovate. Outer lip denticulate. Columellar callus narrowly extended onto body whorl and strongly denticulate at anterior.

TYPE SPECIMENS

SYNTYPES: *Nassarius sublirellus*, SAM, T-580.

DISTRIBUTION

Mitchellian - Kalimnan (Late Miocene - Pliocene): Victoria (VIC060 (TL), VIC061).

REMARKS

Cernohorsky (1981) proposed that *N. (N.) nigellus* is the forerunner to the recent species *N. (N.) sublirellus.* The distinction is based on the more elongate shell and less rounded aperture outline of *N. (N.) nigellus* and the more clearly bordered columellar callus and more prominent denticulation along the columella in *N (N.) sublirellus*.

***Nassarius (Niotha) crassigranosus*** (Tate, 1888)

Plate 3, figs. 1a, b.

1888 *Nassa crassigranosa* Tate, p.170, pl. 12, figs. 6a, b.
1928 *Nassarius crassigranosus* Chapman, p.164.
1970 *Tavaniotha crassigranosa* Darragh, p.164.
1981 *Nassarius (Niotha) crassigranosus* Cernohorsky, p.162, figs. 42-44.

DIAGNOSIS

Shell ovate. Sutures threadlike leading onto concave and distinctive ramp marked with nodules. Sculpture nodular where axial and spiral sculpture intersect. Outer lip smooth or weakly denticulate. Columellar callus fairly narrow, bordered, smooth. Siphonal fasciole with oblique cords. Broad varix on body whorl in some specimens.

TYPE SPECIMENS

SYNTYPES: *Nassarius (Niotha) crassigranosus* SAM, T586.

DISTRIBUTION

Mitchellian - Kalimnan (Late Miocene - Pliocene): Victoria (VIC060 (TL), VIC061-063).

REMARKS

This species is easily distinguished from other species of *Niotha* due to the angular and shallowly sloping sutural shoulder creating a more stepped shell outline.

## Subgenus **ZEUXIS** H. & A. Adams, 1853

1853 *Zeuxis* H. & A. Adams, p.119.
1881 *Venassa* v. Martens, p.109.
1969 *Glabrinassa* Shuto, p.145.
1976 *Bathynassa* Ladd, p.131.

TYPE SPECIES

*Buccinum taenia* Gmelin, 1791 by subsequent designation (Cossman, 1901) = *Buccinum olivaceum* Bruguiere, 1789. Recent, Indo-Pacific.

DIAGNOSIS

Shell moderate sized for family, whorls convex. Shell sculpture of axial costae, spiral striae, grooves. Aperture generally wide. Columellar callus narrow, denticulation variable. Outer lip slightly thickened, less variced than species of *Niotha,* can be denticulate or lirate interiorly. Siphonal canal short.

DISTRIBUTION

Miocene - Recent. Tropical Indo-Pacific.

REMARKS

Cernohorsky (1984) suggested that, like the subgenus *Niotha*, the definition of this subgenus is not well constrained and some species may be easily placed in either subgenera. See remarks section of *Niotha* for discussion. Three species of the subgenus *Zeuxis* are found in the Cenozoic sediments of southeastern Australia.

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Sculpture intersection nodulate.............................................Go to 2.
   Sculpture lacking nodulose appearance. ..............................*spiraliscabrus*

2. Outer lip denticulate along margin.........................................p*yrrhus*
   Outer lip lirate interiorly..........................................................*subcopiosus*

### ***Nassarius (Zeuxis) spiraliscabrus*** (Chapman & Gabriel, 1914)

Plate 3, figs. 2a, b.

1914 *Nassa spiraliscabra* Chapman & Gabriel, p.325, pl. 28, fig. 34.
1928 *Nassarius spiraliscabrus* Chapman, p.164.
1958 *Hinia (Reticunassa) spiraliscabra* Ludbrook, p.65, pl.3, fig. 2.
1970 *Reticunassa spiraliscabra* Darragh, p.195.
1981 *Nassarius (Zeuxis) spiraliscabrus* Cernohorsky, p.172, figs. 61, 62.

DIAGNOSIS

Shell small, elongate-ovate. Sculpture of irregularly spaced, slender axial costae and spiral grooves, weak or strong. Siphonal fasciole with oblique cords. Outer lip variced, interiorly lirate or denticulate. Columellar callus well defined. Distinct siphonal notch.

TYPE SPECIMENS

HOLOTYPE: *Nassarius (Zeuxis) spiraliscabrus*, NMV, P12491.

DISTRIBUTION

Kalimnan – Yatalan (Pliocene – Early Pleistocene): Victoria, Western Australia (VIC063, VIC078 (TL), SA031, SA032, WA027).

REMARKS

The weaker spiral sculpture in this species separates it from the very similar *N. (Z.) subcopiosus*.

### ***Nassarius (Zeuxis) pyrrhus*** (Menke, 1843)

1822 *Buccinum fasciatum* Lamarck, p.211.
1834 *Buccinum jacksonianum* Kiener, p.64, pl. 19, fig. 73 (non Quoy & Gaimard, 1833).
1843 *Buccinum pyrrhum* Menke, p.21 (nom. subst. pro *Buccinum fasciatum* Lamarck, 1822).
1853 *Nassa (Tritia) dealbata* A. Adams, p.112.
1853 *Nassa fasciata* Reeve, pl.6, fig. 40.
1913 *Alectrion fasciata* Suter, p.397, pl.45, fig. 16.

1915 *Alectrion victorianus* Iredale, p.467 (nom. subst. pro *Buccinum fasciatum* Lamarck, 1822).

1916 *Arcularia victoriana* Iredale, Hedley, p.61

1921 *Nassarius victorianus* Iredale, May, p.82

1936 *Nassarius pyrrhus* Gabriel, p.12, textfig.

1938 *Niotha pyrrhus* Cotton & Godfrey, p.24.

1972 *Nassarius (Zeuxis) pyrrhus* Cernohorsky, p.171, fig. 121, 142.

*Refer to Cernohorsky (1981) for full synonymy.*

DIAGNOSIS

Shell elongate-ovate. Coarse spiral threads intersect moderately fine, angulate, axial costae creating a nodular sculpture. Columellar callus narrow and well defined, irregularly denticulate along entire length, frequently doubled. Outer lip denticulate along margin. Aperture ovate, smooth interiorly.

TYPE SPECIMENS

HOLOTYPE: *Nassarius dealbatus* (worn specimen), BMNH, 197331.

SYNTYPES: ?*Buccinum fasciatum*, *Nassarius pyrrhus* and *Alectrion victorianus* MHNG, 1296/7.

DISTRIBUTION

Mitchellian – Recent (Pliocene – Recent): Victoria, South Australia Western Australia, Tasmania (VIC056, VIC062, VIC064-077, TAS008-033, SA003, SA007-029, WA007, WA010-025).

REMARKS

Cernohorsky (1972) noted that *N. (Z.) pyrrhus* is often assigned to the subgenus *Niotha* but the narrow and clearly defined columellar callus is more similar to other species of the subgenus *Zeuxis*.

***Nassarius (Zeuxis) subcopiosus*** (Ludbrook, 1958)

1958 *Hinia (Reticunassa) subcopiosa* Ludbrook, p.64, pl. 3., fig. 1.

1970 *Reticunassa subcopiosa* Darragh, p.197.

1978 *Nassarius (Reticunassa) subcopiosa* Ludbrook p.150, pl. 17, figs. 1, 2.

1981 *Nassarius (Zeuxis) subcopiosus* Cernohorsky, p.170, figs. 59, 60.

DIAGNOSIS

Shell elongate-ovate. Sculpture of fairly fine axial costae intersecting with spiral cords to create a nodular appearance. Outer lip interiorly lirate, weakly variced on margin. Columellar callus narrow, well defined, denticulate. Parietal denticle present.

TYPE SPECIMENS

HOLOTYPE: *Nassarius subcopiosus*, SAM, F15403.

DISTRIBUTION

Kalimnan – Yatalan (Late Pliocene): South Australia, Western Australia (SA030 (TL), WA026).

REMARKS

This species shows a resemblance to *N. (Z.) pyrrhus* but differs in its less numerous mature whorls and more numerous protoconch whorls, the smaller sized adult shell and the thickening of the columellar callus above the parietal wall. *N. (Z.) subcopiosus* is also similar to *N. (Z.) spiraliscabrus* except for a more nodulose sculpture on the spire. Sculpture in both species shows variation.

### Subgenus **PLICARCULARIA** Thiele, 1929

1826 *Eione* Risso, p.171.

1929 *Nassarius (Plicarcularia)* Thiele, p.324.

1936 *Parcanassa* Iredale, p.322.

1956 *Austronassaria* C. & J. Laseron, p.71 (non S. V. Wood, 1872) = *Buccinum jonasii* Dunker, 1846.

1969 *Retiarcularia* Shuto, p.23 (nomen nudum)

1969 *Chelenassa* Shuto, p.142.

TYPE SPECIES

*Nassa (Plicarcularia) thersites* (Bruguiére, 1789) by monotypy = *Buccinum pullus* Linnaeus, 1758. Recent, Indo-Pacific.

DIAGNOSIS

Shell small for family, more elongate than *Nassarius sensu stricto*, mainly ovate in shape. Columellar callus longitudinally extended, often considerably. Aperture small, generally narrow, denticulate or plicate. Shell sculpture of axial costae, spiral threads. Short siphonal canal.

DISTRIBUTION

Pliocene - Recent. Tropical and temperate Indo-Pacific.

REMARKS

The columellar callus is more extended than in other subgenera, often overlapping a large proportion of the body whorl. Only two species of this subgenus are found in Australia, of which only one is found as a fossil in the Cenozoic sediments of southeastern Australia.

***Nassarius (Plicarcularia) burchardi*** (Dunker in Philippi, 1849)

Plate 3, figs. 3a, b.

1849 *Buccinum burchardi* Dunker in Philippi, p.69, pl.2, fig.14.
1852 *Nassa labecula* A. Adams, p.98.
1868 *Nassa (Arcularia) labecula* Cox, p.5.
1901 *Nassa burchardi* Tate & May, p.358.
1918 *Nassarius burchardi* Hedley, M88.
1936 *Parcanassa ellana* Iredale, p.322.
1955 *Parcanassa burchardi* Cotton, p.2, fig. 6.
1961 *Nassarius (Parcanassa) ellana* Rippingale & McMichael, p. 105, pl. 13, fig. 18.
1972 *Nassarius (Plicarcularia) burchardi* Cernohorsky, p.139, figs. 31, 32, fig. 56.
*Refer to Cernohorsky (1981) for full synonymy.*

DIAGNOSIS

Shell elongate-ovate. Axial costae on body whorl slender, often swollen, corrugated, nodular at suture and usually very weak at outer lip. Spiral threads present, interstices often smooth. Columellar callus greatly extended and reaching suture on body whorl, denticles on anterior. Outer lip smooth or denticulate on margin. Aperture ovate, smooth.

TYPE SPECIMENS

HOLOTYPE: *Nassarius (Plicarcularia) burchardi* , ZHMU (no specimen number available).
SYNTYPES: *Nassarius labecula*, BMNH, 197344; *Nassarius ellana*, AMS, C-12999.

DISTRIBUTION

Mitchellian – Recent (Pliocene – Recent): Queensland to Western Australia and Tasmania (QLD001-020, NSW001-036, VIC052-059, SA003 (TL), SA004-009, TAS003-007, WA001-009).

REMARKS

The presence of an extended columellar callus makes this species easily recognisable as belonging to the subgenus *Plicarcularia*.

## Subgenus **HIMA** Leach in Gray, 1852

| | |
|---|---|
| 1852 | *Hima* Leach in Gray, p.123. |
| 1852 | *Tritonella* A. Adams, p.111 (non Swainson, 1839). |
| 1931 | *Mirua* Marwick, p.115. |
| 1936 | *Reticunassa* Iredale, p.322. |

TYPE SPECIES

*Buccinum minutum* Pennent, 1777 by subsequent designation (Marwick, 1931) = *Buccinum incrassatum* Ström, 1768. Recent, Mediterranean.

DIAGNOSIS

Shell small for family, ovate or elongate-ovate. Sutures distinct, often canaliculate. Whorls convex. Sculpture of axial costae, prominent spiral striae. Aperture small, roundly ovate. Columella callused, plicate or irregularly denticulate. Outer lip often denticulate, variced. Siphonal canal short.

DISTRIBUTION

Miocene - Recent. Cosmopolitan.

REMARKS

Cernohorsky (1972, 1984) dicussed in some detail the homonymy and type desginations of the subgenus *Hima*, in particular the confusion between the use of *Tritonella* A. Adams and *Hima* Leach in Gray. Only one species of the subgenera *Hima* is found in the Cenozoic sediments of southeastern Australia.

***Nassarius (Hima) tatei tatei*** (Tenison-Woods, 1879)

Plate 3, figs. 4a, b.

| | |
|---|---|
| 1879 | *Nassa tatei* Tenison-Woods, p.230, pl.21, fig. 13. |
| 1928 | *Nassarius tatei* Tension-Woods, Chapman, p.164. |
| 1970 | *Reticunassa tatei* Darragh, p.200. |
| 1981 | *Nassarius (Hima) tatei tatei* Cernohorsky, p.175, figs. 68-70. |

DIAGNOSIS

Shell small, ovate or elongate-ovate. Sutures somewhat impressed or canaliculate. Sculpture of intersecting axial costae and spiral threads creating nodular appearance. Outer lip variced, denticulate. Columellar callus well defined, narrow. Parietal denticle often present. Siphonal canal oblique cords.

TYPE SPECIMENS

SYNTYPES: *Nassarius tatei*, AMS, F-1771.

DISTRIBUTION

Janjukian – Yatalan (Late Oligocene – Pleistocene): Victoria, South Australia, Western Australia (VIC022-023, VIC061, VIC079-085, SA001 (TL), SA033, WA028-029).

REMARKS

This species is diverse in form with a high degree of variability in shape and sculpture. Harris (1897) examined a large number of specimens concluding that despite the diversity in form all belong to the one species due to the gradual changes in shape and sculpture.

## PLATE 3 – NASSARIIDAE

**Figure 1** *Nassarius (Niotha) crassigranosus,* T586, syntype, Muddy Creek Marl of Muddy Creek, VIC:

a) Shell (length = 14mm)

b) Protoconch

**Figure 2** *Nassarius (Zeuxis) spiraliscabrus,* P12491, holotype, unknown formation of Mallee Bore No. 8, VIC:

a) Shell (length = 10.3mm)

b) Protoconch

**Figure 3** *Nassarius (Plicarcularia) burchardi,* no specimen number*,* non-type, Jemmys Point Formation of Jemmys Point, VIC:

a) Shell (length = 9mm)

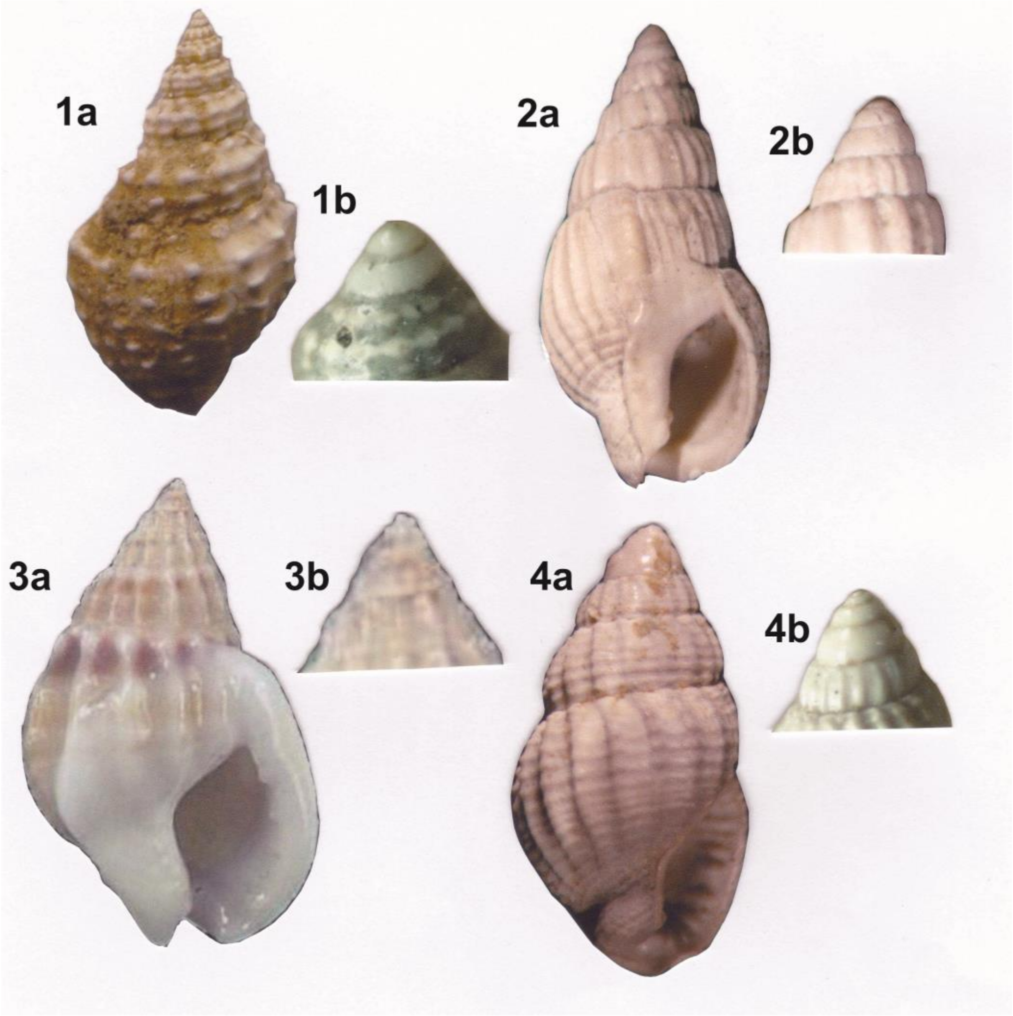
b) Protoconch

**Figure 4** *Nassarius (Hima) tatei tatei,* P316706, non-type, Muddy Creek Marl of Muddy Creek, VIC:

a) Shell (length = 7.5mm)

b) Protoconch

## PLATE 3 – NASSARIIDAE



## 3.3 FAMILY RAPHITOMIDAE

The gastropod family Raphitomidae is assigned to the superfamily Conoidea within the Neogastropoda. Until recently the Raphitomidae has been classified as a subfamily of the Turridae, based on shell morphology and radula form (e.g. Powell, 1966; Rosenberg, 2009). A revised classification of the Conoidea based on shell morphology, radula and foregut anatomy (Taylor et al., 1993) resulted in a significant rearrangement of taxa but was met with resistance (e.g. Rosenberg, 1998) and was generally not adopted. Following this, advances in molecular phylogenetics of living “turrids” placed most turrid species in the family Conidae (Puillandre et al., 2008) significantly reducing the number of true turrid species. Again, this new classification was not well recieved with some researchers suggesting that the phylogeny was not robust enough to move away from the traditional classification of turrid species. The most recent classification of the Conoidea is based on a combination of phylogeny (Puillandre et al., 2008), anatomy, radula and shell morphology (Bouchet et al., 2011) at genus level. This study resulted in the reclassification of the originally polyphyletic Turridae family into thirteen monophyletic families of which the family Raphitomidae is one. However, this new classification only takes into account living taxa and as a result many fossil “turrids” do not perfectly fit owing to the lack of genetic, anatomical and radula data.

The family Raphitomidae is considered to be the largest and most variable of all Conoidea families in terms of species as well as having the greatest vertical range in terms of water depth, from intertidal to trench zones (Bouchet et al., 2011). According to the most recent classification of living species (Bouchet et al., 2011), the family is comprised of 63 genera of which six are only tentatively assigned to the family due to an ambiguous morphological fit. There is currently no revised taxonomy for this family as a whole in Australia for either living or fossil species.

### **3.3.1** SYSTEMATIC PALAEONTOLOGY

Only two species of raphitomid fossil are in included in this taxonomy which is unlikely to reflect the true diversity in Cenozoic southeastern Australia. There are almost certainly a great deal more species but due to the difficulty in assigning fossil genera to the newly erected Raphitomidae family on shell morphology alone, only two can be assigned to the family confidently. Generic assignment follows Bouchet et al. (2011). Species have been assigned to genera based on examination of type material and other Australian species.

CLASS **GASTROPODA**

ORDER **NEOGASTROPODA**

SUPERFAMILY **CONOIDEA** Fleming, 1822

Family **RAPHITOMIDAE** A. Bellardi, 1875

1875 Raphitomidae A. Bellardi, p. 20.

DIAGNOSIS

Shell size and shape variable. Protoconch typically multispiral, striated initially, then cancellate, spiral striations when paucispiral. Sculpture development variable, smooth to strong axial and spiral sculpture. Traces of anal sinus growth. Inner lip often smooth. Siphonal canal short to long.

DISTRIBUTION

Palaeocene – Recent. Cosmopolitan.

REMARKS

Despite being the largest and most diverse family within the superfamily Conoidea, very few fossil species from this family are found in the field area. The genera *Daphnella* and *Teleochilus* were originally assigned to the family Turridae in older literature but have here been assigned to the family Raphitomidae following Bouchet et al. (2011).

**KEY TO GENERA FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Multispiral protoconch, cancellate sculpture. ........................................ *Daphnella*
2. Spiral lirae on paucispiral protoconch, dominant spiral sculpture. ............ *Teleochilus*

## Genus **DAPHNELLA** Hinds, 1844

1844 *Daphnella* Hinds, p. 25.
1844 *Daphnella (Daphnella)* Hinds, p. 25.
1918 *Hemidaphne* Hedley, p. 79.
1933 *Eudaphnella* Bartsch, p.76.
1954 *Paradaphne* Laseron, p. 208.

### TYPE SPECIES

*Pleurotoma lymnaeformis* Kiener by subsequent designation (Herrmannsen, 1947). Recent, Indian Ocean.

### DIAGNOSIS

Shell elongate-ovate to ovate-fusiform. Multispiral, pointed, cancellate sinusigerid protoconch. Whorls convex. Sculpture usually cancellate. Reduced canal.

### DISTRIBUTION

?Palaeocene – Recent. Cosmopolitan.

### REMARKS

Whilst it is not within the scope of this study, this genus needs to be reviewed in the future due to the difficulty in finding distribution data and a clear description outlining the diagnostic characteristics. Only one species of this genus is found in the study area although many others are found in other global regions. It is placed in the family Raphitomidae based on molecular phylogenetic analysis in Bouchet et al. (2011).

### ***Daphnella cuspidatus*** (Chapple, 1934)

Plate 4, figs. 1a, b.

1934 *Guraleus cuspidatus* Chapple, p. 164.
1944 *Daphnella cuspidatus* Powell, p. 59.

DIAGNOSIS

Shell elongate-fusiform, whorls medially convex, turreted spire. Whorls shouldered posteriorly. Axial sculpture of oblique costae, obsolete anteriorly. Spiral sculpture of closely spaced fine threads, coarsest on spire whorls. Outer lip smooth, Siphonal canal wide, short.

TYPE SPECIMENS

HOLOTYPE: *Daphnella cuspidatus* NMV, P13691.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC022 (TL), VIC028).

REMARKS

Some features of this species are atypical of the genus but as the majority of characters are consistent with the genus *Daphnella* it remains in this genus (see Powell, 1944 for discussion). Chapple (1934) remarked on its similarity to the living species *Guraleus cuspis* (Sowerby).

### Genus **TELEOCHILUS** Harris, 1897

1897 *Teleochilus* Harris, p. 64.

TYPE SPECIES

*Daphnella gracillima* Tenison-Woods by original designation. Early Miocene, Tasmania.

DIAGNOSIS

Shell elongate-fusiform. Paucispiral protoconch with spiral lirae. Whorls slightly convex. Axial sculpture of weak costae, growth lines faint. Spiral sculpture of prominent spiral cords and threads. Columella plaited. Aperture callused.

DISTRIBUTION

Miocene – Recent. Southeastern Australia.

REMARKS

This genus is exclusively found in southeastern Australia and is characterised by the spiral lirae present on the paucispiral protoconch and dominance of spiral sculpture rather than axial elements.

***Teleochilus gracillima*** (Tenison-Woods, 1877)

Plate 4, figs. 2a, b.

1877 *Daphnella gracillima* Tenison-Woods, p. 106.
1944 *Teleochilus gracillimus* Powell, p. 64.

DIAGNOSIS

Shell fusiform, glazed, whorls convex. Axial sculpture of strong, broad costae. Spiral sculpture of few, distantly spaced, flat cords, one broad cord at suture. Outer lip thin. Siphonal canal short, wide.

TYPE SPECIMENS

HOLOTYPE: *Daphnella gracillima* TM, Z207.

DISTRIBUTION

Longfordian (Early Miocene): Tasmania (?TAS001, ?TAS002).

REMARKS

This species is easily distinguished by its distinct broad costae and wide spiral interspaces.

## PLATE 4 – RAPHITOMIDAE

**Figure 1** *Daphnella cuspidatus,* P13691, holotype, Fyansford Formation of Fossil Beach, VIC:

a) Shell (length = 14mm)

b) Protoconch

**Figure 2** *Teleochilus gracillima,* no specimen number, non-type, Fossil Bluff Sandstone of Table Cape, TAS:

a) Shell (length = 15mm)

b) Protoconch

## PLATE 4 – RAPHITOMIDAE

1a

1b

2a

2b

## 3.4 FAMILY BORSONIIDAE

The gastropod family Borsoniidae is assigned to the superfamily Conoidea within the Neogastropoda. Traditionally, the Borsoniidae has been assigned as a subfamily to the family Turridae based on shell and radula characters (e.g. Powell, 1966; McLean, 1971). The generally unadopted classification of Taylor et al. (1993) included borsoniid gastropods in the subfamily Clathurellinae. Molecular phylogenetic analysis of living conoidean gastropods (Puillandre et al., 2008) also placed the borsoniids in the subfamily Clathurellinae which in turn was assigned to the family Conoidae. As outlined previously neither of these taxonomic revisions were well receieved and as a result until very recently Borsoniinae has remained a subfamily of the Turridae. Combined examination of molecular data, anatomy, radula and shell morphology has resulted in the promotion of Borsoniinae to family status as one of thirteen monophyletic families within the superfamily Conoidea (Bouchet et al., 2011). However, this newest classification does not include fossil species due to the lack of anatomical and molecular data and as a result the family Borsoniidae still needs to be revised in terms of assignment of fossil taxa.

The literature procides little insight into the ecology of the Borsoniidae itself, but as borsoniid species were originally assigned to the family Turridae it is suggested that they are carnivorous organisms found at a variety of water depths (Roy, 2002). The Borsoniidae is considered to be one of the more heterogeneous groupings within the Conoidea comprising a number of conchologically variable clades (Bouchet et al., 2011). Some of the most ancient conoideans (e.g. *Tomopleura*, *Bathytoma*, *Zemacies*) are included in this family, with first occurrences as far back as the earliest Palaeogene in Australia. The family comprises thirty genera of which four are considered tentative. There is currently no revised taxonomy for this family as a whole in Australia on either living or fossil species.

### **3.4.1** SYSTEMATIC PALAEONTOLOGY

The taxonomy that follows comprises fourteen species assigned to six genera. Difficulty in assigning fossil taxa due to conchological variability makes it unlikely that the taxa here account for all fossil borsoniids in Cenozoic southeastern Australia. Generic assignment follows Bouchet et al. (2011). Species have been assigned to genera based on examination of type material and other Australian species.

## CLASS **GASTROPODA**

## ORDER **NEOGASTROPODA**

## SUPERFAMILY **CONOIDEA** Fleming, 1822

### Family **BORSONIIDAE**, A. Bellardi, 1875

1875 Borsoninae, A. Bellardi, p.20.
2003 Zemaciinae, Sysoev, p. 86.
2011 Borsoniidae, Bouchet et al., p. 276.

DIAGNOSIS

Shell small to large, fusiform to biconic. Protoconch paucispiral or multispiral, sometimes with axial costae. Sculpture of coarse axial costae, sometimes obsolete or absent and spiral threads and cords often well developed. Columellar plaits strong to obsolete. Aperture elliptical to oval. Short to moderately long siphonal canal. Siphonal notch deep.

DISTRIBUTION

Palaeocene – Recent. Cosmopolitan.

REMARKS

This rather heterogeneous group is yet to be fully resolved and is still in need of attention despite the efforts of Bouchet et al. (2011). Conchological variability may be the result of the inclusion of some of the most ancient conoideans (e.g. *Zemacies, Borsonia, Tomopleura*) from the Palaeocene (see Bouchet et al., 2011 for discussion).

**KEY TO GENERA FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Shell elongate-fusiform. ........................................ Go to 2.
   Shell ovate-fusiform to biconic. ........................................ Go to 4.
   Shell claviform. ........................................ *Tomopleura*.

2. Shell whorls shouldered. ........................................ Go to 3.

Shell whorls angulated. ........................................................*Cryptocordieria*.

3. Siphonal notch absent. ........................................................*Borsonia*.
   Siphonal canal long. ........................................................*Zemacies*.

4. Axial sculpture of growth lines only. ....................................*Microdrillia*.
   Axial sculpture of costae or nodules. ....................................*Bathytoma*.

### Genus **TOMOPLEURA** Casey, 1904

1904 *Tomopleura* Casey, p. 138.

TYPE SPECIES

*Pleurotoma nivea* Philippi, 1851 by original designation. Recent, Formosa.

DIAGNOSIS

Shell claviform, slender, elongate. Multispiralled protoconch. Axial sculpture of coarsely incised growth lines. Spiral sculpture of two large, conspicuous principal carinae, one below suture, one medial, smaller carinae present. Small, deep anal sinus between two principal carinae. Columella with one to two plaits.

DISTRIBUTION

?Upper Cretaceous – Recent. Asia, Australasia, Africa, Indo-Pacific.

REMARKS

Finding the distribution data for this genus is extremely difficult as it is often not clearly outlined in the literature and so a review of the genus may confirm temporal and spatial occurrences to be more extensive than suggested here. The genus is characterised by the spiral keel and by the multispiral protoconch.

***Tomopleura dilectoides*** (Chapman & Gabriel, 1914)

Plate 5, figs. 1a, b.

1914 *Pleurotoma (Drillia) dilectoides* Chapman & Gabriel, p. 327.
1944 *Tomopleura dilectoides* Powell, p. 38.

DIAGNOSIS

Shell fusiform, acute apex, sloping shoulder. Whorls contracted at base. Axial sculpture of growth lines. Spiral sculpture of spire bicarinate, increasing in number on body whorl, weakest at anterior, interspaces with sigmoidal, closely spaced threads.

TYPE SPECIMENS

HOLOTYPE: *Tomopleura dilectoides* NMV, P12494.

DISTRIBUTION

Mitchellian - Kalimnan (Pliocene): Victoria (VIC059 (TL), VIC078, VIC117).

REMARKS

This species is one of only two fossil species of this genus to occur in Australia. The other, *T. ludbrookae,* is not included in this taxonomy due to specimens being unavailable for examination.

### Genus **CRYPTOCORDIERIA** Long, 1981

1981 *Cryptocordieria* Long, p. 36.

TYPE SPECIES

*Cryptocordieria variabilis* Long, 1981 by original designation. Eocene, Australia.

DIAGNOSIS

Shell elongate-fusiform, whorls angulated. Paucispiral protoconch. Axial sculpture of slightly sigmoidal costae extending suture to suture, more spaced and weakening towards body whorl. Spiral sculpture of numerous threads, sometimes obsolete. Outer lip sharp. Posterior sinus shallow, on shoulder slope.

DISTRIBUTION

?Eocene. ?Australasia.

REMARKS

Only one species from this genus appears in the fossil record of southeastern Australia. It has been placed in this family due to its thick shell, shallow posterior sinus and twisted, slightly thickened columella.

***Cryptocordieria variabilis*** Long, 1981

Plate 5, figs. 2a, b.

1981 *Cryptocordieria variabilis* Long, p. 36.

DIAGNOSIS

Shell elongate-fusiform, tall spire, whorls medially inflated, shallow, concave shoulder. Axial sculpture of sigmoidal costae extending from suture to suture, anteriorly obsolete on body whorl, nodulate on and around periphery. Spiral sculpture of numerous fine threads, strongest anteriorly, of variable strength, sometimes reticulate where intersecting with growth lines. Short, wide siphonal canal.

TYPE SPECIMENS

HOLOTYPE: *Cryptocordieria variabilis* NMV, P33395.

PARATYPES: *Cryptocordieria variabilis* NMV, P42857, P33394.

DISTRIBUTION

Johannian - Aldingan (Late Eocene): Victoria (VIC091, VIC092, VIC114 (TL)).

REMARKS

Axial and spiral sculpture is variable in this species but still falls within the expected range of variability for a single species (see Long, 1981 for discussion).

### Genus **BORSONIA** Bellardi, 1839

1839 *Borsonia* Bellardi, p.30.

### TYPE SPECIES

*Borsonia prima* Bellardi, 1839 by monotypy. Miocene, Italy.

### DIAGNOSIS

Shell elongate-fusiform, whorls often shouldered. Protoconch small, paucispiral. Columella with one, sometimes two medial plaits. Aperture narrowly pyriform, slightly flexed anterior canal. Outer lip sharp. Posterior sinus rounded, relatively deep, covering whole shoulder slope. Siphonal notch absent.

### DISTRIBUTION

Palaeocene – Recent. Cosmopolitan (except Antarctica).

### REMARKS

This genus is slightly unusual for the family in that the siphonal notch is absent. Relatively little literature defines this genus and, like the family as a whole, some work is needed in order to constrain the characters that define this genus.

### KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:

| | | |
|---|---|---|
| 1. | Siphonal canal short. | Go to 2 |
| | Siphonal canal long. | Go to 3 |
| 2. | Axial sculpture of rounded, spinose costae. | *balteata* |
| | Axial sculpture of faint growth lines. | *torquayensis* |
| 3. | Spiral sculpture of closely spaced threads. | Go to 4 |
| | Spiral sculpture of relatively strong cords. | *tatei* |
| 4. | Whorls shouldered. | Go to 5 |
| | Whorls without shoulder. | *protensa* |
| 5. | Aperture narrow. | *otwayensis* |
| | Aperture wide. | *polycesta* |

***Borsonia balteata*** Tate, 1897

Plate 5, figs. 3a, b.

1897 *Borsonia balteata* Tate, p.395, pl. 19, fig. 10.

DIAGNOSIS

Shell fusiform, whorls carinated medially, narrow convex rib at anterior suture. Axial sculpture of rounded, spinose costae becoming obsolete posteriorly. Faint growth lines. Spiral sculpture of closely spaced cords and threads. Nodulate at intersection of axial and spiral sculpture. Aperture elongate-pyriform. Columella with two strong plaits. Siphonal canal short.

TYPE SPECIMENS

HOLOTYPE: *Borsonia balteata* SAM, T326.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC014 (TL), VIC005).

REMARKS

This species is distinguished by the nodulate appearance of the intersection of axial and spiral sculpture.

***Borsonia torquayensis*** Powell, 1944

1944 *Borsonia torquayensis* Powell, p. 42, pl. 1, fig. 11.

DIAGNOSIS

Shell fusiform-biconic, medially carinated, body whorl tumid. Axial sculpture of faint growth lines. Spiral sculpture of distinct, strong spiral cords. Spiral cords strongest anteriorly below carinae. Columella with two strong plaits. Siphonal canal short, wide.

TYPE SPECIMENS

HOLOTYPE: *Borsonia torquayensis* AIM, 70943.

DISTRIBUTION

Janjukian (Late Oligocene): Victoria (VIC005 (TL)).

REMARKS

This species is similar to *B. balteata* but differs in its reduced axial sculpture and weaker subsutural margining (Powell, 1944).

***Borsonia tatei*** Powell, 1944

1944 *Borsonia tatei* Powell, p.42, pl. 3, fig. 8.

1981 *Borsonia tatei eocenica* Long, p.35, pl. 5, fig.18.

DIAGNOSIS

Shell elongate-fusiform, slender, whorls shouldered medially. Axial sculpture of sub-spinose costae, nodular at periphery, obsolete posteriorly. Spiral sculpture of fine threads and relatively well-developed cords, strongest anteriorly. Inner lip glazed. Columella with one plait. Siphonal canal long.

TYPE SPECIMENS

HOLOTYPE: *Borsonia tatei* AIM, 70942.

DISTRIBUTION

Johannian – Longfordian (Late Eocene – Early Miocene): Victoria (VIC115 (TL), VIC092, ?VIC113).

REMARKS

This species is characterised by the strong medial shoulder, well developed costae and presence of spiral cords. Long (1981) erected the subspecies *Borsonia tatei eocenica* due to variation in sculpture between species found in Browns Creek and those found in Spring Creek. However, the variability is not considerable and as a result this subspecies has been included under the species name *Borsonia tatei*.

***Borsonia protensa*** Tate, 1897

1897 *Borsonia protensa* Tate, p.394, pl. 19, fig. 6.

DIAGNOSIS

Shell elongate-fusiform, slender, whorls rounded. Axial sculpture of poorly developed costae on spire whorls, absent on body whorl. Spiral sculpture of closely spaced faint threads. Columella with two strong plaits. Siphonal canal long and reflexed slightly.

TYPE SPECIMENS

HOLOTYPE: *Borsonia protensa* SAM, T340D.

SYNTYPES: *Borsonia protensa* SAM, T340A-C.

DISTRIBUTION

Aldingan - Willungan (Late Eocene – Early Oligocene): Victoria (VIC002 (TL)).

REMARKS

Long (1981) considered *B. protensa, B. polycesta* and *B. otwayensis* to all be variations of a single species (*Cordieria protensa)*. However, *B. protensa* lacks the angulated shoulder and strongly developed sculpture seen in the other two species and this is probably outside of the spectrum of variability expected within a single species. As a result *B. protensa* is treated as a species in its own right.

***Borsonia otwayensis*** Tate, 1897

1896 *Borsonia otwayensis* Cossmann, p.98 (figure of protoconch only. Specific name not valid).

1897 *Borsonia otwayensis* Tate, p.394, pl. 19, fig. 4.

DIAGNOSIS

Shell fusiform, body whorl tumid, spire whorls shouldered post-medially. Axial sculpture of broad costae on anterior of spire whorls, obsolete on body whorl, faint growth lines. Spiral sculpture of closely spaced threads. Aperture elongate-narrow. Inner lip glazed. Columella with two strong plaits. Siphonal canal long, wide.

TYPE SPECIMENS

HOLOTYPE: *Borsonia otwayensis* SAM, T320D.

SYNTYPES: *Borsonia otwayensis* SAM, T320A-C, E-G.

DISTRIBUTION

Aldingan - Willungan (Late Eocene – Early Oligocene): Victoria (VIC002 (TL)).

REMARKS

This species closely resembles *B. polycesta* except that this species is less nodulate, spire whorls are less convex and the aperture is narrower. As already noted, Long (1981) considered *B. protensa, B. polycesta* and *B. otwayensis* to all be variations of a single species. From examination of type material this species is considered to be distinct.

***Borsonia polycesta*** Tate, 1897

1897 *Borsonia polycesta* Tate, p.395, pl. 19, fig. 2.

DIAGNOSIS

Shell fusiform, body whorl tumid, spire whorls shouldered. Spire whorls convex. Axial sculpture of costae on spire whorls, nodulate at shoulder, obsolete on body whorl. Spiral sculpture of closely spaced threads. Inner lip glazed. Columella with two strong plaits. Siphonal canal wide, moderately long.

TYPE SPECIMENS

HOLOTYPE: *Borsonia polycesta* SAM, T327C.

SYNTYPES: *Borsonia polycesta* SAM, T327A, B, D-H, J.

DISTRIBUTION

Aldingan - Willungan (Late Eocene – Early Oligocene): Victoria (VIC002 (TL)).

REMARKS

This species closely resembles *B. otwayensis* except that this species is more nodulate, spire whorls are convex and the aperture is far wider. As already noted, Long (1981) considered *B. protensa, B. polycesta* and *B. otwayensis* to all be variations of a single species. From examination of type material this species is considered to be separate.

## Genus **ZEMACIES** Finlay, 1926

1926 *Zemacies* Finlay, p. 252.

TYPE SPECIES

*Zemacies elatior* Finlay, 1926 by original designation. Miocene, New Zealand.

DIAGNOSIS

Shell large, slender. Protoconch multispiral, axial costae at juncture with teleoconch. Very deep anal sinus on shoulder. Outer lip extended past origin at suture.

DISTRIBUTION

Palaeocene to Recent. Australasia.

REMARKS

The original description of this species is based on comparison with other genera. If a review of the Borsoniidae was to be undertaken then a clearer definition of this genus and its distribution would be necessary. Darragh (1997) noted that there are many similarities to the genus *Apiotoma*_and suggests that they may comprise the same genus. However, Bouchet et al. (2011) treated them as separate genera and molecular phylogenetic analysis finds them to be assigned to different families. As a result, *Zemacies* is here left as its own genera.

### ***Zemacies procerior*** Darragh, 1997

Plate 5, figs. 4a, b.

1997 *Zemacies procerior* Darragh, p. 81, figs. 5 O-P, U.

DIAGNOSIS

Shell elongate-fusiform, tall spire. Whorls with blunt shoulder, concave ramp. Axial sculpture of low, broad opisthocline costae on shoulder, becoming weaker/obsolete on later whorls. Spiral sculpture of closely spaced fine threads over whole shell. Outer lip with deep notch. Columella callused. Siphonal canal long.

TYPE SPECIMENS

FIGURED: *Zemacies procerior* NMV, P98421, P98419.

DISTRIBUTION

Wangerripian (Late Palaeocene): Victoria (VIC118 (TL)).

REMARKS

Only one complete mature specimen is found in museum collections of *Z. procerior*, other specimens are of juveniles or are weathered.

## Genus **MICRODRILLIA** Casey, 1903

1903 *Microdrillia* Casey, p. 252.

TYPE SPECIES

*Pleurotoma cossmanni* Meyer, 1887 by subsequent designation (Cossmann, 1906). Upper Eocene, Jackson, Mississippi, USA.

DIAGNOSIS

Shell small, slender, truncated anteriorly. Protoconch multispiralled, axially ribbed. Axial sculpture of growth lines. Spiral sculpture of strong cords. Sinus on shoulder between subsutural keel and posterior keel. Columella smooth or plicate.

DISTRIBUTION

Eocene – Recent. Cosmopolitan.

REMARKS

This genus is distinguished by its deep sinus, multispiralled protoconch and axially ribbed protoconch whorls.

### ***Microdrillia steiroides*** (Chapman, 1928)

Plate 5, figs. 5a, b.

1928 *Filodrillia steiroides* Chapman, p. 121, pl. 9, fig. 57.

1944 *Microdrillia steiroides* Powell, p. 30.

DIAGNOSIS

Shell biconical, apex acute, whorls convex, angulate, shoulder carinate. Suture canaliculate. Axial sculpture of closely spaced costae on spire whorls. Spiral sculpture of one strong cord above shoulder, intermediate fine threads. Inner lip callused.

TYPE SPECIMENS

HOLOTYPE: *Microdrillia steiroides* NMV, P14469.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene - Late Miocene): Victoria (VIC022 (TL), VIC119, VIC038, VIC023).

REMARKS

This species is distinguished by its acute spire, sharp apex and ribbed spire whorls.

### Genus **BATHYTOMA** Harris & Burrows, 1891

1891 *Bathytoma* Harris & Burrows, p. 113.

1936 *Micantapex* Iredale, p.319.

1951 *Riuguhdrillia* Oyama, p.80.

1961 *Parabathytoma* Shuto, p.87.

TYPE SPECIES

*Bathytoma cataphractus* Brocchi, 1814 by original designation. Pliocene, Europe.

DIAGNOSIS

Shell oval-fusiform to biconic, whorls angular, concave posteriorly. Sculpture of spiral cords and costae, nodular, sometimes smooth. Protoconch blunt, smooth, paucispiral. Columella with one strong plait. Aperture narrowly subpyriform, slightly curved anterior canal. Outer lip sometimes crenulated. Siphonal fasciole distinct.

DISTRIBUTION

Eocene – Recent. Europe, Asia, Australasia, North America, Indo-Pacific.

REMARKS

A formal description of this genus is hard to find in the literature and as a result a critical review of the diagnostic characters is necessary. The genus is distinguished by the dense beaded lirations occurring on the shoulder of the whorls.

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Siphonal canal short. .................................................... Got to 2.
   Siphonal canal relatively long. ..................................... *rhomboidalis*.

2. Spiral sculpture strongest anteriorly. ........................... Go to 3.
   Spiral sculpture strongest posteriorly. ......................... *fontinalis.*

3. Spiral threads coarse and beaded. ................................ *decomposita*.
   Spiral threads beaded only at intersection on shoulder. .. *pritchardi*.

***Bathytoma rhomboidalis*** (Tenison-Woods, 1880)

1880 *Pleurotoma rhomboidalis* Tenison-Woods, p. 10, pl. 2, fig. 9.
1894 *Genotia angustifrons* Tate, p. 175, pl. 10, fig. 7.
1897 *Bathytoma angustifrons* Harris, p. 49.
1914 *Bathytoma rhomboidalis* Chapman, p. 19.

DIAGNOSIS

Shell elongate - fusiform, tall spired, whorls keeled at posterior suture. Axial sculpture of sinuous growth lines. Spiral sculpture of strong cords and threads, cords strongest anteriorly on body whorl. Subsutural fold bearing two beaded threads. Inner lip glazed. Outer lip sharp. Siphonal canal moderately long, narrow.

TYPE SPECIMENS

SYNTYPES: *Bathytoma angustifrons* SAM, T 1525A-K.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene - Late Miocene): Victoria and South Australia (VIC038 (TL), VIC022, VIC023, SA001).

REMARKS

This species is distinguished by its elongate-fusiform outline and the subsutural beaded threads.

***Bathytoma fontinalis*** (Tate, 1894)

1893 *Dolichotoma fontinalis* Tate & Dennant (*nomen nudum*), p. 221.
1894 *Genotia fontinalis* Tate, p. 175, pl. 10, fig. 4.
1896 *Bathytoma fontinalis* Cossmann, p. 103.

DIAGNOSIS

Shell fusiform, whorls medially concave. Whorls inflated at anterior suture, nodular-beaded. Axial sculpture of growth lines. Spiral sculpture of spiral threads, strongest posteriorly, sometimes granulose on body whorl. Inner lip callused. Outer lip sharp. Siphonal canal short, relatively wide.

TYPE SPECIMENS

SYNTYPES: *Genotia fontinalis* SAM, T1520A-F.

DISTRIBUTION

Janjukian – Bairnsdalian (Late Oligocene – Middle Miocene): Victoria (VIC005, VIC038, VIC115).

REMARKS

This species is distinguished by the beading along the anterior suture and the granulose spiral threads on the body whorl.

***Bathytoma decomposita*** (Tate, 1894)

1893 *Dolichotoma decomposita* Tate & Dennant (*nomen nudum*), p. 221.
1894 *Genotia decomposita* Tate, p. 175, pl. 10, fig. 8.

1896 *Bathytoma gellibrandi* Cossmann, p. 103.

1897 *Bathytoma decomposita* Harris, p. 50.

DIAGNOSIS

Shell fusiform-biconic, whorls medially concave. Whorls inflated at anterior suture. Axial sculpture of strong growth lines. Spiral sculpture of coarse beaded threads, most prominent on anterior of body whorl. Inner lip callused. Outer lip sharp. Siphonal canal short, slightly closed.

TYPE SPECIMENS

SYNTYPES: *Genotia decomposita* SAM, T1509A-M.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene - Late Miocene): Victoria (VIC005, VIC022-023, VIC033, VIC081 (TL), VIC116).

REMARKS

This species is distinguished by its rounded sutural inflation and its coarse beaded spiral threads. Specimens from eastern Victoria are tall-spired with straight outlines compared to the wider specimens found in western Victoria (Powell, 1944).

### ***Bathytoma pritchardi*** (Tate, 1894)

Plate 5, figs. 6a, b.

1894 *Genotia pritchardi* Tate, p. 175, pl. 10, fig. 9.

1944 *Bathytoma pritchardi* Powell, p. 14.

DIAGNOSIS

Shell fusiform, whorls medially concave, shouldered. Axial sculpture of coarse growth lines. Spiral sculpture of strong cords, strongest anteriorly. Nodulate-beaded at intersection on shoulder. Inner lip callused. Outer lip sharp. Siphonal canal short.

TYPE SPECIMENS

SYNTYPES: *Bathytoma pritchardi* SAM, T1522 A-C.

DISTRIBUTION

Mitchellian - Kalimnan (Pliocene): Victoria (VIC059).

REMARKS

This species is characterised by its fusiform outline and strong posterior spiral cords.

## PLATE 5 – BORSONIIDAE

**Figure 1** *Tomopleura dilectoides,* P12494, holotype, unknown formation ofMallee Bore No. 8, VIC:

a) Shell (length = 12mm)

b) Protoconch

**Figure 2** *Cryptocordieria variabilis,* P33395, holotype, Browns Creek Clay of Johanna, VIC:

a) Shell (length = 23.2mm)

b) Protoconch

**Figure 3** *Borsonia balteata,* T326, holotype, Fyansford Formationn of the Belmont Shaft, VIC:

a) Shell (length = 9.8mm)

b) Protoconch

**Figure 4** *Zemacies procerior,* P98421, figured specimen, Pebble Point Formation of Dilwyn Cove, VIC:

a) Shell (length = 31mm)

b) Protoconch

**Figure 5** *Microdrillia steiroides,* P14469, holotype, Fyansford Formation of Fossil Beach, VIC:

a) Shell (length = 15mm)

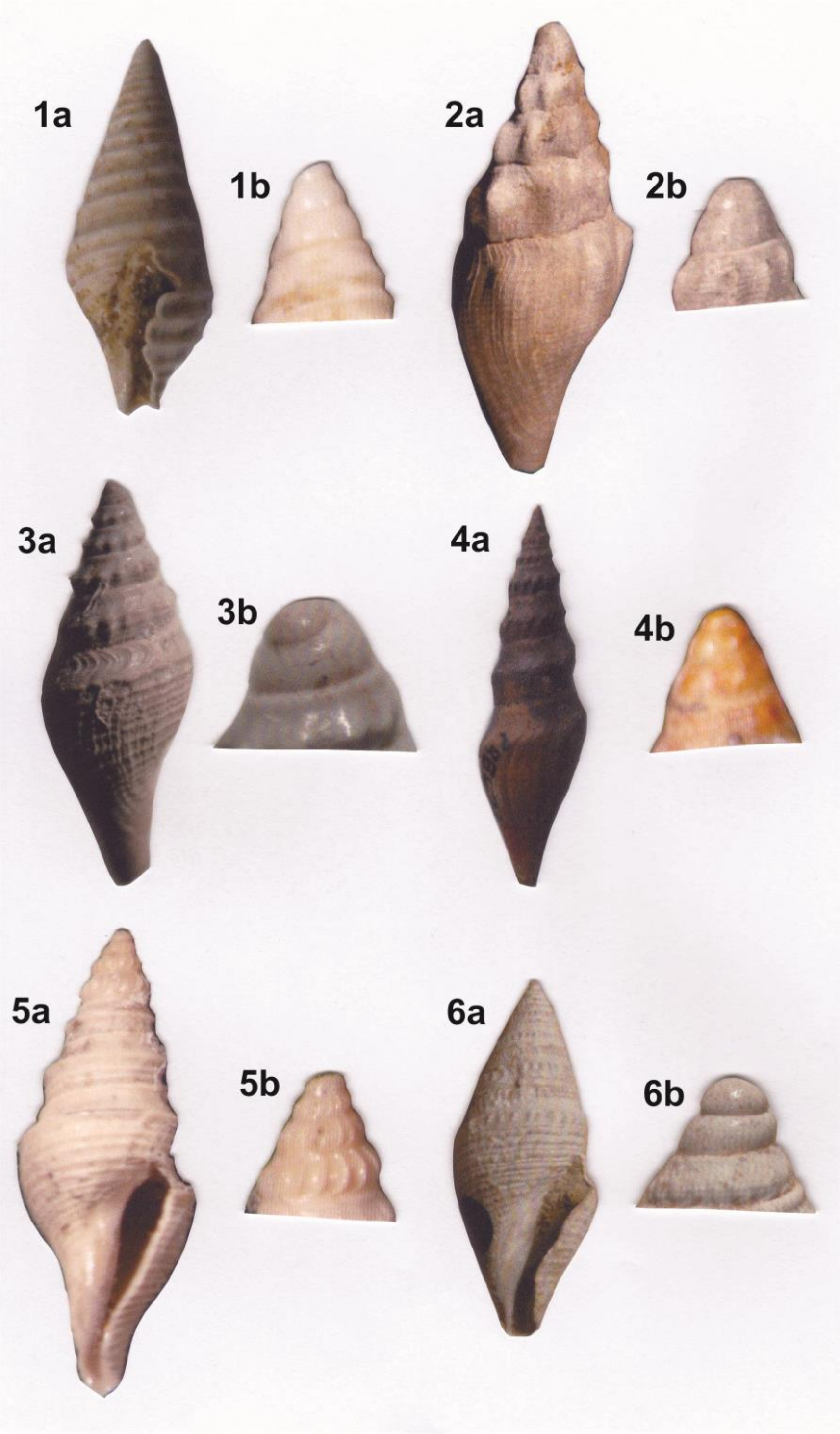
b) Protoconch

**Figure 6** *Bathytoma pritchardi,* T1522, syntype, Pliocene of Gippsland, VIC:

a) Shell (length = 32mm)

b) Protoconch

## PLATE 5 – BORSONIIDAE



## 3.5 FAMILY MANGELIIDAE

The gastropod family Mangeliidae is assigned to the superfamily Conoidea within the Neogastropoda. This family is traditionally accepted as a subfamily of the family Turridae (e.g. Powell, 1966; McLean, 1971) based on both shell morphology and radula. The addition of anatomical characters to radulae did not alter this family's classification in any way (Taylor et al., 1993). Molecular phylogenetic analysis assigned the subfamily Mangeliinae to the family Conoidae (Puillandre et al., 2008) but this new classification was not generally supported and the subfamily remained under the Turridae umbrella. The most recent attempts to reclassify the Conoidea based on the combination of molecular data, shell morphology, radula and anatomy assigns the Mangeliinae to family level. It is now considered to be one of the thirteen monophyletic families comprising the Conoidea (Bouchet et al., 2011). Unfortunately, this newest classification system only takes into account Recent taxa which can lead to difficulties in assigning fossil taxa to this family.

The family comprises fifty-seven genera (of which eight are tentatively placed within this family by Bouchet et al., (2011)) making it one of the more diverse conoidean families. There is currently no revised taxonomy for this family as a whole in Australia for either living or fossil species.

### **3.5.1** SYSTEMATIC PALAEONTOLOGY

The following taxonomy includes six species from three genera found within the field area. It is likely that many more fossil species from this family exist within the field area but it has not been possible to confidently assign more than these six species based on the information available. Generic assignment follows Bouchet et al. (2011). Species have been assigned to genera based on examination of type material.

CLASS **GASTROPODA**

ORDER **NEOGASTROPODA**

SUPERFAMILY **CONOIDEA** Fleming, 1822

Family **MANGELIIDAE** P. Fischer, 1883

| | |
|---|---|
| 1883 | Mangeliinae P. Fischer, p. 587. |
| 1929 | Cytharinae Thiele, p. 365. |
| 1987 | Oenopotinae Bogdanov, p. 35. |
| 2011 | Mangeliidae, Bouchet et al., p. 281. |

DIAGNOSIS

Shell ovate – fusiform, low spired, whorls often shouldered/angulate. Axial sculpture of costae dominate. Spiral sculpture well developed, variable. Deep sinus with thick callus on shoulder slope of outer lip. Outer lip reinforced. Aperture narrow, ovate-elongate, rarely denticulate. Short, truncated siphonal canal.

DISTRIBUTION

Palaeocene – Recent. Cosmopolitan.

REMARKS

Bouchet et al. (2011) combined the subfamilies Mangeliinae, Oenopotinae and Cytharinae and promote them to the new rank of family (Mangeliidae) following the molecular phylogeny of Puillandre et al. (2011). Morphologically the family is characterised by the reinforced outer lip.

**KEY TO GENERA FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

| | | |
|---|---|---|
| 1. | Outer lip thin. | Got to 2. |
| | Outer lip variced. | *Antiguraleus* |
| 2. | Spiral sculpture weakly developed. | *Guraleus* |
| | Spiral sculpture of fine threads over whole shell. | *Macteola* |

## Genus **ANTIGURALEUS** Powell, 1942

1942 *Antiguraleus* Powell, p. 146.

TYPE SPECIES

*Antiguraleus otagoensis* Powell, 1942 by original designation. Recent, New Zealand.

DIAGNOSIS

Shell claviform-fusiform, blunt apex, relatively wide aperture. Whorls flattened below suture. Protoconch paucispiral, usually smooth. Axial sculpture of costae, often crenulating suture. Spiral sculpture of threads overprinting axial sculpture. Outer lip with strong to weak varix. Inner lip smooth. Siphonal canal shallow.

DISTRIBUTION

?Miocene – Recent. Australasia, Africa, Asia, Indo-Pacific.

REMARKS

The spatial and temporal distribution of this genus may be greater than outlined here. This is the result of a paucity of distribution data in the literature.

### ***Antiguraleus incisus*** (Powell, 1944)

Plate 6, figs. 1a, b.

1944 *Guraleus (Paraguraleus) incisus* Powell, p.51, pl. 5, fig. 15.
1970 *Antiguraleus incisus* Darragh, p. 175.

DIAGNOSIS

Shell elongate-fusiform, whorls gently convex, whorls very slightly shouldered posteriorly. . Axial sculpture of sinuous costae, thirteen per whorl extending suture to suture, obsolete on anterior of body whorl. Spiral sculpture of incised grooves, intersecting axial sculpture. Outer lip with recurve, lightly varixed externally. Posterior sinus rounded, covering shoulder.

TYPE SPECIMENS

HOLOTYPE: *Guraleus (Paraguraleus) incisus* AIM, 71000.

DSITRIBUTION

Kalimnan - Yatalan (Pliocene): South Australia (SA032 (TL)).

REMARKS

This species has distinctive curved costae and the outer lip is supported by a thick external varix. As a result it has been placed in the genus *Antiguraleus* following Darragh (1970).

## Genus **GURALEUS** Hedley, 1918

1918 *Guraleus* Hedley, p. 79.

1947 *Euguraleus* Cotton, p. 15.

TYPE SPECIES

*Mangilia picta* Adams & Angas, 1864 by original designation. Recent, New South Wales.

DIAGNOSIS

Shell elongate-fusiform tall, turreted spired. Protoconch multispiral, conical, smooth, sometimes with distinct tip and brephic axials. Body whorl narrow. Axial sculpture of dominant costae. Spiral sculpture of weakly developed cords and threads. Aperture narrow, outer lip thin. Posterior sinus broad, shallow, covering majority of shoulder slope.

DISTRIBUTION

Eocene – Recent. Australasia, Africa, Asia, Indo-Pacific.

REMARKS

The spatial distribution of this genus may be greater than outlined here. Due to a paucity of distribution data in the literature this information provides the best estimate.

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Periphery subangulate.................................................Go to 2.

Periphery angulate. .................................................. *eocenicus*
Periphery carinate. .................................................. *adelaidensis*

2. Six costae per whorl. .................................................. *volutiformis*
One costae per whorl. .................................................. *subnitidus*

***Guraleus eocenicus*** Long, 1981

Plate 6, figs. 2a, b.

1981 *Guraleus eocenicus* Long, p. 43, pl. 7, fig. 2.

DIAGNOSIS

Shell buccinoid-fusiform, whorls angulated, shoulder slope gently concave. Axial sculpture of narrow costae, wide interspaces, extending suture to suture, weakest on shoulder. Spiral sculpture of threads and fine cords overprinting axial sculpture. Outer lip sharp, inner lip smooth. Siphonal canal short, open.

TYPE SPECIMENS

HOLOTYPE: *Guraleus eocenicus* NMV, P42871.
PARATYPES: *Guraleus eocenicus* NMV, P42872, P42873.

DISTRIBUTION

Johannian - Willungan (Late Eocene – Early Oligocene): Victoria, South Australia (VIC091 (TL), VIC002, SA034, SA049).

REMARKS

There is a degree of variability between specimens from different localities but this appears to fall within the range expected from a single species and so no attempts to split the taxon have been made.

***Guraleus adelaidensis*** Powell, 1944

1944 *Guraleus adelaidensis* Powell, p. 49, pl. 6, fig. 13.

DIAGNOSIS

Shell fusiform, periphery carinate. Axial sculpture of costae, ten per whorl, extending from periphery to suture. Spiral sculpture of three broad, flat cords and grooves per whorl, intersecting axial sculpture.

TYPE SPECIMENS

HOLOTYPE: *Guraleus adelaidensis* AIM, 70991.

DISTRIBUTION

Kalimnan - Yatalan (Pliocene): South Australia (SA032 (TL)).

REMARKS

This species is distinguished by having ten axial costae per whorl.

***Guraleus volutiformis*** Chapman & Crespin, 1928

1928 *Guraleus volutiformis* Chapman & Crespin, p. 123, pl. 9, fig. 62.

DIAGNOSIS

Shell biconic-fusiform, whorls angulated posteriorly, anteriorly tapered. Axial sculpture of six strongly developed costae, weakest posteriorly, interspaces wide. Spiral sculpture of relatively strong spiral cords and threads, strongest on penultimate and body whorl. Outer lip thin, shouldered, inner lip narrowly callused.

TYPE SPECIMENS

HOLOTYPE: *Guraleus volutiformis* NMV, P14479.

DISTRIBUTION

Balcombian - Bairnsdalian (Middle Micoene): Victoria (VIC119 (TL), VIC038).

REMARKS

This species is distinguished by having six axial costae per whorl.

***Guraleus subnitidus*** Ludbrook, 1941

1941 *Guraleus subnitidus* Ludbrook, p. 99, pl. 5, fig. 22.

1947 *Euguraleus subnitidus* Cotton, p.15.

1958 *Guraleus (Euguraleus) subnitidus* Ludbrook, p. 90.

1970 *Euguraleus subnitidus* Darragh, p. 197.

DIAGNOSIS

Shell fusiform, whorls subangulate. Axial sculpture of costae, one per whorl, extending from angulation to suture. Spiral sculpture of broad, flat cords and grooves, intersecting axial sculpture.

TYPE SPECIMENS

HOLOTYPE: *Guraleus subnitidus* SAM, T1664.

DISTRIBUTION

Kalimnan - Yatalan (Pliocene): South Australia (SA032 (TL), SA031).

REMARKS

This species is distinguished by the single axial rib per whorl.

### Genus **MACTEOLA** Hedley, 1918

1918 *Macteola* Hedley, p. 146.

TYPE SPECIES

*Purpura (Cronia) anomala* Angas, 1877 by original designation. Recent, New South Wales.

DIAGNOSIS

Shell biconic. Protoconch paucispiral, smooth, blunt. Axial sculpture of broad costae, obsolete on shoulder slope, fading anteriorly. Spiral sculpture of fine threads over whole shell, intersecting axial sculpture. Aperture subovate. Outer lip thin. Weakly developed posterior sinus covering shoulder slope. Siphonal canal short, unnotched.

### DISTRIBUTION

?Eocene – Recent. Australasia, ?North America, Asia, Indo-Pacific.

### REMARKS

The temporal and spatial distribution of this genus may be more extensive than outlined here. A review of the genus as a whole may shed light on its true distribution.

## ***Macetola eocenica*** Long, 1981

Plate 6, figs. 3a, b.

1981 *Macteola eocenica* Long, p. 44, pl. 7, fig. 6.

### DIAGNOSIS

Shell fusiform, whorls turretted, whorls shouldered and angulate. Axial sculpture of spaced, narrow costae, aligned whorl to whorl, obsolete on anterior of body whorl, carinate at periphery, faint growth lines. Spiral sculpture of incised grooves on spire, cords on body whorl. Outer lip sharp, nearly straight. Posterior sinus on peripheral angulation.

### TYPE SPECIMENS

HOLOTYPE: *Macteola eocenica* NMV, P42874.
PARATYPES: *Macteola eocenica* NMV, P42875, P42876.

### DSITRIBUTION

Johannian - Aldingan (Late Eocene): Victoria (VIC091 (TL), VIC092).

### REMARKS

This is the only species of *Macteola* recorded from southeastern Australia. Long (1981) discusses the generic placement of the species.

## PLATE 6 – MANGELIIDAE

**Figure 1** *Antiguraleus incisus,* no specimen number, non-type, Hallett Cove Sandstone of Hallett Cove, SA:

a) Shell (length = 15.9mm)

b) Protoconch

**Figure 2** *Guraleus eocenicus,* P42871, holotype, Browns Creek Clay of Johanna, VIC:

a) Shell (length = 6.2mm)

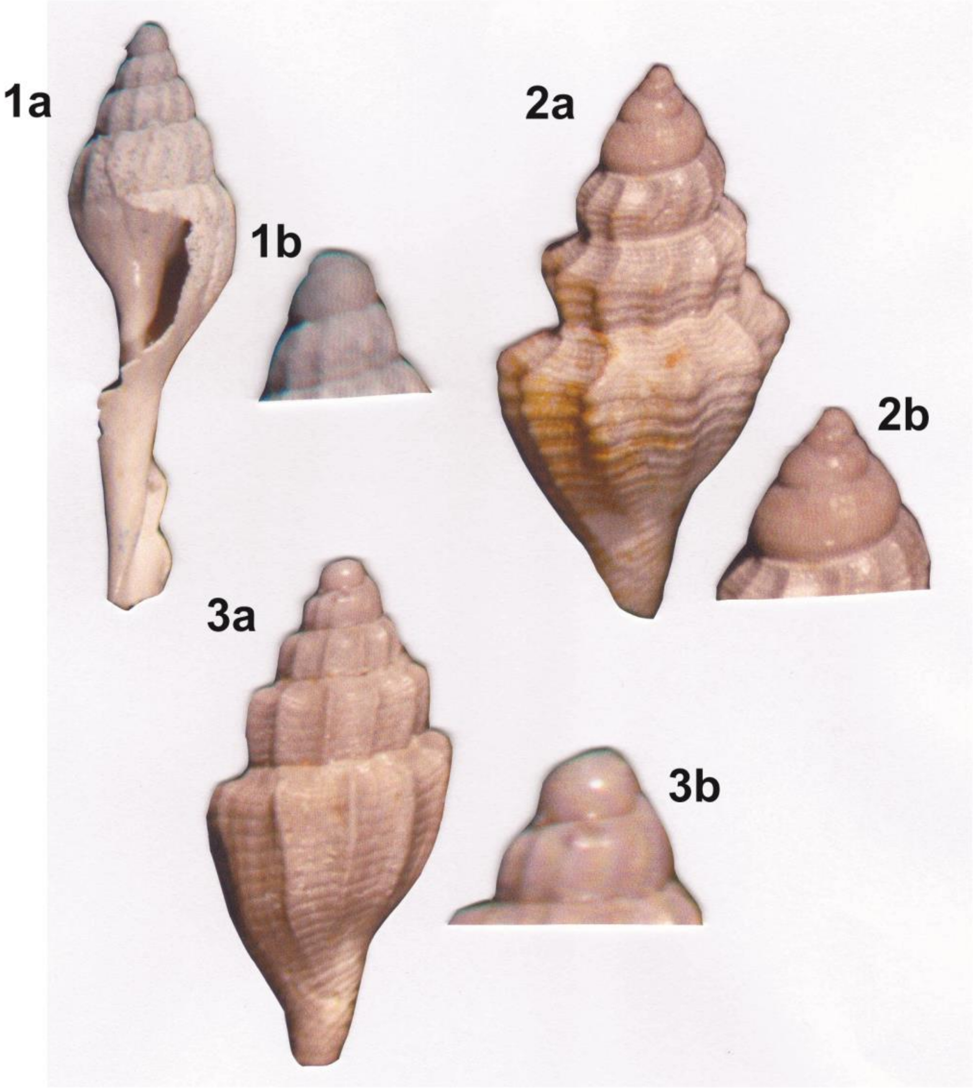
b) Protoconch

**Figure 3** *Macteola eocenica,* P42874, holotype, Browns Creek Clay of Johanna, VIC:

a) Shell (length = 4.5mm)

b) Protoconch

## PLATE 6 – MANGELIIDAE



## 3.6 FAMILY TURRIDAE

The gastropod family Turridae is assigned to the superfamily Conoidea within the Neogastropoda. The family Turridae has long been considered one of the most complex and taxonomically confusing groups of gastropod and as result most authors have dealt either with specific subfamilies or particular geographic regions (e.g. Hedley, 1922; Powell, 1942, 1944, 1964, 1966, 1969; McLean, 1971; Hickman, 1976; Long, 1981; Kilburn, 1983, 1985, 1986, 1988, 1989, 1991; Chang 1995, 2001; Figueira & Absalão, 2010). Genera were assigned to eight subfamilies by Powell (1944, 1966): Turrinae, Turriculinae, Cochlespirinae, Conorbinae, Clavinae, Borsoniinae, Mangeliinae and Daphnellinae. This subfamilial division was generally used in published literature (e.g. Long, 1981) until Bouchet & Rocroi (2005) established a more concise classification of five subfamilies (Turrinae, Cochlespirinae, Crassispirinae, Zemacinae and Zonulispirinae). Reclassification of the Superfamily Toxoglossa based on shell morphology and radula corroborated this classification scheme (Tucker & Tenorio, 2009) which was further supported by molecular phylogenetic analysis (Puillandre et al., 2008). However, despite these attempts to reduce the complexity of turrid taxonomy confusion still existed due to the great variability in shell morphology. The most recent classification uses molecular data, shell morphology, anatomy and radula to try and resolve taxonomy within the Conoidea (Bouchet et al., 2011). The study resolved thirteen monophyletic families from the originally polyphyletic family Turridae greatly reducing the number of “turrid” taxa. Bouchet et al. (2011) included fourteen genera within the family Turridae, but it should be noted that fossil taxa have not been taken into account.

As there is no recent publication examining the whole family Turridae (living or fossil) within southeastern Australia it is difficult to estimate the number of species assigned to the family.  Some older studies have attempted to undertake this task using previous classification schemes (e.g. Powell, 1944, 1966; Long, 1981). The family Turridae is still in great need of attention. However, it is not within the scope of this thesis to undertake a task of this enormity.

## 3.6.1 SYSTEMATIC PALAEONTOLOGY

Six species from three genera included in this revision. This does not reflect the true diversity of this family in this region in any way. Due to difficulties in assigning genera and species based on the newest classification system only those species that can be confidently assigned to the family Turridae have been included. Examination of type material and comparison with other Australian species has been used to assign species to genera. Generic assignment is based on Bouchet et al. (2011).

CLASS **GASTROPODA**
ORDER **NEOGASTROPODA**
SUPERFAMILY **CONOIDEA** Fleming, 1822
Family **TURRIDAE** H. & A. Adams, 1853

1853 Turridae, H. & A. Adams, p.87.

### DIAGNOSIS

Shell fusiform, high spired, typically with long siphonal canal. Protoconch often multispiral with riblets or paucispiral and smooth. Axial sculpture weak or absent. Spiral sculpture variable. Posterior sinus on periphery of whorl, “V” shaped. Columella smooth.

### DISTRIBUTION

Palaeocene – Recent. Cosmopolitan.

### REMARKS

The family Turridae as it was defined in Bouchet & Rocroi (2005) is considered to be one of the most complex families to classify due to the numerous supra-specific taxa and high diversity. The most recent classification outlined by Bouchet et al. (2011) has attempted to remedy the taxonomic complications of this family using anatomical data and molecular phylogenies of living taxa (from Puillandre et al., 2008) resulting in the previously polyphyletic family Turridae being reclassified as 13 monophyletic families (including Raphitomidae, Mangeliidae, Borsoniidae and Turridae). This taxonomy follows these latest advances in classifying the “turrids”.

**KEY TO GENERA FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Peripheral keel with gemmules.......................................*Gemmula*
   Peripheral keel without gemmules...............................Go to 2

2. Posterior sinus "V" shaped..........................................*Lophiotoma*
   Posterior sinus "U" shaped..........................................Go to 3

3. Sulcation in front of suture.........................................*Turris*
   Posterior sinus above peripheral keel..........................*Optoturris*

Genus **GEMMULA** Weinkauff, 1875

1875 *Gemmula* Weinkauff, p. 285.
1931 *Eugemmula* Iredale, p.226.

TYPE SPECIES

*Pleurotoma gemmata* Reeve, 1843 by subsequent designation (Cossmann, 1906) = *Gemmula hindsiana* Berry, 1958. Recent, Indo-Pacific.

DIAGNOSIS

Shell elongate-fusiform, tall spire, long siphonal canal, siphonal notch absent. Protoconch multispiral, costate. Spiral sculpture of keels and cords, with gemmulate peripheral keel. Posterior sinus deep, narrow, peripheral.

DISTRIBUTION

?Cretaceous – Recent. Cosmopolitan.

REMARKS

This genus has a wide distribution, mostly in warm seas, and a long fossil record. The genus is distinguished by the gemmulate keel and narrow, conical, multispiral protoconch.

***Gemmula gellibrandensis*** Chapple (1934)

Plate 7, figs. 1a, b.

1934 *Gemmula gellibrandensis* Chapple, p. 163, pl. 19, figs. 3, 3a.

DIAGNOSIS

Shell narrow-fusiform, tall spired, whorls shouldered. Axial sculpture of close set growth lines. Spiral sculpture of closely spaced, coarse, granulose cords on keel, rounded on whorls, threads in interspaces. Outer lip lirate. Posterior sinus wide, deep. Siphonal canal relatively short.

TYPE SPECIMENS

HOLOTYPE: *Gemmula gellibrandensis* NMV, P13688.

PARATYPE: *Gemmula gellibrandensis* NMV, P13689.

DSITRIBUTION

Longfordian (Early Miocene): Victoria (VIC081).

REMARKS

This species is distinguished by the granulose keel.

### Subgenus **CLAVOGEMMULA** Long, 1981

1981 *Clavogemmula* Long, p. 31.

TYPE SPECIES

*Gemmula (Clavogemmula) prima* Long, 1981 by monotypy. Eocene, Australia.

DAIGNOSIS

Shell fusiform, tall spire, short siphonal canal. Spiral sculpture of threads and cords dominant. Peripheral cord gemmulate, weakening on later whorls. Posterior sinus deep, “V” shaped, narrowing at periphery.

DISTRIBUTION

Eocene. Australia.

REMARKS

Long (1981) erected this subgenera by distinguishing it from *Gemmula* s.s. by its smooth protoconch, short twisted siphonal canal and weakly developed axial gemmules.

***Gemmula (Clavogemmula) prima*** Long, 1981

Plate 7, figs. 2a, b.

1981 *Gemmula (Clavogemmula) prima* Long, p. 32, pl. 5, figs. 9, 10.

DIAGNOSIS

Shell fusiform, tall spire, median angulation, concave shoulder. Axial sculpture of strong, elongate gemmulations centred on the periphery and faint growth lines. Spiral sculpture of narrow threads and a simple or double threaded peripheral keel. Siphonal canal short, straight, twisted left.

TYPE SPECIMENS

HOLOTYPE: *Gemmula (Clavogemmula) prima* NMV, P33350.

PARATYPES: *Gemmula (Clavogemmula) prima* NMV, P42852, P42851.

DSITRIBUTION

Johannian - Aldingan (Late Eocene): Victoria (VIC092 (TL)).

REMARKS

The spiral sculpture of this species is somewhat variable. The diagnostic characters of this species are as in the subgenus description.

## Genus **LOPHIOTOMA** Casey, 1904

1904 *Lophiotoma* Casey, p. 130.

1964 *Lophioturris* Powell, p. 407.

TYPE SPECIES

*Pleurotoma tigrina* Lamarck, 1822 by subsequent designation (Woodring, 1928). Recent, Indo-Pacific.

DIAGNOSIS

Shell elongate-fusiform, attenuated spire, siphonal canal long, straight. Protoconch paucispiral to mulitspiral, conical or papillate followed by half whorl with brephic axials. Axial sculpture of obsolete growth lines. Spiral sculpture of elevated, close-set threads. Aperture ovate. Columella smooth. Posterior sinus "V" shaped on the flat or concave peripheral carina.

DISTRIBUTION

Miocene – Recent. ?Cosmopolitan.

REMARKS

This genus is characterised by the position of the posterior sinus. It is restricted to the peripheral keel or the most prominent spiral.

**KEY TO SPECIES FOUND AS FOSSILS IN SOUTHEASTERN AUSTRALIA:**

1. Slender outline, strong peripheral keel.......................................*murrayana*
2. Granulose sculpture near sinus, weak peripheral keel..................*murndaliana*

***Lophiotoma murrayana*** (Pritchard, 1904)

Plate 7, figs. 3a, b.

1904 *Pleurotoma murrayana* Pritchard, p. 335, pl. 19, fig. 10.

DIAGNOSIS

Shell elongate-fusiform, apex blunt, slender, elongate spire. Spire whorls flat to slightly convex. Suture channelled. Axial sculpture of weak growth lines and undulating striae. Spiral sculpture of strong cords and threads, median nodulose keel. Columella smooth, straight. Posterior sinus on peripheral keel.

TYPE SPECIMENS

HOLOTYPE: *Lophiotoma murrayana* NMV, P127950.

DISTRIBUTION

Batesfodian (Middle Miocene): South Australia (SA001 (TL)).

REMARKS

This species closely resembles *L. murndaliana* but differs in its more slender outline, stronger peripheral keel and weaker subsidiary keels.

***Lophiotoma murndaliana*** (Tenison-Woods, 1879)

1879 *Pleurotoma murndaliana* Tenison-Woods, p. 226, pl. 20, fig. 5.
1896 *Hemipleurotoma murndaliana* Cossmann, p. 79.
1944 *Lophiotoma murndaliana* Powell, p. 9.

TYPE SPECIMENS

HOLOTYPE: *Pleurotoma murndaliana* AMS, F1700

DIAGNOSIS

Shell elongate-fusiform, whorls convex. Protoconch multispiral, initially slightly globose. Axial sculpture of growth lines. Spiral sculpture of coarse, irregular cords and threads, granulose near sinus. Canal long, narrow, twisted. Posterior sinus large, situated away from suture.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC038 (TL), VIC083).

REMARKS

Powell (1944) noted that the recording of this species from Limestone Creek, Glenelg River by Dennant & Kitson (1903) is erroneous and is therefore excluded from the geographic range of the species.

## Genus **TURRIS** Batsch, 1789

1799 *Pleurotoma* Lamarck, p. 73.
1966 *Annulaturris* Powell, p. 51.

### TYPE SPECIES

*Murex babylonius* Linnaeus, 1758 by subsequent designation (Dall, 1909). Recent, Indo-Pacific.

### DIAGNOSIS

Shell elongate-fusiform, attenuated spire, siphonal canal long, straight, open. Protoconch multispiral, smooth, papillate. Sculpture variable. Aperture ovate. Columella smooth. Posterior sinus "U" shaped, deep, on a rounded costae above the peripheral keel.

### DISTRIBUTION

?Palaeocene – Recent. ?Cosmopolitan.

### REMARKS

Australian turris species from the Middle Cenozoic differ slightly to the conventional turris description in that they have a short, twisted siphonal canal. Powell (1944) discussed this is more detail.

### ***Turris septemliratus*** (Harris, 1897)

Plate 7, figs. 4a, b.

1897 *Pleurotoma septemlirata* Harris, p. 39, pl. 2, figs. 10a-d.
1900 *Pleurotoma perarata* Cossmann & Pissarro, p. 24.
1944 *Turris septemliratus* Powell, p. 8.

### DIAGNOSIS

Shell fusiform, siphonal canal very short, wide. Suture canaliculate. Axial sculpture of growth lines. Spiral sculpture of cords and threads, increasing in number on later whorls. Aperture large, ovate. Columella smooth. Posterior sinus broad, deep, situated away from suture. Deep, broad sulcation in front of suture.

TYPE SPECIMENS:

SYNTYPES: *Pleurotoma septemlirata* BMNH, G4231, G4233, G5501, G5499.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC038 (TL), VIC028, VIC034).

REMARKS

Harris (1897) separated this species from *Lophiotoma murndaliana*, which he saw as very similar, based on the larger, more tumid shell, the shorter siphonal canal and the characteristic deep, broad sulcation in front of the suture.

## Genus **OPTOTURRIS** Powell, 1944

1944 *Optoturris* Powell, p.12.

TYPE SPECIES

*Pleurotoma optata* Harris, 1897 by original designation. Middle Miocene, Australia.

DIAGNOSIS

Shell fusiform, blunt spire, siphonal canal short, straight. Protoconch multispiral, small, asymmetric, no definite brephic stages. Posterior sinus "U" shaped, shallow, extended over shoulder, situated at the weak peripheral keel.

DISTRBUTION

Miocene. Australia.

REMARKS

Powell's (1944) description is somewhat vague with the emphasis heavily placed on the posterior sinus.

### ***Optoturris optatus*** (Harris, 1897)

Plate 7, figs. 5a, b.

1897 *Pleurotoma optata* Harris, p. 44, pl.3, figs. 4a-b.

1944 *Optoturris optatus* Powell, p. 12.

DIAGNOSIS

Shell fusiform, whorls slightly convex. Axial sculpture of growth lines and costae in early whorls. Spiral sculpture of closely-spaced threads. Suture bound anteriorly and posterior by keels, anterior keel dominant. Aperture elongate- pyriform. Outer lip thin. Posterior sinus shallow, wide. Siphonal canal long, recurved.

TYPE SPECIMENS

HOLOTYPE: *Pleurotoma optata* BMNH, 48052.

DISTRIBUTION

Janjukian – Mitchellian (Late Oligocene – Late Miocene): Victoria (VIC022 (TL), VIC038).

REMARKS

The dominant anterior keel characterises this species.

## PLATE 7 – TURRIDAE

**Figure 1** *Gemmula gellibrandensis,* P13688, holotype, Gellibrand Marl of Gellibrand, VIC:

a) Shell (length = 18mm)

b) Protoconch

**Figure 2** *Gemmula (Clavogemmula) prima,* P33350, holotype, Browns Creek Clay of Johanna, VIC:

a) Shell (length = 13.4mm)

b) Protoconch

**Figure 3** *Lophiotoma murrayana,* P127950, holotype, Cadell Formation of the River Murray, SA:

a) Shell (length = 28mm)

b) Protoconch

**Figure 4** *Turris septemliratus,* no specimen number, non-type, Muddy Creek Marl of Muddy Creek, VIC:

a) Shell (length = 45mm)

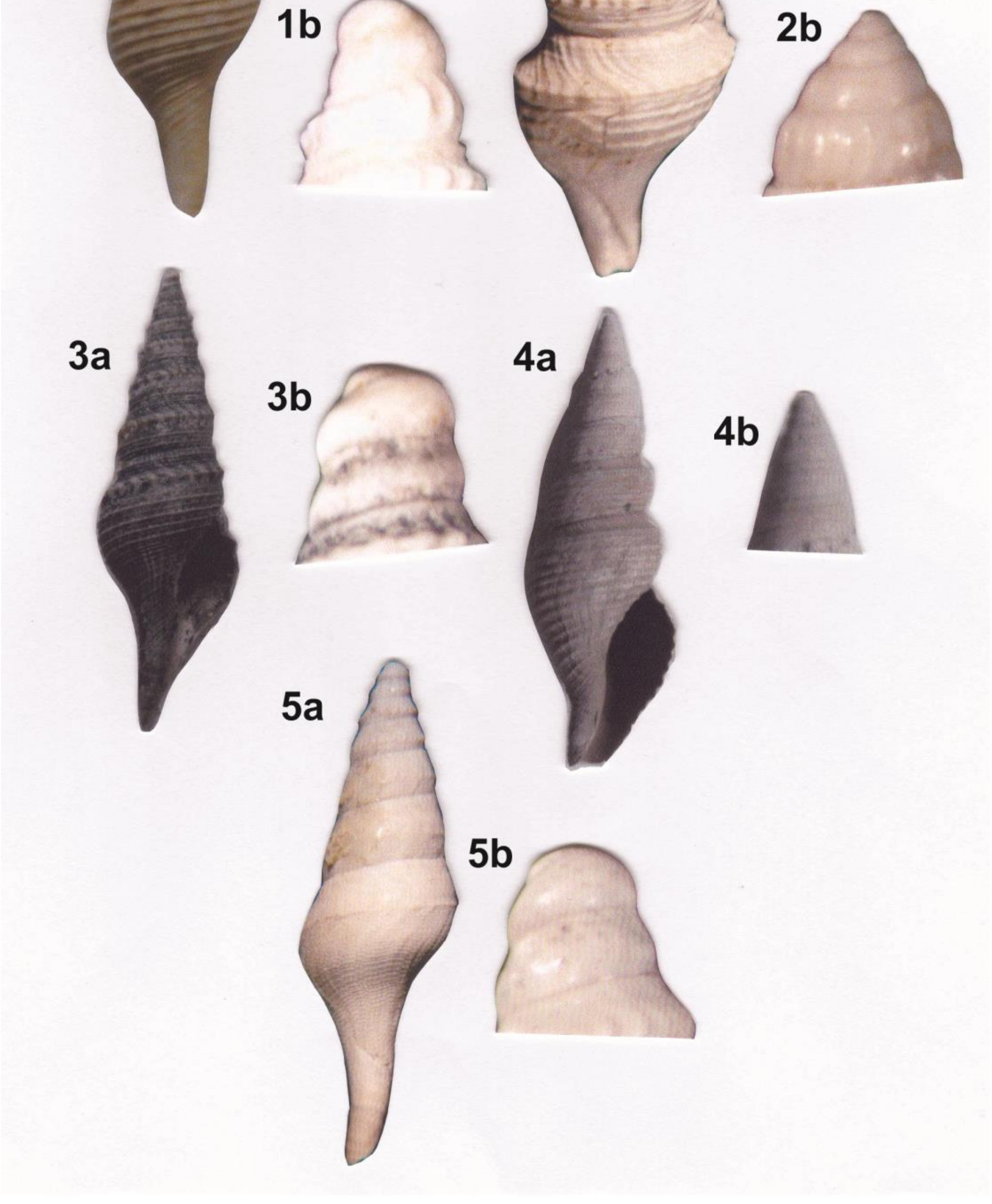
b) Protoconch

**Figure 5** *Optoturris optatus,* P6832, non-type, Fyansford Formation of Fossil Beach, VIC:

a) Shell (length = 16.5mm)

b) Protoconch

## PLATE 7 – TURRIDAE



# CHAPTER 4

# PHYLOGENETIC ANALYSES OF CENOZOIC GASTROPODS FROM SOUTHEASTERN AUSTRALIA

In this chapter the evolutionary relationships of the gastropod taxa included in this thesis are considered. Phylogenetic analyses are used to establish the relationships between taxa and this will be later used to determine the plesiomorphic larval strategy and the order and timing of switches in developmental mode (Chapter 5).

Within the literature, concerns have been raised about the difficulties of inferring reliable phylogenies from fossil gastropods (e.g. Harasewych, 1984; Emberton, 1995; Frýda, 1999; Wagner, 2001). Many specimens can only offer teleoconch (adult) characters due to loss of anatomical and genetic material. There is a general assumption that gastropod shells are simple structures offering few informative characters and characters states (e.g. Schopf et al., 1975; Smith, 1994).

The potential problems in morphologically based phylogenetic analyses are dealt with in some detail by Wagner (2001). The number of teleoconch characters may depend on which taxonomic level studies are carried out at (e.g. Wagner, 1999; 2001). It is noted that teleoconch characters are often highly homoplastic and as a result do not reveal true phylogenetic signals (Wagner, 2001). However, the same study also suggests that phylogenetic patterns do influence the distribution of teleoconch characters. As more sophisticated methods are developed and our understanding of characters and characters states improve, robust phylogenetic trees may yet be resolved from fossil gastropods (Bieler, 1992; Wagner, 2001).

A number of studies have combined morphological and anatomical data of extant taxa to expand the number of available characters for particular groups of gastropods (e.g. Reid, 1989; Allmon, 1990; Ponder, 1997; Haasl, 2000; Collin, 2003). Recent studies focusing entirely on shell morphology have sought to find innovative approaches to character selection and coding such as separating juvenile and adult characters (Papadopoulos et al.,

2004) or examining the geometric morphometrics of gastropod shells (Smith & Hendricks, 2013).

Many studies examining the evolutionary relationships of gastropods concentrate on molecular phylogenies. These studies generally exclude “unreliable” morphological characters, instead concentrating on DNA sequences (and sometimes radula) to resolve phylogenies, with varying levels of success. The neogastropods have been one area of focus (e.g. Haarasewych et al., 1997; Cunha et al., 2009), whilst other researchers have concentrated on examining the complex relationships within the Conoidea, in particular the “turrids” (e.g. Puillandre et al., 2008, 2011; Fedosov et al., 2011).

Of the families included in this thesis the “turrids” (= Raphitomidae, Borsoniidae, Mangeliidae and Turridae) are the most well resolved in terms of phylogenetic analysis (e.g. Puillandre et al., 2008, 2011; Bouchet et al., 2011), although most of this work has concentrated purely on molecular data from living species at higher taxonomic levels and fossil species are yet to be fully examined. The nassariids have received scant attention, although Haasl (2000) has attempted to resolve phylogenetic relationships at generic level based on conchological and anatomical data. Of all the families in this thesis, it is the volutes that are most in need of attention. A single paper examines the evolutionary relationships between different genera (Bondarev, 1995), but the taxonomic division of the subfamilies has since been re-evaluated (e.g. Darragh, 1988) suggesting that this group needs to undergo further phylogenetic analyses to resolve subfamilial and generic relationships.

## 4.1 METHODS

The phylogenetic relationships of Cenozoic gastropods from southeastern Australia are resolved through cladistic analyses using morphological characters for all taxa examined as part of the taxonomic revision (see Chapter 3).

| | **Species** | **Genus** | **Subfamily** |
|---|---|---|---|
| **Volutidae** | √<br>(Athletinae & Volutinae) | √<br>(Amoriinae & Zidoninae) | √ |
| **Nassariidae** | - | √ | - |
| **Rapitomidae** | - | - | - |
| **Borsoniidae** | - | √ | - |
| **Mangeliidae** | - | √ | - |
| **Turridae** | - | √ | - |

**Table 4.1** Table showing taxonomic level of analysis carried out for each family. Ticks indicate the taxonomic level that analysis has been carried out at for each family. Subfamily level analysis is only carried out for the Volutidae as no other families include subfamilies.

Species level analysis is carried out for genera with more than one developmental mode (Volutidae: Athletinae & Volutinae). Genus level analysis is performed for all families or subfamilies except the Raphitomidae, which has too few taxa to be analysed. Genus level analysis is based on the type species of each genus to avoid complications associated with intragreneric variability, even if the type species is not present in the Cenozoic of southeastern Australia. Families or subfamilies with only one or two genera are analysed as part of larger composite trees. Subfamilial analysis is performed only for the family Volutidae because others families either have no representatives from Cenozoic southeastern Australia from other subfamilies or have not been assigned subfamilies. A summary of analyses carried out on the taxa included in this study is presented in Table 4.1.

Due to the small number of available characters, larger trees are created as composites of genus and species level trees using representatives from each subfamily or family. A composite tree of all genera included in this thesis is based on analysis by Cunha et al. (2009) which is one of the most recent articles examining the molecular phylogeny of neogastropod families.

Characters used in the analyses come from examination of specimens during the taxonomic revision of the species used in this research (see Chapter 3, Fig. 3.1 for main morphological characters examined). Wherever possible characters are based on structural differences in shell morphology and "soft characters", such as overall size, are avoided. Where size-based characters are used, they are presented as ratios to avoid the issue of large features being due to overall body size. Where a character has only two character states (e.g. absent and present), they are coded as 0 and 1. Where a character is given more than two states, they are assigned 0, 1, 2, 3 etc., from simple to complex or small to large. Metric characters have been measured with electronic callipers to the nearest 0.1mm and character states for metric characters are established using gap analysis. Metric characters with more than two states have been ordered. Within the data matrix, missing or unknown characters are coded as question marks. Characters are assigned equal weighting. Where character information for the type genus is not known, characters are based on the species used within this study. Characters relating to the protoconch are not included to avoid circularity when examining switches in larval mode (Chapter 5).

Phylogenetic analysis is carried out using the Macintosh application PAUP v. 4.0b10 (Swofford, 2002). Due to the small size of the datasets used in this research it is possible to use the most comprehensive search possible, an exhaustive search, which will find the most parsimonious tree or trees (MPT), unlike other methods such as heuristic and branch and bound searches which cannot definitely find the MPT. Where an exhaustive search produces more than one tree, common components of these trees are analysed using a majority rule consensus. Where more than four trees are produced by an exhaustive search, characters are rescaled to the Rescaled Consistency Index (RCI). This method gives the maximum weight to characters showing no homoplasy and down-weights homoplaseous characters based on the numbers of times they have evolved.

The consistency index (CI) and retention index (RI) are reported as a measure of robustness. Tree support is measured using two statistical methods. The Bootstrap method randomly chooses characters from the data matrix to create a dataset of the same size as the original before determining the most parsimonious solution of this new dataset. This process is repeated (usually ~1000 times) and the results are compared with the original MPT. The higher the bootstrap percentage, the stronger the phylogenetic signal. Bootstrap values less than 50% are not presented. Bremer support is a method commonly used for small, morphologically-based datasets and is therefore the most useful method for assessing tree strength when only fossil taxa are considered. The method examines the number of extra steps required for the MPT to collapse. The greater the number of steps required for the tree to collapse, the more robust the tree.

## 4.2 FAMILY VOLUTIDAE

Analysis of the family Volutidae is initially split into subfamilies, and generic or species level analysis is carried out. A composite tree is based on subfamilial level phylogenetic analysis. Species level analysis is carried out on the subfamilies Athletinae and Volutinae. Generic level analysis is carried out on the subfamilies Amoriinae and Zidoninae. The subfamily Scaphellinae is only included in the composite tree.

### **4.2.1** SUBFAMILY ATHLETINAE

All nine species assigned to the subfamily Athletinae as part of the taxonomic revision (Chapter 3) belong to the genus *Athleta (Ternivoluta).* Of the nine species one is planktotrophic and eight are direct developers. As a result phylogenetic analysis is carried out at species level. The species *Mitra (Mitra) mitra* (the type species of the genus *Mitra*) is selected as the outgroup for this analysis due to its close relationship with the family Volutidae.

The 24 characters and their states are shown in Table 4.2 and the data matrix is shown in Table 4.3.

An exhaustive search produced a single MPT with a tree length of 67 steps, CI = 0.6269, RI = 0.5192 (Figure 4.1). Bootstrap values for this tree are extremely low suggesting the tree is poorly supported. Bremer support also suggests this tree is not strongly supported with all nodes collapsing after a single step increase (68 steps). The tree supports the close relationship between the subspecies of *Athleta (Ternivoluta) antiscalaris*, particularly the closely related *A. (t.) antiscalaris antiscalaris* and *A. (T.) antiscalaris levior*, but the non-monophyletic relationship between subspecies of *A. (T.) anticingulata* seems to need more attention based on this analysis, either to re-evaluate the taxonomic position of these subspecies or to examine the evolution of the subspecies in more detail. In the taxonomic revision of this subfamily, assignment of *Athleta (Athleta) wangerrip* was revised and the decision was made to move the species into the subgenus *Athleta (Ternivoluta)*. Based on the phylogenetic analysis this decision would seem to be appropriate.

**Characters and states**

1. *Shell height to width ratio*: Up to 2.5 (0); 2.5 or more (1).
2.* *Body whorl height to spire height ratio*: Up to 3.0 (0); 3.0 – 3.9 (1); 4.0 – 4.9 (2); 5.0 or more (3).
3.* *Aperture height to width ratio*: Up to 4.0 (0); 4.0 – 5.0 (1); 5.0 or more (2).
4.* *Body whorl height to aperture height ratio*: 1.0 or less (0); 1.1 – 1.5 (1); 1.6 or more (2).
5. *Shell shape*: Elongate fusiform (0); fusiform (1); narrowly fusiform (2); pyriform (3).
6. *Spire form*: Subconical (0); gradate (1); high gradate (2).
7. *Axial sculpture development*: Weakly developed (0); strongly developed (1).
8. *Axial sculpture on early teleoconch whorls*: Absent (0); present (1).
9. *Axial sculpture on late teleoconch whorls*: Absent (0); wide, strong costae (1); narrow, strong costae (2).
10. *Axial costae interspaces*: Absent (0); wide (1); narrow (2).
11. *Axial sculpture extension*: Absent (0); confined to posterior third of body whorl (1); extending over half of body whorl (2).
12. *Number of costae present on body whorl*: Absent (0); 1-19 (1); 20 or more (2).
13. *Axial costae form*: Absent (0); sigmoidal (1); non-sigmoidal (2).
14. *Axial costae form at shoulder*: Absent (0); rounded (1); subspinose (2); spinose (3); nodulose (4).
15. *Spiral sculpture development*: Weakly developed (0); strongly developed (1).
16. *Spiral sculpture on early teleoconch whorls*: Absent (0); present (1).
17. *Spiral sculpture on body whorl*: Weakly developed (0); strongly developed (1).
18. *Extension of spiral sculpture on body whorl*: Restricted to anterior (0); covering whole body whorl (1).
19. *Suture type*: Simple, flush with shell (0); whorls concave at suture, ledged (1); canaliculate, distinct groove (2).
20. *Subsutural nodules*: Absent (0); subspinose (1); spinose (2).
21. *Whorl shouldered/angulate*: Angulate (0); shouldered (1).
22. *Whorl shoulder slope*: Absent (0); convex (1); concave (2).
23. *Columella major plaits*: Less than 3 (0); 3 or more (1).
24. *Columella minor plaits*: Less than 2 (0); 2 or more (1).

**Table 4.2** Characters and states used in species level phylogenetic analysis of the subfamily Athletinae. * = ordered characters.

| **Character matrix** | |
|---|---|
| *Mitra (Mitra) mitra ** | 10120 00000 00000 00000 001? |
| *Athleta (Ternivoluta) wangerrip* | 01101 01111 21230 01012 1100 |
| *Athleta (Ternivoluta) curvicostata* | 00112 11122 22110 01021 1100 |
| *Athleta (Ternivoluta) anticingulata anticingulata* | 01011 11121 21110 01011 1111 |
| *Athleta (Ternivoluta) anticingulata craticula* | 00211 11122 22241 11111 1111 |
| *Athleta (Ternivoluta) subcrenulifera* | 10110 21122 12221 11122 1101 |
| *Athleta (Ternivoluta) antiscalaris antiscalaris* | 01011 11111 11131 11112 1201 |
| *Athleta (Ternivoluta) antiscalaris levior* | 02111 11111 11131 01012 1211 |
| *Athleta (Ternivoluta) antiscalaris antispinosa* | 03113 01111 21230 00012 1211 |
| *Athleta (Ternivoluta) bungae* | 03213 01112 02240 01020 0011 |

**Table 4.3** Data matrix for nine *Athleta* species plus the outgroup *Mitra (Mitra) mitra* (*).

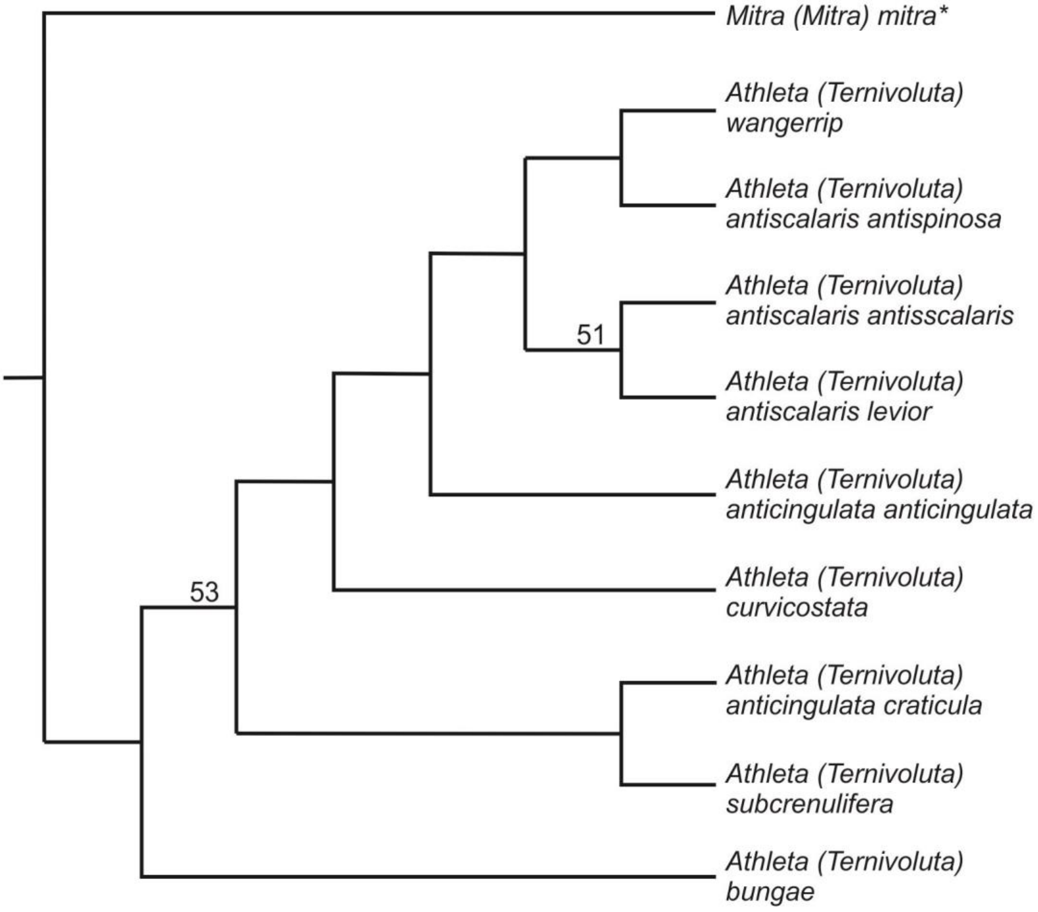


**Figure 4.1** Cladogram for Cenozoic species of the subgenus Athleta (Ternivoluta) plus the outgroup *Mitra (Mitra) mitra**. Bootstrap support values based on 1000 replicates are indicated for each branch.

### **4.2.2** SUBFAMILY VOLUTINAE

In this thesis the subfamily Volutinae includes five species from two genera (*Lyria* and *Leptoscapha*) of which one is planktotrophic, two are lecithotrophic and two are direct developers. Phylogenetic analysis is carried out at species level. The species *Mitra (Mitra) mitra* is selected as the outgroup. The 21 characters and their states are shown in Table 4.4 and the data matrix is shown in Table 4.5.

**Characters and states**

1.* *Shell height to width ratio*: Less than 2.0 (0); 2.0 – 2.9 (1); 3.0 or more (2).
2. *Body whorl height to spire height ratio*: Less than 2.5 (0); 2.5 or more (1).
3. *Aperture height to width ratio*: Less than 3.0 (0); 3.0 or more (1).
4. *Body whorl height to aperture height ratio*: Less than 1.5 (0); 1.5 or more (1).
5. *Shell shape*: Elongate-fusiform (0); elongate-ovate (1); ovate (2).
6. *Axial sculpture development*: Weakly developed (0); strongly developed (1).
7. *Axial sculpture on early teleoconch whorls*: Absent (0); present (1).
8. *Axial sculpture on late teleoconch whorls*: Absent (0); weakly developed (1) strongly developed (2).
9. *Axial costae interspaces*: Absent (0); narrow (1); wide (2).
10. *Extension of axial costae on body whorl*: Absent (0); obsolete anteriorly (1); covering whole whorl (2).
11. *Number of costae present on body whorl*: Absent (0); less than 20 (1); more than 20 (2).
12. *Spiral sculpture development*: Absent (0); present (1).
13. *Spiral sculpture on early teleoconch whorls*: Absent (0); present (1).
14. *Spiral sculpture on body whorl*: Absent (0); present (1).
15. *Extension of spiral sculpture on body whorl*: Absent (0); restricted to anterior (1); covering whole whorl (2).
16. *Suture type*: Simple, flush with shell (0); ledged, whorls concave at suture (1); canaliculate, distinct groove (2).
17. *Columella plaits*: Two (0); three (1); more than three (2).
18. *Posterior denticle*: Absent (0); present (1).
19. *Siphonal notch*: Absent (0); shallow (1); deep (2).
20. *Spire form*: Subconical (0); acute (1); squat (2); gradate (3).
21. *Outer lip*: Sharp (0); thickened (1).

**Table 4.4** Characters and states used in phylogenetic analysis of the subfamily Volutinae. * = ordered character.

**Character matrix**

| | |
|---|---|
| *Mitra (Mitra) mitra** | 20110 00000 01011 02120 1 |
| *Lyria semiacuticostata* | 11111 11211 20000 21121 0 |
| *Lyria acuticostulata* | 11012 11222 21112 20012 0 |
| *Lyria harpularia* | 01002 11222 21111 20023 0 |
| *Lyria gemmata* | 10102 11211 21011 20110 1 |
| *Leptoscapha crassilabrum* | 10102 00100 11112 11100 1 |

**Table 4.5** Data matrix for five Volutinae species plus the outgroup *Mitra (Mitra) mitra* (*).

An exhaustive search produced a single MPT with a tree length of 39 steps, CI = 0.8462, RI = 0.6667 (Figure 4.2). Bootstrap values are moderately high and Bremer support shows that all nodes collapse after an additional 4 steps (43 steps) indicating that the tree is moderately well supported. The close relationship between *L. acuticostulata* and *L. harpularia* is the most strongly supported. However, the tree does not strongly support the suggestion in the taxonomic revision that *L. semiacuticostata* and *L. gemmata* are the most similar of these taxa. The tree supports the monophyletic genus *Lyria*.

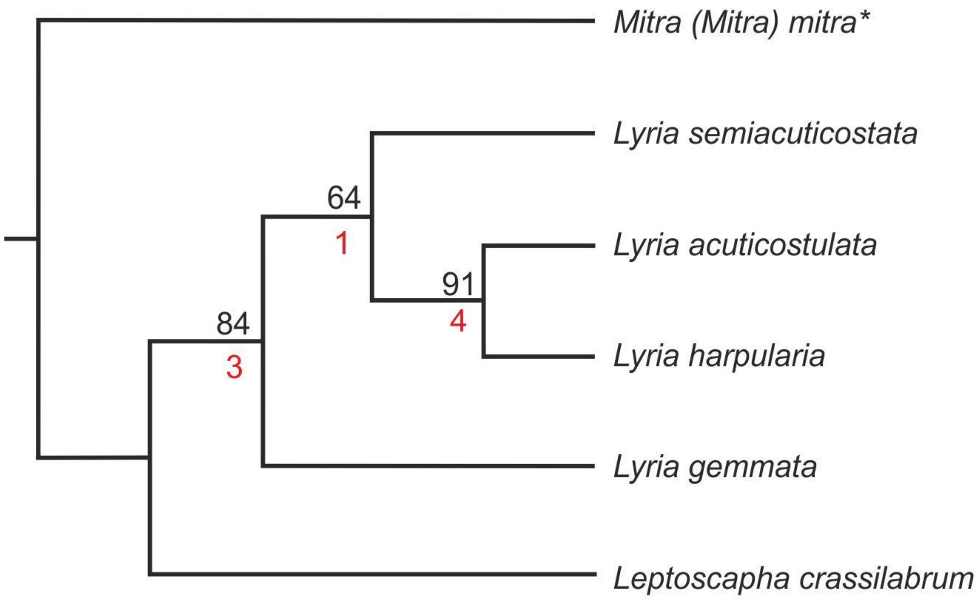


**Figure 4.2** Cladogram for Cenozoic species of the subfamily Volutinae plus *Mitra (Mitra) mitra**. Bootstrap support % based on 1000 replicates indicated for each branch (in black). Bremer support values indicated at each node (in red).

### **4.2.3** SUBFAMILY AMORIINAE

The taxonomic revision of this family includes 24 direct developing species assigned to three genera: *Amoria, Nannamoria* and *Notovoluta*. Phylogenetic analysis is carried out at genus level using the type species for each genus. The genus *Mitra* is selected as the outgroup.

The 18 characters and their states used in this phylogenetic analysis are shown in Table 4.6 and the data matrix is shown below in Table 4.7.

**Characters and states**

1. *Shell height to width ratio*: 2.5 or less (0); more than 2.5 (1).
2. *Body whorl height to spire height ratio*: 2.5 or less (0); more than 2.5 (1).
3. *Aperture height to width ratio*: Less than 5.0 (0), 5.0 or more (1).
4. *Body whorl height to aperture height ratio*: Less than 1.5 (0); 1.5 or more (1).
5. *Shell shape*: Ovate (0); fusiform (1); elongate-fusiform (2).
6. *Axial sculpture development*: Weakly developed (0); strongly developed (1).
7. *Axial sculpture on early teleoconch whorls*: Absent (0); present (1).
8. *Axial sculpture on late teleoconch whorls*: Absent (0); present (1).
9. *Spiral sculpture*: Absent (0); present (1).
10. *Suture type*: Flush (0); ledged (1).
11. *Whorl form*: Angulate (0); shouldered (1).
12. *Columella major plaits*: 4(0); 5 (1).
13. *Columella minor plaits*: 1 (0); 2 (1).
14. *Aperture form*: Elongate (0); narrowly-elliptical (1).
15. *Siphonal canal dorsally reflexed*: Absent (0); present (1).
16. *Siphonal notch development*: Weakly developed (0); strongly developed (1).
17. *Siphonal fasciole development*: Weakly developed (0); strongly developed (1).
18. *Outer lip thickening*: Absent (0); present (1).

**Table 4.6** Characters and states used in generic level phylogenetic analysis of the subfamily Amoriinae. * = ordered characters.

**Character matrix**

| | |
|---|---|
| *Mitra** | 10012 00010 01?00 1?0 |
| *Amoria* | 01101 00001 00010 101 |
| *Nannamoria* | 00100 01111 00000 001 |
| *Notovoluta* | 10001 11111 10111 110 |

**Table 4.7** Data matrix for the subfamily Amoriinae plus the outgroup *Mitra* (*).

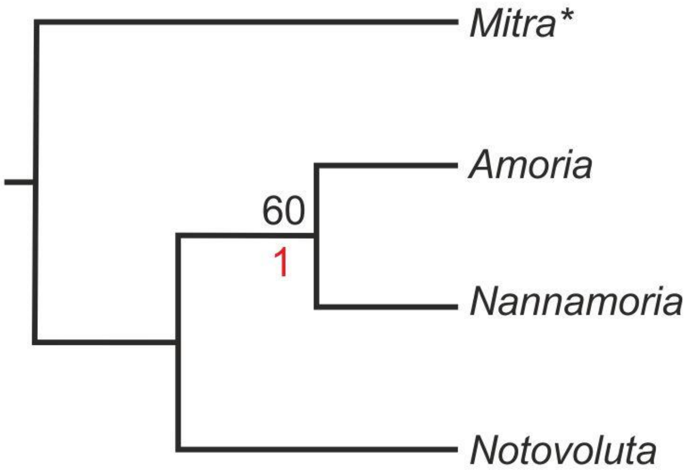


**Figure 4.3** Cladogram for Cenozoic Amoriinae genera plus *Mitra**. Bootstrap support % based on 1000 replicates indicated for each branch (in black). Bremer support values indicated at each node (in red).

An exhaustive search produced a single MPT with a tree length of 22 steps, CI = 0.8636, RI = 0.5000 (Figure 4.3). Bootstrap and Bremer support values indicate that the tree is not very well supported. However, the analysis does support the taxonomy laid out in the previous chapter in identifying *Amoria* and *Nannamoria* as sister taxa.

### **4.2.4** SUBFAMILY ZIDONINAE

Phylogenetic analysis is carried out at generic level for the subfamily Zidoninae and includes 30 species assigned to six genera (*Alcithoe (Alcithoe), Alcithoe (Waihaoia), Ericusa, Livonia, Notopeplum, Cymbiola*). Of these 30 species, 29 are direct developers and one is planktotrophic. The genus *Mitra* is selected as the outgroup.

The 19 characters and their states used in this phylogenetic analysis are shown in Table 4.8 and the data matrix is shown below in Table 4.9.

**Characters and states**

1.* *Shell height to width ratio*: Less than 2.0 (0); 2.0 – 2.9 (1); 3.0 or more (2).
2. *Body whorl height to spire height ratio*: Less than 5.0 (0); 5.0 or more (1).
3.* *Aperture height to width ratio*: Less than 3.0 (0); 3.1 – 4.0 (1); 4.1 – 5.0 (2); 5.0 or more (3).
4. *Body whorl height to aperture height ratio*: Less than 1.5 (0); 1.5 or more (1).
5. *Shell shape*: Broadly fusiform (0); ovate-fusiform (1); ovate (2).
6. *Axial sculpture development*: Weakly developed (0); strongly developed (1).
7. *Axial sculpture on early teleoconch whorls*: Absent (0); present (1).
8. *Axial sculpture on late teleoconch whorls*: Absent (0); present (1).
9. *Costae form at shoulder*: Absent (0); rounded (1); nodulate (2); spinose (3).
10. *Whorl shoulder/angulate*: Angulate (0); shouldered (1).
11. *Spiral sculpture*: Absent (0); present (1).
12. *Suture form*: Flush (0); ledged (1).
13. *Spire form*: Subconical (0); elongate (1); gradate (2); rapidly tapered (3).
14. *Columella plaits*: Less than 4 (0); 4 or more (1).
15. *Outer lip reflexed*: Absent (0); present (1).
16. *Outer lip wing-like extension*: Absent (0); present (1).
17. *Aperture form*: Elongate (0); ovate (1); lenticular (2).
18. *Siphonal notch*: Shallow (0); deep (1).
19. *Siphonal fasciole*: Absent (0); weakly developed (1); strongly developed (2).

**Table 4.8** Characters and states used in generic level phylogenetic analysis of the subfamily Zidoninae. * = ordered characters.

**Character matrix**

| | |
|---|---|
| *Mitra ** | 20210 00000 10011 001? |
| *Alcithoe (Alcithoe)* | 10100 11120 01111 1012 |
| *Alcithoe (Waihaoia)* | 10110 11110 11111 0101 |
| *Ericusa* | 10001 00000 11100 1200 |
| *Livonia* | 01002 00000 11201 1200 |
| *Notopeplum* | 11312 00000 01300 0201 |
| *Cymbiola* | 11202 11131 01210 0012 |

**Table 4.9** Data matrix for the six genera of the subfamily Zidoninae plus the outgroup *Mitra* (*).

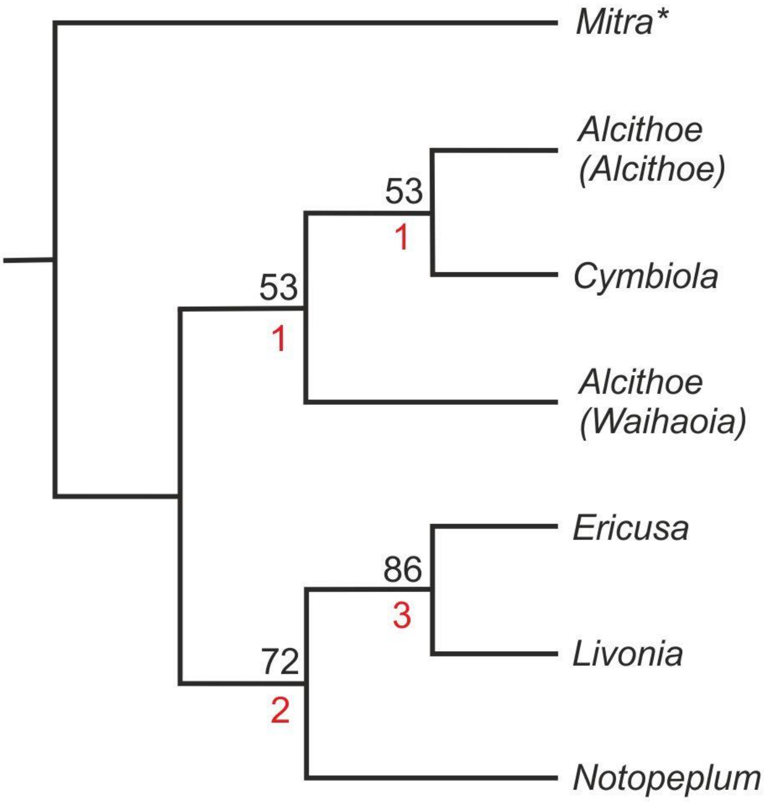


**Figure 4.4** Cladogram for Cenozoic genera from the subfamily Zidoninae plus *Mitra**. Bootstrap support % based on 1000 replicates indicated for each branch (in black). Bremer support values indicated at each node (in red).

An exhaustive search produced a single MPT with a tree length of 41 steps, CI = 0.7073, RI = 0.6000 (Figure 4.4). Bootstrap values suggest that the tree is moderately well supported. Bremer support values indicate that all nodes on the tree collapse after an additional 3 steps (44 steps). The tree indicates that there are two major clades within the subfamily Zidoninae. Bootstrap values suggest the *Ericusa* + *Livonia* + *Notopeplum* clade is more strongly supported than the *Alcithoe (Alcithoe)* + *Cymbiola* + *Alcithoe (Waihaoia*) clade. Surprisingly, the tree does not place *Alcithoe (Alcithoe)* and *Alcithoe (Waihaoia)* as sister taxa suggesting either a review of the taxonomy of this genus is needed or that attempts to resolve this relationship using anatomical or molecular phylogenies are necessary.

### **4.2.5** FAMILY VOLUTIDAE COMPOSITE TREE

Taxa from the family Volutidae include all three larval strategies considered as part of this thesis: planktotrophy, lecithotrophy and direct development. Subfamilial level phylogenetic analysis is carried out on five subfamilies (Athletinae, Volutinae, Scaphellinae, Amoriinae and Zidoninae) using a representative genus from each (*Athleta (Ternivoluta)*, *Lyria*, *Scaphella (Aurinia)*, *Amoria* and *Livonia*, respectively). The family Scaphellinae has not been dealt with in previous analyses in this chapter due to the fact that only a single species from this family is included in this thesis. The genus *Notovoluta* is also included due to some controversy regarding its placement in the subfamily Amoriinae (Darragh, 1988 for discussion). The genus *Mitra* from the family Mitridae is selected as the outgroup, as has been the case for generic level analyses for individual subfamilies. Anatomical data for the genera used in this analysis is extremely limited and is therefore excluded from this analysis. The 22 characters and their states used in this phylogenetic analysis are shown in Table 4.10 and the data matrix is shown in Table 4.11.

| | **Characters and states** |
|---|---|
| 1. | *Shell height to width ratio*: Less than 2.5 (0); 2.5 or more (1). |
| 2.* | *Body whorl height to spire height ratio*: Less than 2.5 (0); 2.5 – 5.0 (1); 5.0 or more (2). |
| 3.* | *Aperture height to width ratio*: Less than 3.0 (0); 3.0 – 5.0 (1); 5.0 or more (2). |
| 4. | *Body whorl height to aperture height ratio*: Less than 1.5 (0); 1.5 or more (1). |
| 5. | *Shell shape*: Elongate-fusiform (0); fusiform (1); ovate-fusiform (2); ovate (3). |
| 6. | *Spire form*: Subconical (0); gradate (1); elongate conical (2). |
| 7. | *Aperture form*: Elongate (0); elliptical (1); lenticular (2). |
| 8. | *Whorl shouldered/angulate*: Angulate (0); shouldered (1). |
| 9. | *Suture form*: Flush (0); ledged (1); canaliculate (2). |
| 10. | *Axial sculpture development*: Weakly developed (0); strongly developed (1). |
| 11. | *Axial sculpture on early teleoconch whorls*: Absent (0); present (1). |
| 12. | *Axial sculpture on late teleoconch whorls*: Absent (0); present (1). |
| 13. | *Spiral development*: Absent (0); present (1). |
| 14. | *Spiral sculpture on early teleoconch whorls*: Absent (0); present (1). |
| 15. | *Spiral sculpture on late teleoconch whorls*: Absent (0); present (1). |
| 16. | *Extension of spiral sculpture*: Absent (0); spire whorls (1); anterior of body whorl (2). |
| 17. | *Major columella plaits*: Less than 3 (0); more than 3 (1). |
| 18. | *Minor columella plaits*: 2 or less (0); more than 2 (1). |
| 19. | *Outer lip form*: Sharp (0); lirate (1); thickened (2); wing-like (3). |
| 20. | *Siphonal canal reflexed*: Absent (0); present (1). |
| 21. | *Siphonal notch development*: Absent (0); shallow (1); deep (2). |
| 22. | *Siphonal fasciole development*: Absent (0); weakly developed (1); strongly developed (2). |

**Table 4.10** Characters and states used in subfamilial level phylogenetic analysis of volutes. * = ordered characters.

| **Character matrix** | |
|---|---|
| Mitridae (*Mitra*)* | 10110 00000 00100 21?20 2? |
| Athletinae (*Athleta (Ternivoluta)*) | 02101 10121 10100 21110 00 |
| Volutinae (*Lyria*) | 01102 10021 11100 20000 12 |
| Scaphellinae (*Scaphella (Aurinia)*) | 11111 01020 10000 10020 00 |
| Amoriinae (*Amoria*) | 12201 01010 00100 01020 21 |
| Amoriinae (*Notovoluta*) | 10101 01111 11111 11001 22 |
| Zidoninae (*Livonia*) | 02003 12010 00111 10030 10 |

**Table 4.11** Data matrix for the five volute subfamilies plus the outgroup *Mitra**.

An initial exhaustive search produced 18 MPTs (CI = 0.6600, RI = 0.3929) with a tree length of 50 steps. Analysis was repeated following a character reweighting according to RCI producing a single MPT (CI = 0.7309, RI = 0.5366) with a tree length of 35 steps (Figure 4.5). Bootstrap values for this tree are extremely low and Bremer support values indicate that all nodes of the tree collapse after an additional two steps (37 steps).

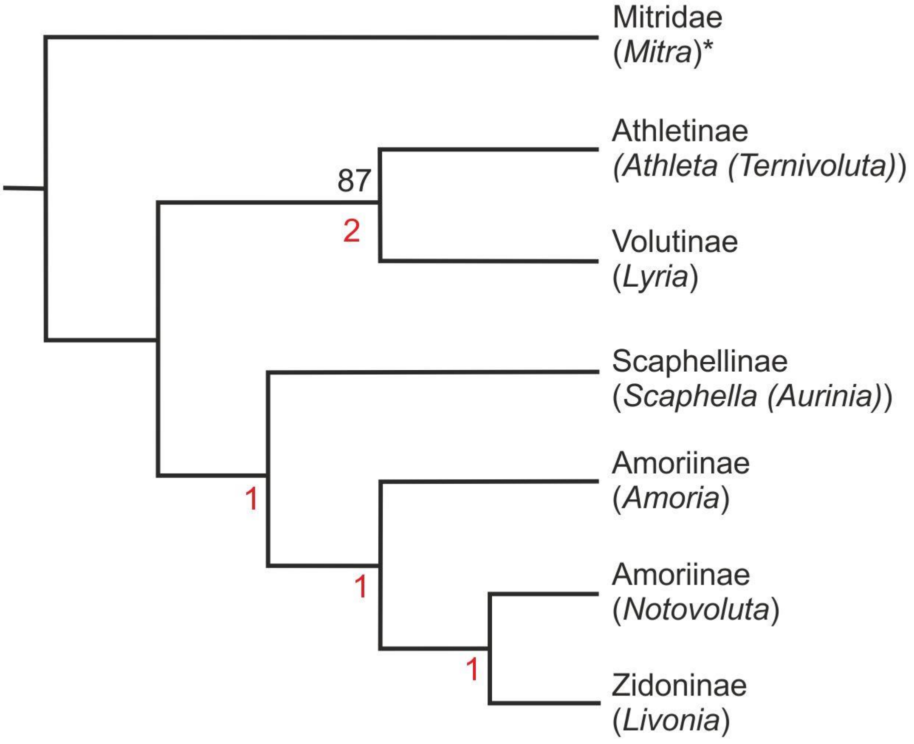


**Figure 4.5** Cladogram of Cenozoic volute subfamilies plus Mitridae. Bootstrap support % based on 1000 replicates indicated for each branch (in black). Bremer support values indicated at each node (in red).

The tree indicates that the clade Athletinae + Volutinae is well supported but that the rest of the tree lacks support. The cladogram suggests that the genus *Notovoluta* may be better placed in the subfamily Zidoninae than in the Amoriinae. The difficulty in placing

*Notovoluta* in a subfamily has been discussed in the Chapter 3. As there is no recent publication that deals with subfamilial phylogenies of this family it is not possible to compare this tree with others that use different methods or characters. As the majority of volute species used in this thesis are fossils, it is only possible to base phylogenetic analyses on morphological characters, which are somewhat limited. A composite tree is presented comprised of individual subfamily trees (Figures 4.1, 4.2, 4.3, 4.4) and the family level tree (Figure 4.6). This composite tree is shown in Figure 4.6. The genus *Notovoluta* is retained in the subfamily Amoriinae.

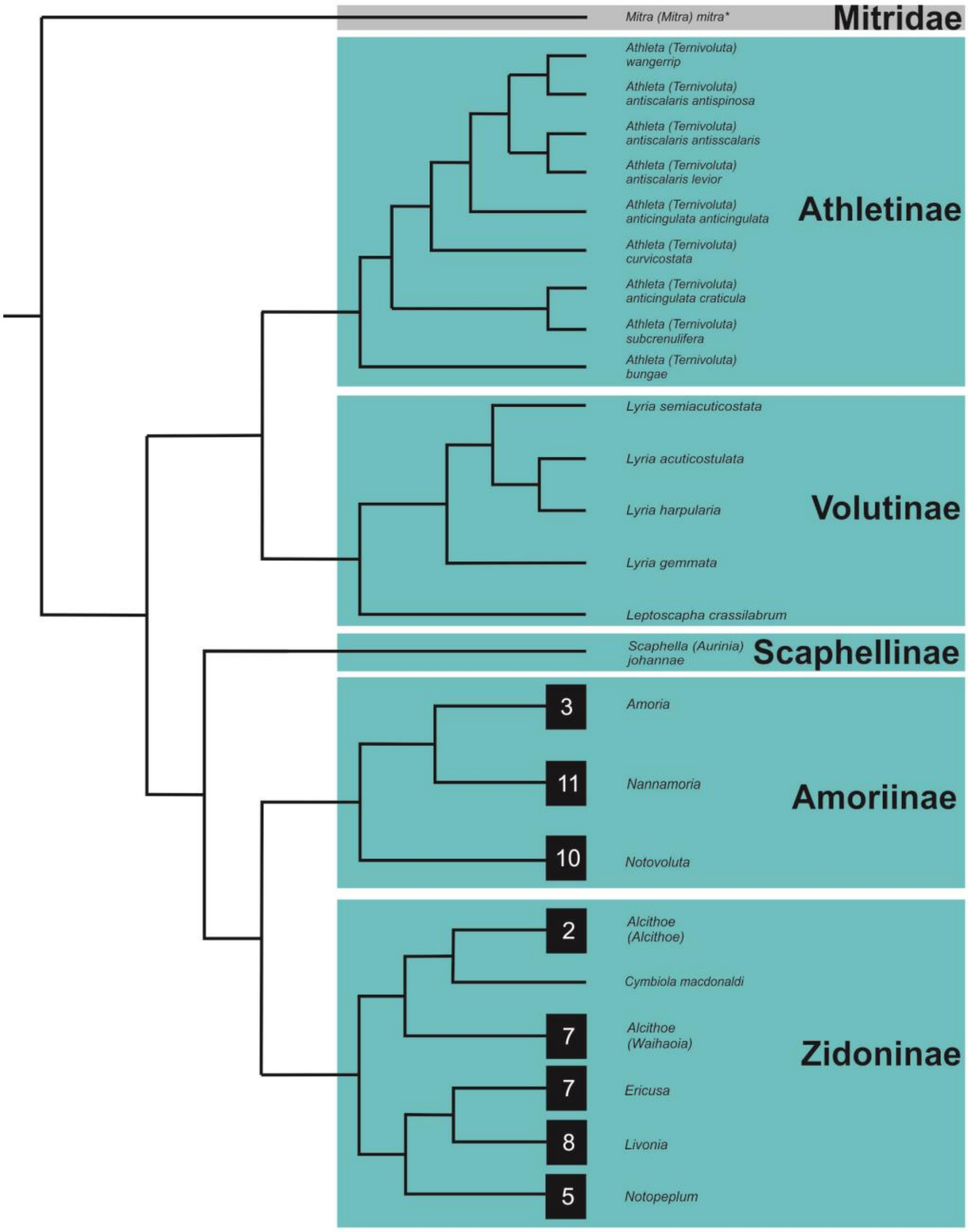


**Figure 4.6** Composite cladogram of the family Volutidae showing the relationships between the subfamilies Athletinae, Volutinae, Scaphellinae, Amoriinae and Zidoninae. The genus *Notovoluta* is retained in the subfamily Amoriinae. Species level analysis was not carried out on the subfamilies Amoriinae and Zidoninae but black boxes indicate the number of species in each genera included in this thesis.

There is a severe lack of phylogenetic analyses of the family Volutidae in the literature. Only one publication deals with the relationships between genera of this family using radula and shell morphology from volute species from Australia (Bondarev, 1995). The author examined the relationships of genera within the subfamilies Cymbiolinae (= Amoriinae) and Zidoninae separately (Figure 4.7). The analysis of Bondarev (1995) supports the analysis of the subfamily Zidoninae carried out in this thesis in establishing *Ericusa* and *Livonia* as sister taxa and *Notopeplum* as the sister taxa to *Ericusa* + *Livonia* within the subfamily Amoriinae. Similarly, both analyses suggest that *Amoria* is the sister genus to *Nannamoria* and that *Notovoluta* is the sister genus to *Amoria* + *Nannamoria* within the subfamily Zidoninae. The genus *Cymbiola* is included in the subfamily Zidoninae in this thesis but in the subfamily Cymbiolinae in Bondarev (1995) making a comparison on its placement difficult.

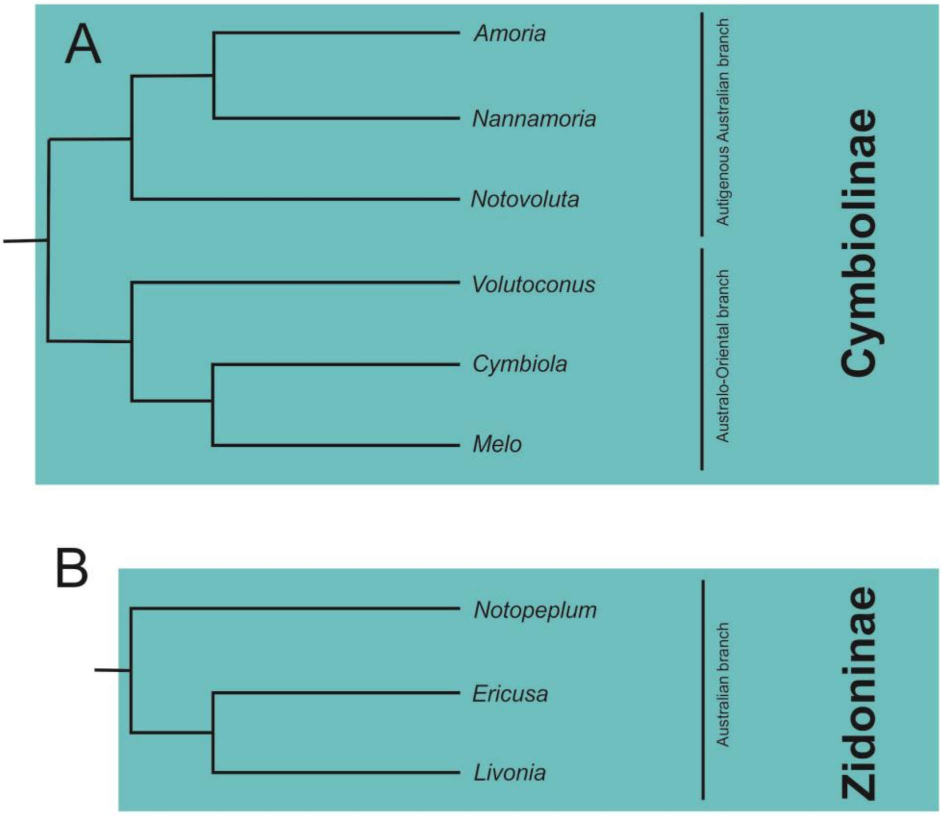


**Figure 4.7** Cladograms redrawn from Bondarev (1995) for the subfamilies Cymbiolinae and Zidoninae.

## 4.3 FAMILY NASSARIIDAE

All species in the family Nassariidae included in this thesis are planktotrophic and, therefore, only generic level analysis is carried out. Four subgenera are included in this analysis: *Niotha, Zeuxis, Plicarcularia* and *Hima*. The genus *Buccinum* is selected as the outgroup for this analysis due to its close relationship with the nassariids. The characters and states used here are based upon Haasl (2000) but with some novel characters added.

The 32 characters and their states used in this phylogenetic analysis are shown in Table 4.12 and the data matrix is shown below in Table 4.13.

**Characters and states**

1.* *Shell height to width ratio*: 1.0 or less (0); 1.1to 1.6 (1); 1.7 or more (2).
2. *Body whorl height to spire height ratio*: Less than 2.0 (0); 2.0 or more (1).
3. *Axial sculpture development*: Weakly developed (0); strongly developed (1).
4. *Axial sculpture on early teleoconch whorls*: Absent (0); present (1).
5. *Axial sculpture on late teleoconch whorls*: Weakly developed costae or cords (0); strongly developed costae (1).
6. *Axial sculpture extension*: Axial costae extended over whole body whorl (0); axial costae becoming obsolete before base of body whorl (1).
7. *Spiral sculpture development*: Weakly developed (0); strongly developed (1).
8. *Spiral sculpture on early teleoconch whorls*: Absent (0); present (1).
9. *Spiral sculpture on late teleoconch whorls*: Strong cords (0); restricted to anterior of body whorl (1).
10.* *Suture type*: Simple, flush with shell (0); whorls concave at suture, ledged (1); canaliculate, distinct groove (2).
11. *Subsutural nodule development*: Absent (0); "beaded" just under suture (1).
12.* *Aperture sculpture form*: Absent (0); lirate (1); denticulate (2).
13. *Terminal columellar fold*: Absent (0); present (1).
14.* *Columellar sculpture*: Absent (0); denticulate anteriorly (1); Denticulate over whole columella (2).
15. *Columellar spur*: Absent (0); present (1).
16. *Columellar callus thickness*: Thin glaze, shell sculpture visible (0); thick enamel, shell sculpture concealed (1).
17.* *Extension of columellar callus*: Restricted to columella (0); relatively extensive, confined to body whorl (1); considerably extended (2).
18. *Columellar callus type*: Flush with shell (0); separated from shell surface (1).
19. *Parietal rib*: Absent (0); present (1).
20. *Parietal notch*: Absent (0); present (1).
21. *Outer lip thickened/variced*: Absent (0); present (1).
22. *Outer lip spines*: Absent (0); present (1).
23. *Labral tooth*: Absent (0); present (1).
24. *Siphonal canal form*: Shortened, prominent (0); abbreviated (1).
25. *Siphonal canal constriction*: Unconstricted, broad (0); constricted, narrow (1).
26. *Eyes*: Absent (0); present, base of cephalic tentacles (1).
27. *Foot*: Unenlarged (0); enlarged (1).
28. *Metapodia*: Zero (0); two (1).

29. *Gastric shield*: Absent (0); present (1).
30. *Rachidian tooth*: Paucicuspate, less than 6 (0); multicuspate, 6 or more (1).
31. *Lateral teeth*: Bicuspate (0); multicuspate (1).
32. *Accessory lateral plates*: Absent (0); present (1).

**Table 4.12** Characters and states used in generic level phylogenetic analysis of nassariids. * = ordered characters.

| Character matrix | |
|---|---|
| *Buccinum** | 01111 11100 01000 10000 00000 10000 10 |
| *Hima* | 20110 01100 02120 01011 10011 10111 01 |
| *Plicarcularia* | 10111 00010 02110 12011 10011 10111 01 |
| *Niotha* | 10111 01101 02111 01111 11111 10111 00 |
| *Zeuxis* | 20011 10012 11121 00111 11111 10111 01 |

**Table 4.13** Data matrix for the five nassariid subgenera plus the outgroup *Buccinum* (*).

An exhaustive search produced a single MPT with a tree length of 42 steps, CI = 0.7857, RI = 0.3571 (Figure 4.8). The tree supports the suggestion laid out in Chapter 3 that the subgenera *Niotha* and *Zeuxis* are very closely related. Bootstrap values are low and Bremer support shows that by 44 steps all nodes have collapsed indicating the tree is not strongly supported.

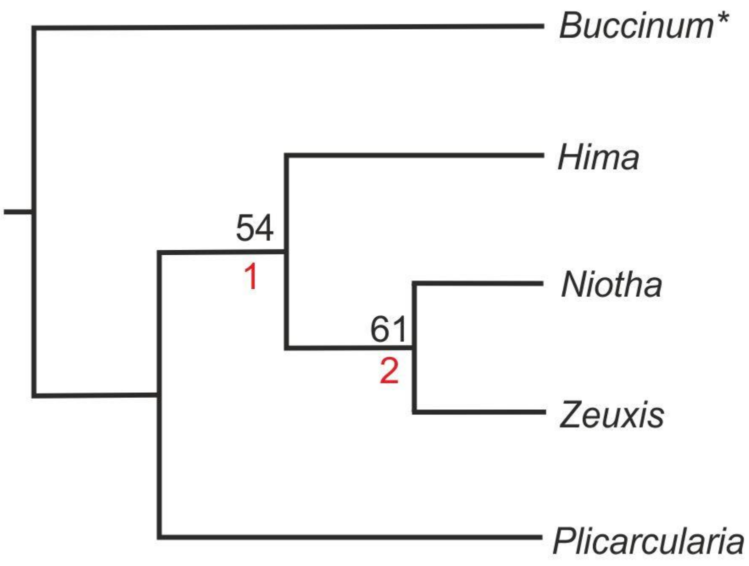


**Figure 4.8** Cladogram for Cenozoic nassariid genera plus *Buccinum**. Bootstrap support % based on 1000 replicates indicated for each branch (in black). Bremer support values indicated at each node (in red).

Analysis of the combined dataset (extant + fossil) from Haasl (2000) suggests that *Niotha* is not as closely related to *Zeuxis* as is predicted by examination of fossil material (Figure 4.9). However, the author notes that the tree is not robust, maybe a result of highly homoplastic data.

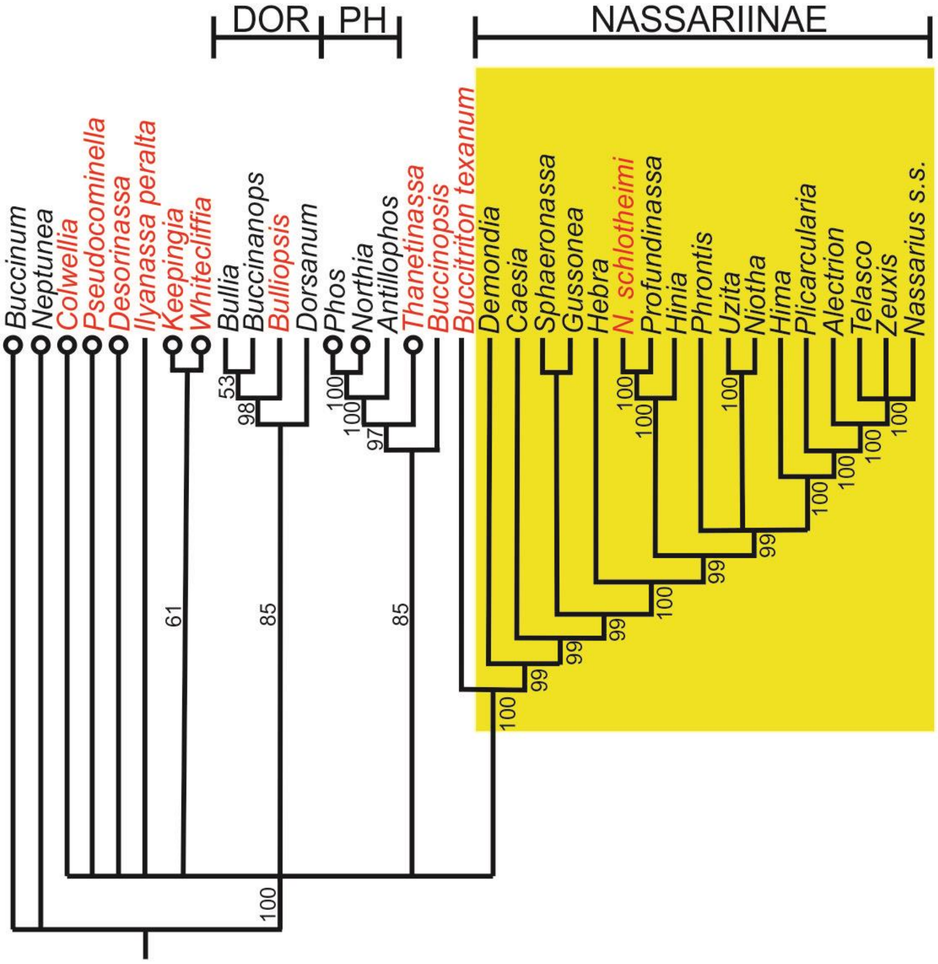


**Figure 4.9** Majority rule consensus tree of 1845 MPTs modified from Haasl (2000). Tree length = 145, CI = 0.359, RI = 0.628. Numbers indicate percentage of MPTs that contained each node. Taxa highlighted in red = fossil. Open circles indicate outgroup taxa. DOR = Dorsaninae, PH = Photinae.

## 4.4 FAMILY RAPHITOMIDAE

Two species from two genera (one planktotroph and one direct developer) are included in the taxonomy of the family Raphitomidae as part of this thesis (Figure 4.10). As a result it is not possible to carry out a phylogenetic analysis on only two taxa. These taxa are included in the summary tree at the end of this chapter.

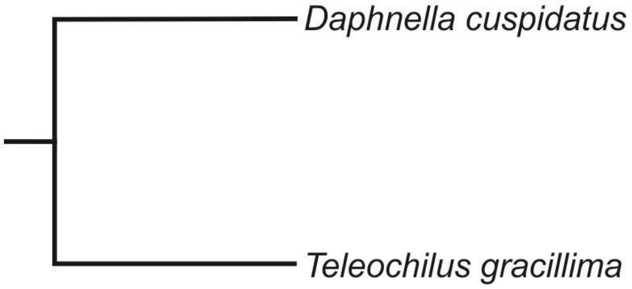


**Figure 4.10** Cladogram of taxa included in the family Raphitomidae as part of this thesis.

## 4.5 FAMILY BORSONIIDAE

Species assigned to the family Borsoniidae in Chapter 3 include three planktotrophic and 11 nonplanktotrophic taxa although there is no intrageneric variation. As a result only a generic level analysis is carried out for this family. Six genera are included in this analysis: *Tomopleura, Cryptocordieria, Borsonia, Zemacies, Microdrillia* and *Bathytoma*. The genus *Conus* is selected as the outgroup due to its close relationship with this family.

The 23 characters and their states used in this phylogenetic analysis are shown in Table 4.14 and the data matrix is shown below in Table 4.15.

**Characters and states**

1.* *Shell height to width ratio*:Less than 2.0 (0); 2.0-2.9 (1); 3.0 – 3.9 (2); 4.0 or more (3).
2.* *Body whorl height to spire height ratio*: Less than 1.4 (0); 1.5 – 2.0 (1); More than 2.0 (2).
3. *Shell shape*: Conical (0); claviform (1); fusiform (2); elongate-fusiform (3).
4. *Axial sculpture development*: Weakly developed (0); strongly developed (1).
5. *Axial sculpture on early teleoconch whorls*: Absent (0); present (1).
6. *Axial sculpture on late teleoconch whorls*: Weakly developed costae or cords (0); strongly developed costae (1).
7. *Axial sculpture extension*: Axial costae extended over whole body whorl (0); axial costae becoming obsolete before base of body whorl (1).
8. *Growth lines*: Weakly developed (0); strongly developed (1).
9. *Spiral sculpture development*: Weakly developed (0); strongly developed (1).
10. *Spiral sculpture on early teleoconch whorls*: Absent (0); present (1).
11. *Spiral sculpture on late teleoconch whorls*: Weak threads only (0); threads and cords (1).
12. *Extension of spiral sculpture*: Strongest anteriorly (0); covering whole body whorl (1).
13.* *Suture type*: Simple, flush with shell (0); whorls concave at suture, ledged (1); canaliculated, distinct groove (2).
14. *Whorl shape*: Straight-sided (0); convex (1).
15. *Whorl shoulder slope*: Flat (0); convex (1); concave (2).
16. *Whorl shouldered/angulate*: Angulate (0); shouldered (1).
17. *Outer lip thickened*: Absent (0); present (1).
18.* *Siphonal canal form*: Abbreviated (0); short, prominent (1); long (2).
19. *Siphonal canal constriction*: Unconstricted, broad (0); constricted, narrow (1).
20. *Sinus depth*: Shallow (0); deep (1).
21. *Position of posterior sinus*: Between two principle keels (0); covering shoulder slope (1).
22. *Aperture shape*: Ovate (0); pyriform (1); elongate (2).
23. *Columella plaits*: Smooth (0); plicate (1).

**Table 4.14** Characters and states used in generic level phylogenetic analysis of borsoniids. * = ordered characters.

| Character matrix | |
|---|---|
| *Conus** | 02000 01000 00000 1000? ?2? |
| *Tomopleura* | 20100 01011 11111 00101 001 |
| *Cryptocordieria* | 10311 11111 11212 10100 110 |
| *Borsonia* | 20211 11111 11112 00111 111 |
| *Zemacies* | 31311 01100 00212 11211 120 |
| *Microdrillia* | 11211 10111 11111 01111 010 |
| *Bathytoma* | 10211 10111 11112 10111 011 |

**Table 4.15** Data matrix for the six borsoniid genera plus the outgroup *Conus**.

An initial exhaustive search produced seven MPTs (CI = 0.6957, RI = 0.4815) with a tree length of 46 steps. The analysis was repeated with the characters reweighted according to the Rescaled Consistency Index (RCI) and three MPTs were produced with a tree length of 26 steps (CI = 0.8150, RI = 0.7056). The 50% majority rule consensus of these trees is shown in Figure 4.11. Bootstrap values are low higher up the tree but the lower part of the tree is more strongly supported. Bremer support showed that all nodes of the tree collapsed after five extra steps (tree length = 31 steps) although the more distal nodes collapsed after only one extra step.

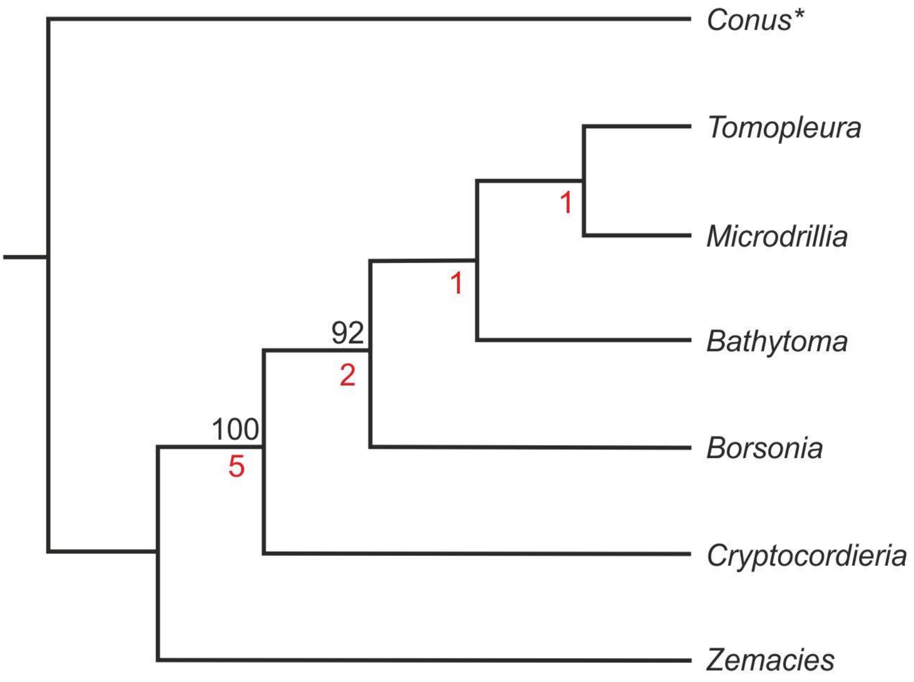


**Figure 4.11** Cladogram for Cenozoic borsoniid genera plus *Conus**. Bootstrap support % based on 1000 replicates indicated for each branch (in black). Bremer support values indicated at each node (in red).

## 4.6 FAMILY MANGELIIDAE

Taxa assigned to the family Mangeliidae in this thesis include four planktotrophic and two lecithotrophic larvae but there is no variation in larval strategy within a single genus. Subsequently only a generic level phylogenetic analysis is carried out for this family. Three genera are included in this analysis: *Antiguraleus, Guraleus* and *Macteola*. The genus *Conus* is selected as the outgroup.

The 21 characters and their states are shown in Table 4.16 and the data matrix is shown in Table 4.17.

**Characters and States**

1. *Shell height to width ratio*:Less than 2.0 (0); 2.0 or more (1).
2. *Body whorl height to spire height ratio*: Less than 2.0 (0); 2.0 or more (1).
3. *Shell shape*: Cone-shaped (0); fusiform (1).
4. *Axial sculpture development*: Weakly developed (0); strongly developed (1).
5. *Axial sculpture on early teleoconch whorls*: Absent (0); present (1).
6. *Axial sculpture of late teleoconch whorls*: Absent (0); weakly developed costae (1); strongly developed costae (2).
7. *Axial costae width and interspaces*: Absent (0); costae narrow with wide interspaces (1); costae wide with narrow interspaces (2).
8. *Spiral sculpture development*: Weakly developed (0); strongly developed (1).
9. *Spiral sculpture on early teleoconch whorls*: Absent (0); present (1).
10. *Spiral sculpture on late teleoconch whorls*: Weak threads only (0); threads and cords (1).
11. *Extension of spiral sculpture*: Strongest anteriorly (0); strongest posteriorly (1); covering whole body whorl (2).
12. *Whorl shape*: Straight-sided (0); convex (1).
13. *Whorl shoulder slope*: Flat (0); convex (1); concave (2).
14. *Suture type*: Simple, flush with shell (0); whorls concave at suture (1).
15. *Outer lip thickened*: Absent (0); present (1).
16. *Siphonal canal form*: Short, prominent (0); abbreviated (1).
17. *Siphonal canal constriction*: Unconstricted, broad (0); constricted, narrow (1).
18. *Position of posterior sinus*:Covering shoulder slope (0); covering peripheral keel (1).
19. *Whorl shouldered or angulate*: Angulate (0); shouldered (1).

20.* *Number of costae per whorl*: Absent (0); less than 10 (1); 10 or more (2).

21. *Periphery form*: Subangulate (0); angulate (1); carinate (2).

**Table 4.16** Characters and states used in generic level phylogenetic analysis of mangeliids. * = ordered characters.

| Character matrix | |
|---|---|
| *Conus** | 01000 00000 00000 10010 2 |
| *Antiguraleus* | 10111 11111 21211 00012 0 |
| *Guraleus* | 10111 22000 11100 0000? 1 |
| *Macteola* | 10111 22010 21200 01111 2 |

**Table 4.17** Data matrix for the three mangeliid genera plus the outgroup *Conus* (*).

An exhaustive search produced a single MPT with a tree length of 30 steps, CI = 0.9000, RI = 0.5000 (Figure 4.12). Bootstrap values are fairly low and Bremer support showed that the nodes collapse after only one extra step (31 steps). The tree suggests that *Antiguraleus* and *Macteola* are more closely related than either is to *Guraleus* which is not necessarily supported by the taxonomic revision in the previous chapter.

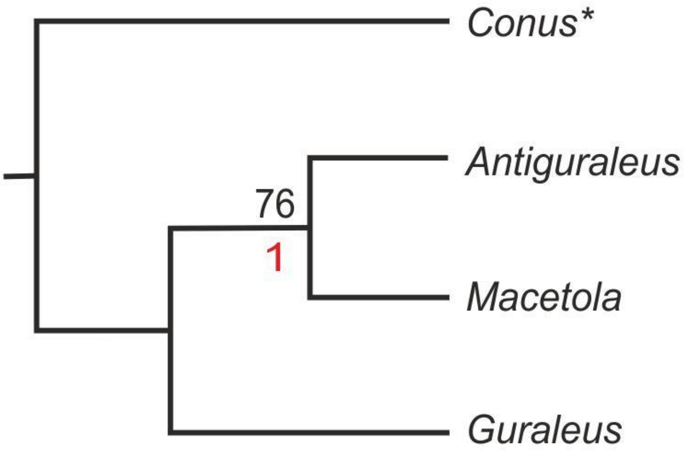


**Figure 4.12** Cladogram for Cenozoic mangeliid genera plus *Conus**. Bootstrap support % based on 1000 replicates indicated for each branch (in black). Bremer support values indicated at each node (in red).

## 4.7 FAMILY TURRIDAE

Of the six species assigned to the family Turridae in Chapter 3 one is planktotrophic and five are lecithotrophic but there is no intrageneric variation in larval mode. Consequently, generic level phylogenetic analysis is carried out for this family. Five genera are included in this analysis: *Gemmula, Gemmula (Clavogemmula), Lophiotoma, Turris* and *Optoturris*. The genus *Conus* was selected as the outgroup. The 21 characters and their states are shown in Table 4.18 and the data matrix is shown in Table 4.19.

**Characters and states**

1. *Shell height to width ratio*:Less than 2.0 (0); 2.0 or more (1).
2. *Body whorl height to spire height ratio*: Less than 2.0 (0); 2.0 or more (1).
3. *Shell shape*: Cone-shaped (0); fusiform (1); elongate-fusiform (2).
4. *Axial sculpture development*: Weakly developed (0); strongly developed (1).
5. *Axial sculpture on early teleoconch whorls*: Absent (0); present (1).
6. *Axial sculpture of late teleoconch whorls*: Absent (0); present (1).
7. *Spiral sculpture development*: Weakly developed (0); strongly developed (1).
8. *Spiral sculpture on early teleoconch whorls*: Absent (0); present (1).
9. *Spiral sculpture on late teleoconch whorls*: Weak threads only (0); Threads and cords (1).
10. *Extension of spiral sculpture*: Strongest anteriorly (0); strongest posteriorly (1); covering whole body whorl (2).
11. *Peripheral keel*: Absent (0); present (1).
12.* *Peripheral keel form*: Absent (0); non-gemmulate (1); gemmulate (2).
13. *Whorl shape*: Straight-sided (0); convex (1).
14. *Whorl shoulder slope*: Flat (0); concave (1).
15.* *Suture type*: Simple, flush with shell (0); whorls concave at suture (1); canaliculate (2).
16. *Outer lip thickened*: Absent (0); present (1).
17.* *Siphonal canal form*: Abbreviated (0); short, prominent (1); long (2).
18. *Siphonal canal constriction*: Unconstricted, broad (0); constricted, narrow (1).
19. *Posterior sinus form*: “V-shaped” (0); “U-shaped” (1).
20. *Position of posterior sinus*: Covering shoulder slope (0); covering peripheral keel (1).
21. *Outer lip lirations: Absent (0); present (1).*
22. *Aperture height to width ratio*: 2.0 or less (0); more than 2.0 (1).

**Table 4.18** Characters and states used in generic level phylogenetic analysis of turrids. * = ordered characters.

| Character matrix | |
|---|---|
| *Conus** | 01000 00000 00000 000?0 01 |
| *Gemmula* | 10200 11110 12112 01111 10 |
| *Gemmula (Clavogemmula)* | 10111 11010 12112 01011 ?0 |
| *Lophiotoma* | 10200 11112 11112 02001 00 |
| *Turris* | 10200 01112 11112 01110 11 |
| *Optoturris* | 10200 00101 11111 11011 01 |

**Table 4.19** Data matrix for the five turrid genera plus the outgroup *Conus**.

An exhaustive search produced a single MPT with a tree length of 34 steps, CI = 0.7941 and RI = 0.5625 (Figure 4.13). Bootstrap values are low, perhaps a result of the small dataset, and Bremer support shows that all nodes of the tree collapse at 36 steps. As would be expected from the taxonomic review of this family, *Gemmula* and *Gemmula (Clavogemmula)* are most closely related to each other than either is to another taxa, although this is only moderately well supported on this tree.

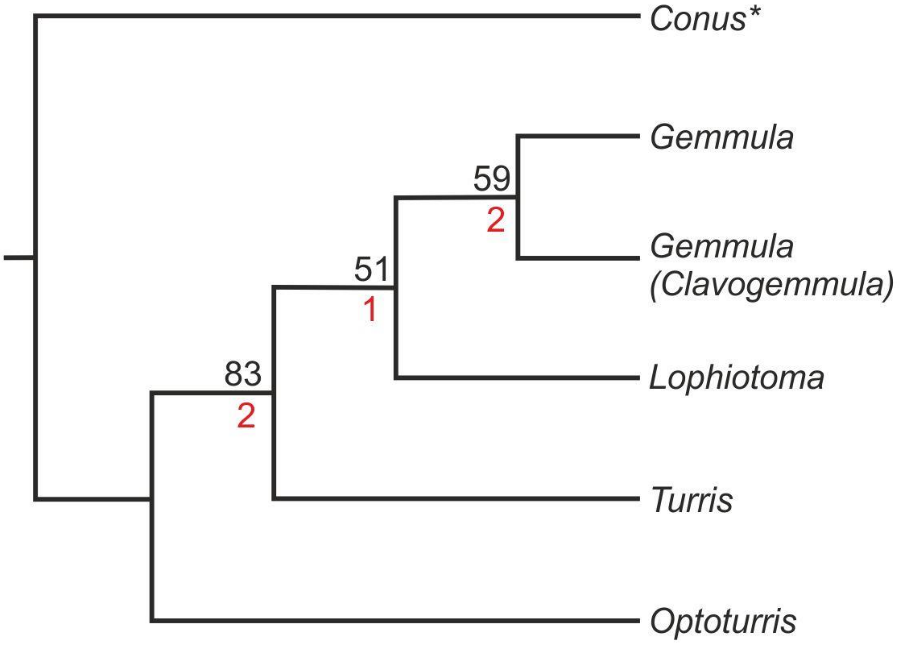


**Figure 4.13** Cladogram for Cenozoic turrid genera plus *Conus**. Bootstrap support % based on 1000 replicates indicated for each branch (in black). Bremer support values indicated at each node (in red).

## 4.8 SUPERFAMILY CONOIDEA

Families assigned to the superfamily Conoidea include planktotrophic, lecithotrophic and direct developing taxa with variation confined to generic level. Family level phylogenetic analysis is carried out on four families (Raphitomidae, Borsoniidae, Mangeliidae and Turridae) using one genus from each as representatives for each family. The genus *Conus* is selected as the outgroup, as has been the case for generic level analyses. Anatomical data for the genera used in this analysis is extremely limited and is therefore excluded from this analysis. The 24 characters and their states used in this phylogenetic analysis are shown in Table 4.20 and the data matrix is shown in Table 4.21.

**Characters and states**

1.* *Shell height to width ratio:* Less than 2.0 (0); 2.1-3.0 (1); More than 3.0(2).
2.* *Body whorl height to spire height ratio*: 1.0 or less (0); 1.1 to 2.0 (1); More than 2.0 (2).
3.* *Aperture height to width ratio*: Up to 2.5 (0); 2.5 to 5.0 (1); More than 5.0 (2).
4. *Shell shape*: Cone-shaped (0); ovate (1); fusiform (2); elongate-fusiform (3).
5. *Axial sculpture development*: Weakly developed (0); strongly developed (1).
6. *Axial sculpture on early teleoconch whorls*: Absent (0); present (1).
7. *Axial sculpture on late teleoconch whorls*: Absent (0); weakly developed (1); strongly developed (2).
8. *Axial sculpture extension*: Over whole body whorl (0); obsolete before base of body whorl (1).
9. *Growth lines*: Weakly developed (0); strongly developed (1).
10. *Spiral sculpture development*: Weakly developed (0); strongly developed (1).
11. *Spiral sculpture on early teleoconch whorls*: Absent (0); present (1).
12. *Spiral sculpture on late teleoconch whorls*: Weak threads only (0); threads and cords (1).
13. *Spiral sculpture extension*: Strongest anteriorly (0); strongest posteriorly (1); covering whole body whorl (2).
14. *Whorl shape*: Straight-sided (0); convex (1).
15. *Whorl angulate/shouldered*: Angulate (0); shouldered (1).
16. *Whorl shoulder slope form*: Absent (0); flat (1); concave (2).
17.* *Suture form*: Simple, flush with shell (0); whorls concave at suture, ledged (1); canaliculate, distinct groove (2).
18. *Aperture shape*: Ovate (0); pyriform (1); elongate (2).
19. *Outer lip thickened*: Absent (0); present (1).
20. *Outer lip lirations*: Absent (0); present (1).
21.* *Siphonal canal form*: Abbreviated (0); short, prominent (1).
22. *Siphonal canal constriction*: Unconstricted, broad (0); constricted, narrow (1).
23. *Posterior sinus depth*: Shallow (0); deep (1).
24. *Position of posterior sinus*: Covering shoulder slope (0); covering peripheral keel (1).

**Table 4.20** Characters and states used in generic level phylogenetic analysis of conoideans. * = ordered characters.

| | Character matrix |
|---|---|
| Conidae (*Conus**) | 02200 00100 00001 10200 00?? |
| Raphitomidae (*Daphnella*) | 11111 11101 11210 01000 1000 |
| Borsoniidae (*Bathytoma*) | 10121 11011 11211 21100 1111 |
| Mangeliidae (*Antiguraleus*) | 11031 11111 11211 21210 1010 |
| Turridae (*Turris*) | 21030 02101 11211 22001 1110 |

**Table 4.21** Data matrix for the four conoidean families plus the outgroup *Conus**.

An exhaustive search produced a single MPT (CI = 0.9167, RI = 0.5000) with a tree length of 36 steps. Bootstrap values are moderately low as indicated on Figure 4.14 and Bremer support showed that all nodes of the tree collapsed after only one extra step.

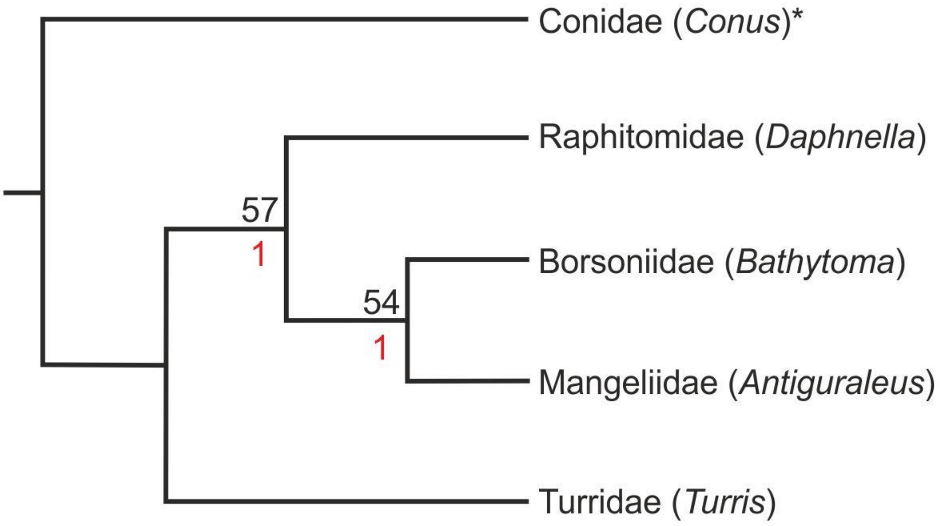


**Figure 4.14** Cladogram of Cenozoic conoidean gastropod families plus Conidae. Bootstrap support % based on 1000 replicates indicated for each branch (in black). Bremer support values indicated at each node (in red).

The molecular phylogeny of the Superfamily Conoidea has been the focus of several publications in recent years (Puillandre et al., 2008, 2011, based on three mitochondrial genes: COI, 12S, 16S) and has resulted in new a classification of this complex superfamily with a number of new families being established (Bouchet et al., 2011). The families Raphitomidae, Borsoniidae, Mangeliidae and Turridae are included in the superfamily Conoidea and their relationship to each other and other conoidean families has been assessed in these studies (Figure 4.15). By pruning the tree of families not included in this thesis, the families Raphitomidae and Mangeliidae are found to be most closely related and are the sister group to the family Borsoniidae whilst the family Turridae is the sister group to Raphitomidae + Mangeliidae + Borsoniidae (Puillandre et al., 2011).

The tree produced as part this study indicates that the families Borsoniidae and Mangeliidae are most closely related with the family Raphitomidae as the sister group. This differs from the tree produced by Puillandre et al. (2011) although the family Turridae is here shown to be the sister group to Borsoniidae + Mangeliidae + Raphitomidae, in agreement with Puillandre et al. (2011). The dataset used in the literature is considerably larger than the one in this thesis, is based on molecular data and is analysed using maximum likelihood which may account for the differences between the trees.

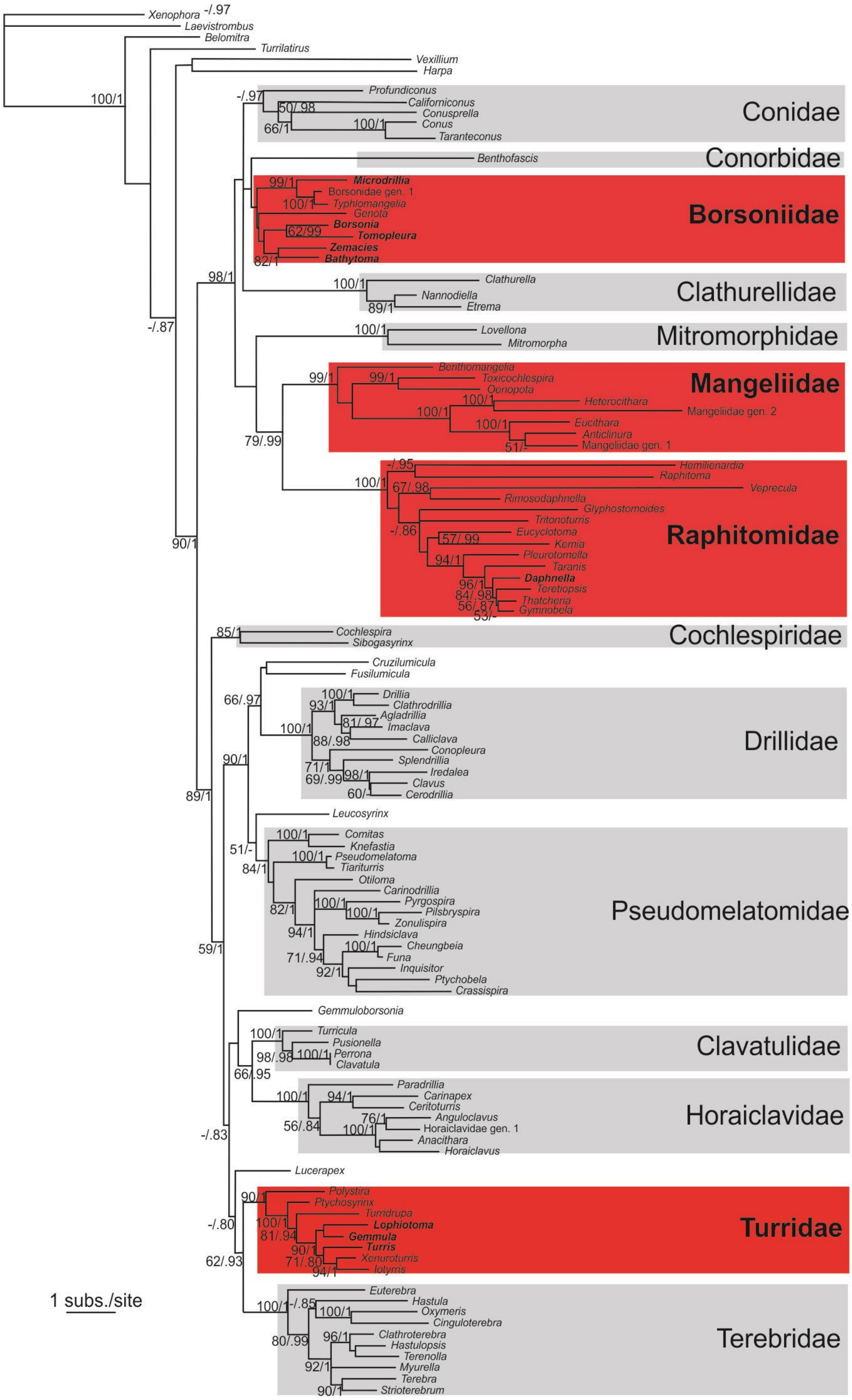


**Figure 4.15** Best MLA tree obtained from molecular phylogenetic analysis for the superfamily Conoidea (modified from Puillandre et al., 2011). Bootstrap values (>50%) and posterior probabilities (>0.8) are indicated for each node. Grey boxes indicate families defined in the most recent classification of the Conoidea (Bouchet et al., 2011). Yellow boxes indicate families included in this thesis with genera in bold indicating those used in this chapter.

As the majority of conoidean species used in this thesis are fossils, phylogenetic analyses are limited to morphological characters. As a result it is not possible to analyse all these species in the way Puillandre et al. (2008, 2011) have done and instead a composite tree is presented comprised of individual family trees (Figures 4.10, 4.11, 4.12, 4.13) and the family level tree (Figure 4.14). This composite tree is shown in Figure 4.16.

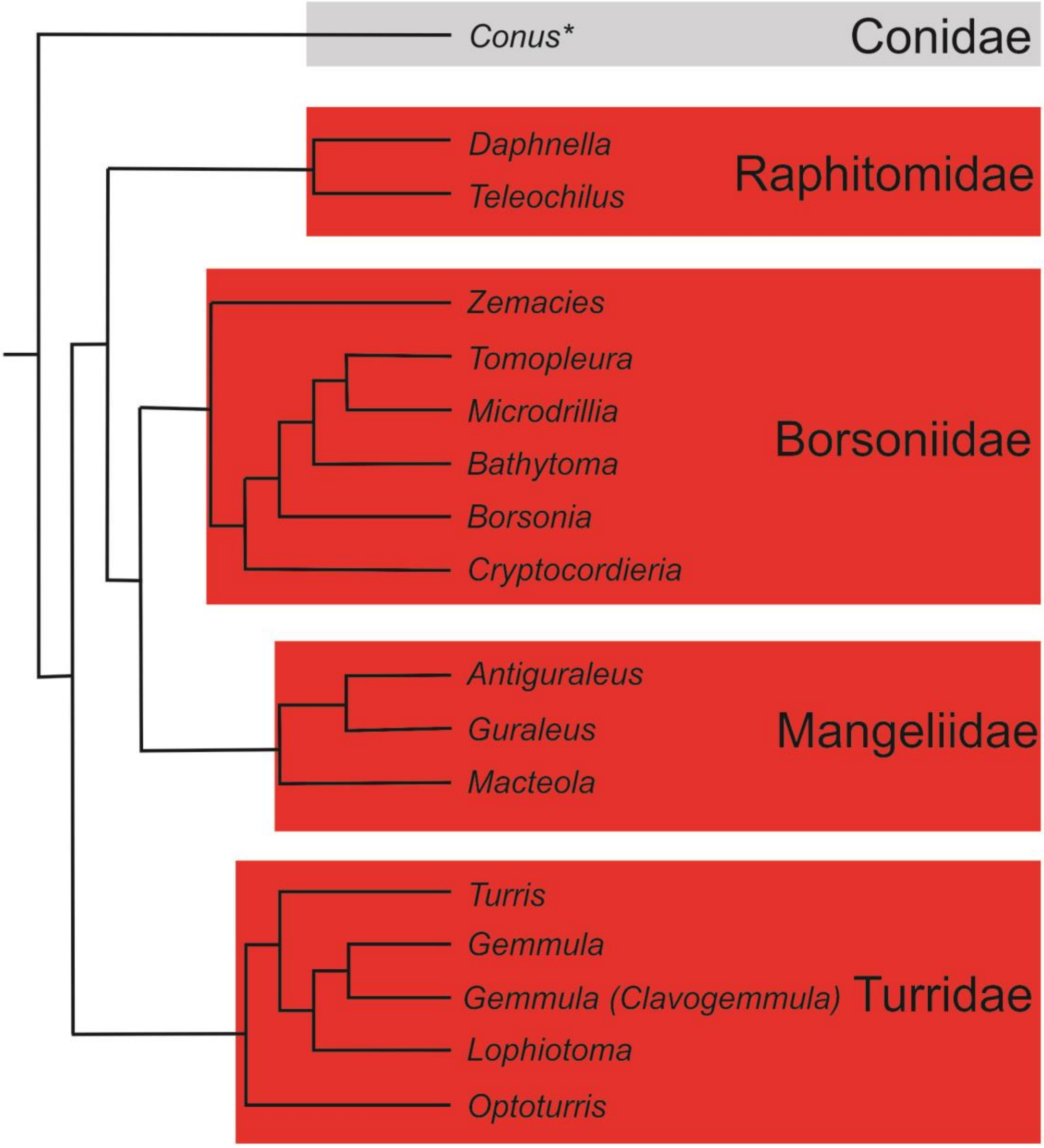


**Figure 4.16** Composite cladogram of the superfamily Conoidea showing the relationships between the families Raphitomidae, Borsoniidae, Mangeliidae and Turridae.

## 4.9 NEOGASTROPOD COMPOSITE TREE

The paucity of informative characters available from fossil gastropods makes creating a large dataset on which to base family level analysis implausible. Examination of anatomical and molecular characters is not within the scope of this thesis and as a result a composite tree for all genera/species included in this study is based on molecular phylogenies by Cunha et al. (2009) which use complete mitochondrial genomes. The study by Cunha et al. (2009) suggests that the Nassariidae and “Turridae” (=Raphitomidae, Borsoniidae, Mangeliidae and Turridae) are sister groups and the family Volutidae is the sister family to Nassariidae + “Turridae” (Figure 4.17).

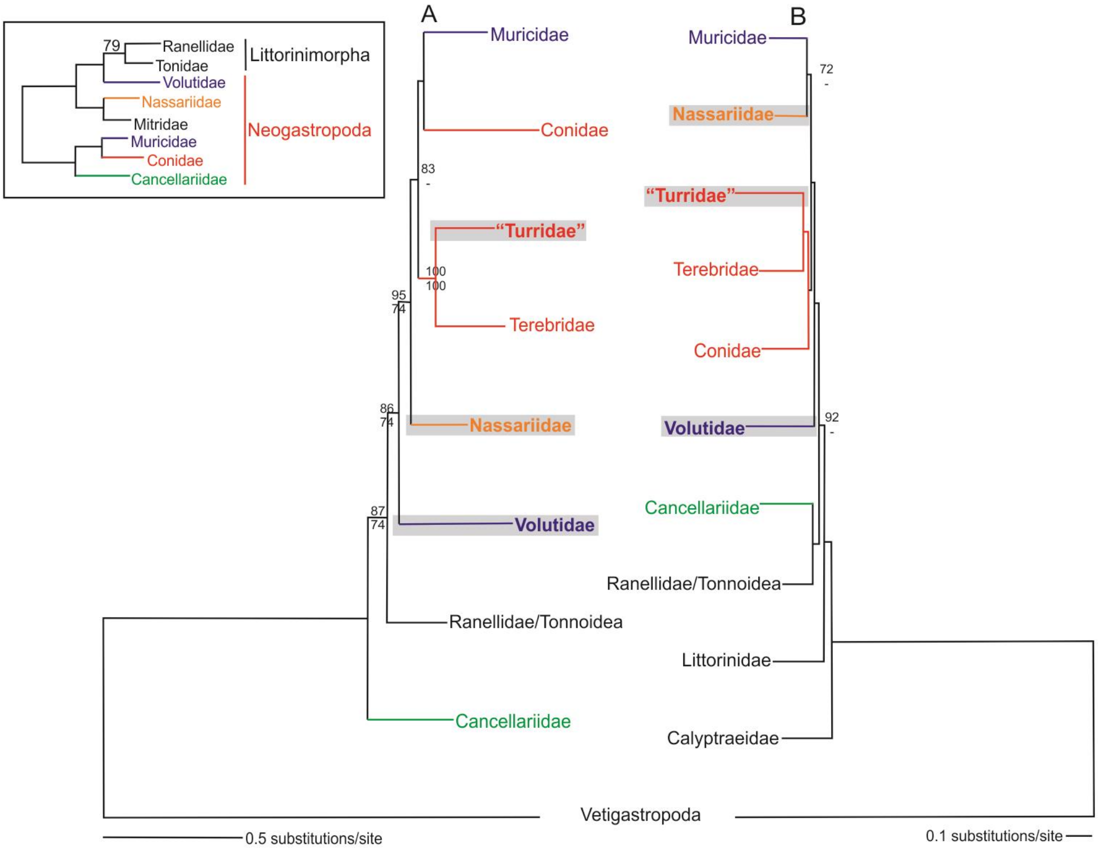


**Figure 4.17** Phylogenetic relationships within Gastropoda modified from Cunha et al. (2009). A) Maximum Likelihood phylogram based on all combined data set. B) ML phylogram based on partial combined dataset. Numbers in nodes correspond to ML bootstrap proportions (above) and BI posterior possibilities (below). Only values >70% represented. Families highlighted in grey boxes and bold are included in this thesis. The inset shows a ML topology based on fragments of mitochondrial and nuclear data (adapted from Colgan et al., 2007). Families highlighted in grey are included in this thesis.

The length of the branches in Figure 4.17 are extremely short suggesting that the taxa are difficult to distinguish from one another. This highlights the difficulties faced in trying to resolve the evolutionary relationships of neogastropods, even where molecular data is available.

A composite tree of the families Nassariidae and Volutidae and the superfamily Conoidea used in this thesis is based on Figure 4.17 where the Nassariidae and Conoidea are presented as more closely related to one another than either is to the Volutidae. This composite tree (Figure 4.18) will provide the means for mapping switches in larval strategy through geological time and determining the plesiomorphic larval condition in the following chapter.

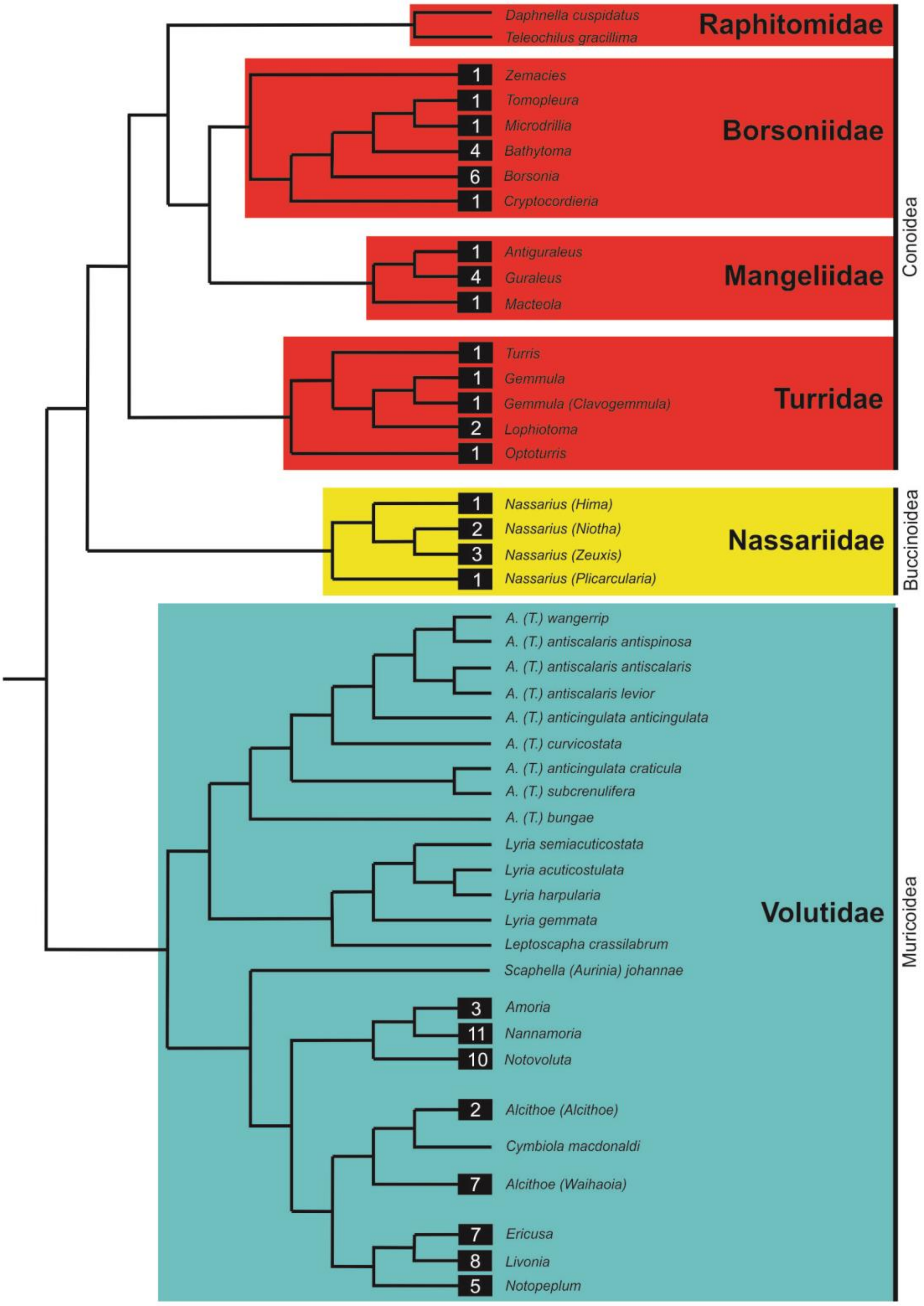


**Figure 4.18** Composite cladogram for the families Volutidae, Nassariidae, Raphitomidae, Borsoniidae, Mangeliidae and Turridae based on arrangement by Cunha et al. (2009). Black boxes indicate the number of species assigned to genera where species level analysis has not been carried out.

# CHAPTER 5

# ORDER AND TIMING OF SWITCHES IN LARVAL MODE

Research into the evolutionary history of developmental mode in fossil gastropods has received very little attention in the published literature. Direct observations of fossilised larvae are hindered by their extremely poor fossil record and problems in attributing larvae to particular adult taxa. In addition, difficulties in constructing well-resolved phylogenies severely hamper our understanding of the evolution of larval strategies of gastropods through geological time. As a result the plesiomorphic developmental mode and the timing and order of switches in larval strategy are yet to be fully investigated.

In this chapter, the larval strategies of the 104 species of fossil gastropods described in Chapter 3 are presented. These developmental modes are then mapped onto the cladograms produced in Chapter 4. This approach allows plesiomorphic larval strategies to be explored and the order and timing of switches in developmental mode in gastropods throughout the Cenozoic of southeastern Australia to be investigated. By examining the time intervals at which switches in larval strategies occur, it is possible to assess whether they are clustered to a particular time period, an approach which has allowed researchers to explore possible external influencing factors (e.g. Jeffery, 1997).

A few researchers have examined the evolutionary patterns of gastropod larval strategies using both phylogenetic and non-phylogenetic techniques (e.g. Hansen, 1982; Reid, 1989; Lieberman et al., 1993). Most studies indicate that whilst planktotrophic species often give rise to nonplanktotrophic species, the reverse is extremely rare. This is often attributed to the presumed difficulty in reacquiring the specialised feeding and swimming structures required for planktotrophic development once they are abandoned (e.g. Strathmann, 1974; 1978).

Planktotrophy has been determined as the primitive larval strategy in a number of gastropod groups using phylogenetic methods, such as the neogastropods (Hansen, 1982), the family Turritellidae (Lieberman et al., 1993), the genus *Conus* (Duda & Palumbi, 1999) and the conoidean genera *Kermia* and *Pseudodaphnella* (Fedosov & Puillandre, 2012). In each of these groups nonplanktotrophic development has been independently gained at least twice and there is no evidence of a reversal to planktotrophy once nonplanktotrophy has been acquired (although Lieberman et al. (1993) do not rule out the possibility). An exception to this general trend is seen in the subfamily Lacuninae of the family Littorinidae (Reid 1989), where a recent reversal from nonplanktotrophy to planktotrophy is inferred. There is some evidence that gastropods can retain the specialised larval structures required for feeding and swimming (e.g. opposed-band ciliary mechanism) in nonplanktotrophic taxa, making a transition from nonfeeding back to feeding development possible (Collin, 2004; Collin et al., 2007) although these intermediary larval forms are yet to be fully understood.

A much overlooked aspect of developmental mode evolution in gastropods is the issue of coordinated switches of larval strategy. If switches in larval mode are concentrated at particular time periods then it may be possible to determine external factors which drive such shifts. Although this topic has been somewhat neglected in studies on gastropods, some light has been shed on coordinated shifts in larval strategies in echinoids (e.g. Jeffery 1997). Near-synchronous shifts to nonplanktotrophic development in nine independent clades during the latest Cretaceous over a wide latitudinal range are thought to have been driven by increased seasonality (Jeffery, 1997). Similarly, shifts to nonplanktotrophy in spatangoid echinoids during the Campanian and Maastrichtian have been attributed to environmental change occurring at this time (Cunningham & Jeffery Abt, 2009). Similar studies on gastropods are yet to be undertaken/published. This study aims to shed light on the possible factors driving switches in larval mode in gastropods from the Cenozoic of southeastern Australia, if such coordinated shifts exist.

## 5.1 INFERRING LARVAL MODE FROM FOSSIL GASTROPODS

Gastropods, as well as a small number of other marine invertebrates including echinoids and bivalves, can be used to infer larval mode from fossil specimens. This is because the different larval strategies are reflected in the size and shape of the protoconch (larval shell) which is often preserved at the tip of the adult shell. The protoconch, or apex, of the gastropod shell forms prior to metamorphosis to the adult body plan and thus is often referred to as the "larval shell" (Figure 5.1a). In this thesis, the "protoconch" refers to the entire shell formed prior to metamorphosis, as in Robertson (1971), Shuto (1974) and Hansen (1978, 1980, 1982, 1983). The protoconch is comprised of two parts, each representing different phases of early development (Figure 5.1b). The Protoconch I, or embryonic shell, is the first part to form prior to hatching and is thought to be secreted by the shell gland (e.g. Iwata, 1980). The Protoconch I always comprises fewer than two volutions and is generally unornamented with a grainy appearance (Robertson, 1971; Jablonski & Lutz, 1983). The Protoconch II represents the second stage of larval shell growth and is produced by deposition of aragonite at the mantle edge (Carriker & Palmer, 1979). The Protoconch II comprises 1.5 to 8 volutions and can be smooth or ornamented (Jablonski & Lutz, 1983). The boundary between these two parts of the protoconch is often difficult to identify due to recrystallisation of the shell, except under the scanning electron microscope. The protoconch is always composed of aragonite, even if the teleoconch is calcitic (Carriker & Palmer, 1979). Often there is little resemblance between the protoconch and teleoconch (adult shell), with distinct differences in ornamentation as well as cases of heterostrophy, where the coiling axes of the protoconch and teleoconch differ in orientation (e.g. Frýda & Ferrová, 2011). These differences often make identification of the protoconch a simple process, even without the aid of a scanning electron microscope.

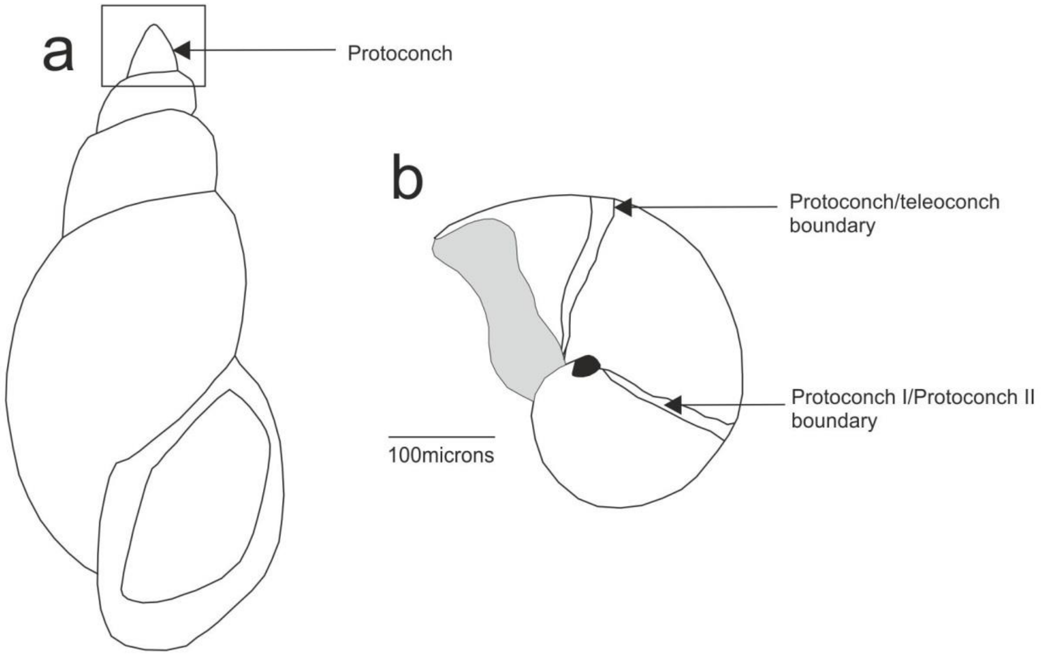


**Figure 5.1** Diagrams of the gastropod protoconch. a) Location of the protoconch at the apex of the shell, b) diagram of the protoconch showing the Protoconch I/II boundary and the protoconch/teleoconch boundary (Scale = 100microns) (modified from Vendetti, 2007).

Inference of larval mode in fossil gastropods is only possible in specimens that have not lost or damaged their protoconch and have therefore retained evidence of their early development.

Modern methods of inferring gastropod larval strategies are commonly based on Thorson's "apex theory" which states that "as a general rule, a clumsy, large apex points to a nonpelagic development, while a narrowly twisted apex, often with delicate sculpture, points to a pelagic development" (Thorson, 1950). This general rule suggests that large, paucispiral protoconchs indicate that the larvae have spent little or no time in the plankton (nonplanktotrophic) having hatched from large, yolk-rich eggs while narrow, multispiral protoconchs indicate a prolonged planktic period (planktotrophic). Whilst this provides a good basis for inference of larval mode, many researchers have sought to develop more precise criteria, aided by advances in microscopy.

Most authors follow or modify the method outlined by Shuto (1974), which is based on prosobranch gastropods, using living taxa whose larval mode is known to test the method. Maximum diameter (D) and number of volutions of the protoconch (V), are combined with qualitative characters such as shape and sculpture to infer larval mode of fossil species. Definitions of volutions and maximum diameter are shown in Figure 5.2.

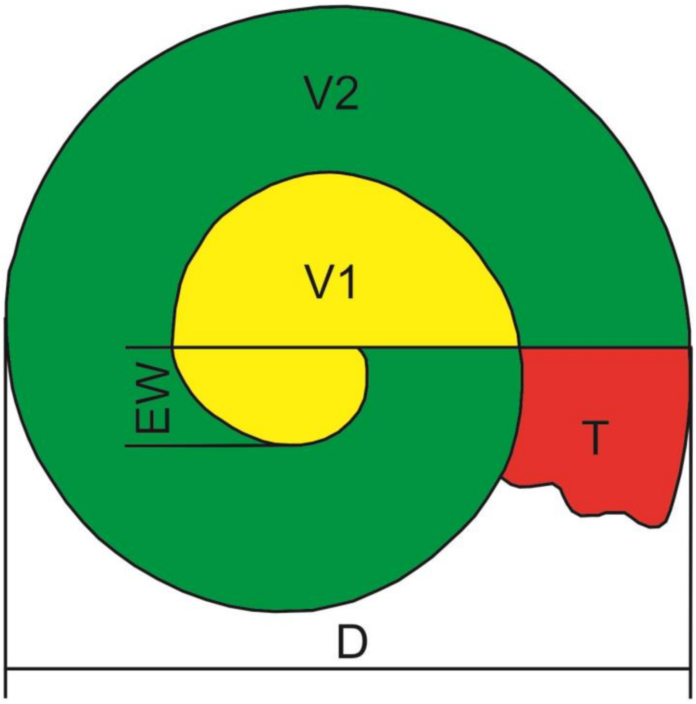


**Figure 5.2** Definitions of maximum diameter (D), volutions (V) and embryonic whorl (EW) of the gastropod protoconch and teleoconch (T). Modified from Hansen (1980).

The method outlines the metric and morphological criteria of planktotrophic, lecithotrophic and, to a lesser extent, direct developing taxa. Species inferred as planktotrophic have a maximum protoconch diameter to number of volutions ratio (D/Vol) of less than 0.3, more than 3 volutions, the presence of a sinusigera riblet (a rib that defines the boundary between the protoconch and teleoconch), possible sculpture of brephic axials and a narrow, high apex. By contrast, lecithotrophic species can be inferred by a D/Vol of 0.3 to 1.0, less than 2.25 volutions, lack of sculpture and a blunt, low apex. Direct developing taxa are defined as having a D/Vol of more than 1.0. Where D/Vol = 0.3 – 1.0 and Vol = <3.0, both planktrotophy and lecithotrophy are possible and morphological criteria must be used to infer larval mode. This method and some others used in the literature are summarised in Table 5.1.

| | **This thesis** | **Thorson (1950) (general)** | **Shuto (1974) (prosobranchs)** | **Hansen (1980) (neogastropods)** | **Gili & Martinell (1994) (nassariids only)** |
|---|---|---|---|---|---|
| **Planktotrophic** | D/Vol <0.3<br>Vol >3.0<br>Narrow, high apex<br>Regular spiral development<br>Small EW | Narrowly twisted apex | D/Vol <0.3<br>Vol >3.0<br>Narrow, high, pointed apex<br>Sinusigera riblet<br>Brephic axials | Vol = 2.5 – 6<br>High, conical spire<br>Sinusigera riblet<br>Brephic axials<br>Small EW | D/Vol <0.39<br>Vol = 2.5+<br>Regular spiral development<br>Small EW |
| **Lecithotrophic** | D/Vol = 0.3 – 1.0<br>Vol <2.25<br>Globose, low apex<br>Irregular spiral development<br>Large EW | Clumsy, large apex | D/Vol = 0.3 – 1.0<br>Vol <2.25<br>Globose, low, blunt apex | Vol = 1 – 3<br>Spire variable, usually blunt and globose<br>Large EW | D/Vol >0.45<br>Vol = 2.25 or less<br>Irregular spiral development<br>Large EW |
| **Direct Development** | D/Vol >1.0<br>Irregular spiral development<br>Large-very large EW | | D/Vol >1.0 | | |

**Table 5.1** Table summarising methods in published literature and method used in this research for inferring larval mode from gastropod protoconchs. D = maximum diameter of protoconch, Vol = number of protoconch volutions, EW = embryonic whorl.

For this research, larval mode is inferred using the method developed by Shuto (1974) because it seems to be the most robust approach in the published literature, using both metric and morphological characters to infer larval strategies in fossil specimens (Table 5.1). In addition, the research presented in this thesis will be easy to compare to other studies as many authors use or modify Shuto's (1974) method. A graphical representation of the protoconch measurements used to infer larval mode is shown in Figure 5.3.

A total of 104 Cenozoic species from the neogastropod families Volutidae, Nassariidae, Raphitomidae, Borsoniidae, Mangeliidae and Turridae of southeastern Australia are examined and larval mode inferred. Although many additional species were examined, only those with an intact protoconch and whose taxonomic position could be confidently assigned were included. Analysed specimens include both museum material and material collected in the field. Wherever possible at least one type specimen from each species was analysed to avoid complications relating to misidentification of species. Material collected from the field and examined as part of this research is deposited in the Department of Earth Sciences and Liverpool University in the UK.

Measurements of the protoconch were taken using electronic callipers, accurate to 0.01mm, and in cases of very small specimens, light microscopy was used to identify the boundary between the protoconch and teleoconch. Morphological data such as general shape and size, sculpture and spiral development was recorded from examination of specimens using light microscopy.

Protoconch measurements of all species included in this study are presented graphically in Figures 5.4 and 5.5. Morphological observations and, where necessary, comparison to closely related living species whose larval mode is known are used to confidently determine the larval strategy of each of the species included in the dataset. The number of species with each larval strategy in each taxonomic family is presented in Table 5.2. Figure 5.6 shows the distribution of larval strategies on the cladograms produced in Chapter 4.

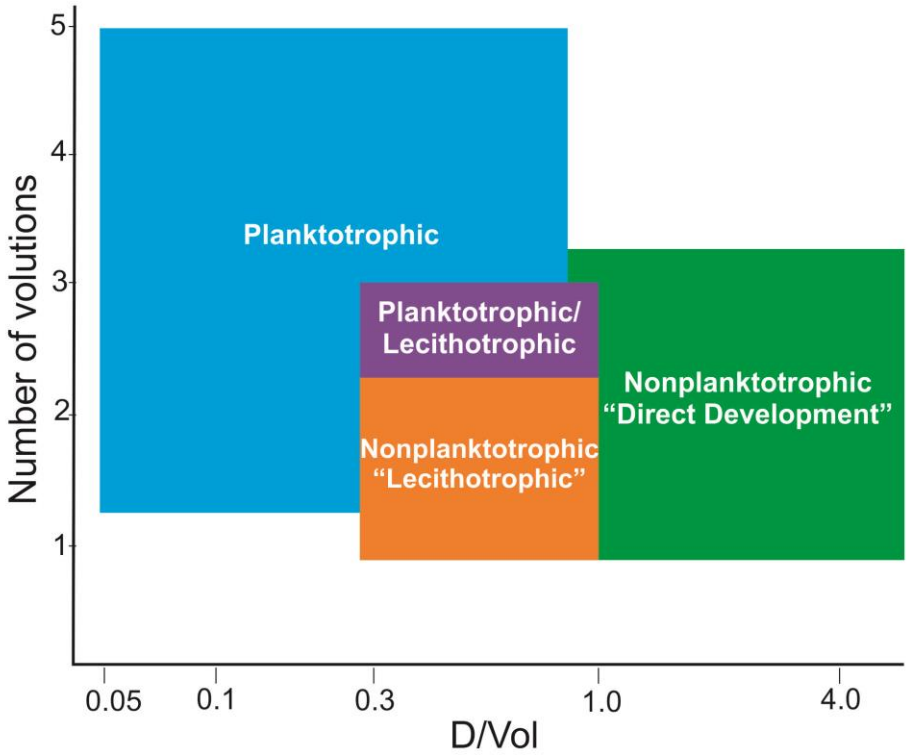


**Figure 5.3** Graphical presentation of metric criteria for inferring larval mode in fossil gastropods based on the method developed by Shuto (1974). Modified from Vendetti (2007).

| | P | L | DD | TOTAL |
|---|---|---|---|---|
| **Volutidae** | 3 | 2 | 64 | **69** |
| **Nassariidae** | 7 | 0 | 0 | **7** |
| **Raphitomidae** | 1 | 0 | 1 | **2** |
| **Borsoniidae** | 3 | 11 | 0 | **14** |
| **Mangeliidae** | 4 | 2 | 0 | **6** |
| **Turridae** | 1 | 5 | 0 | **6** |
| **TOTAL** | **19** | **20** | **65** | **104** |

**Table 5.2** Table showing the number of species with different larval strategies in each family used in this study. P = Planktotrophic, L = Lecithotrophic, DD = Direct developer.

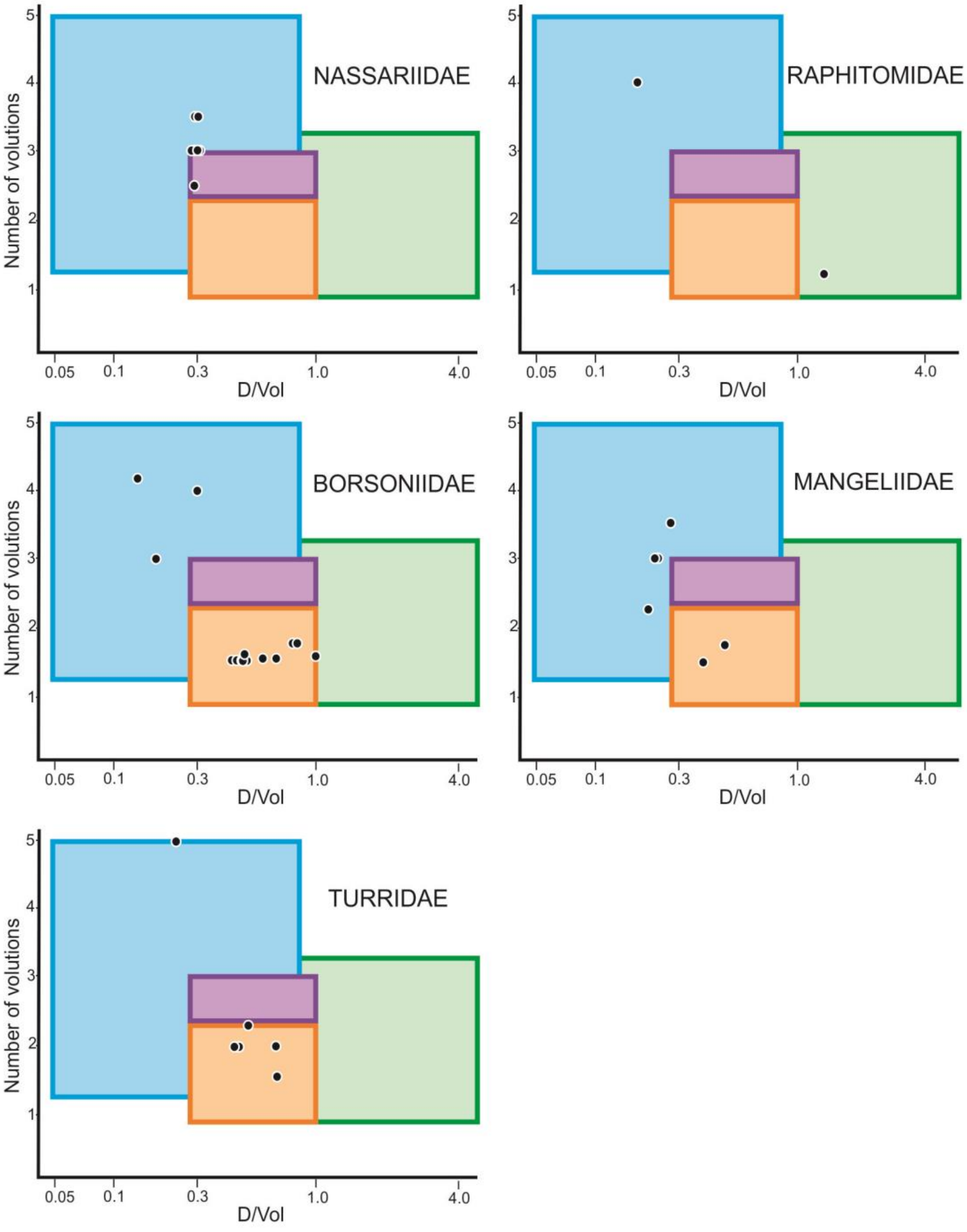


**Figure 5.4** Plot of protoconch measurements for the families Nassariidae, Raphitomidae, Borsoniidae, Mangeliidae and Turridae. Blue box = planktotrophy, orange box = lecithotrophy, green box = direct development, purple box = planktotrophy or lecithotrophy.

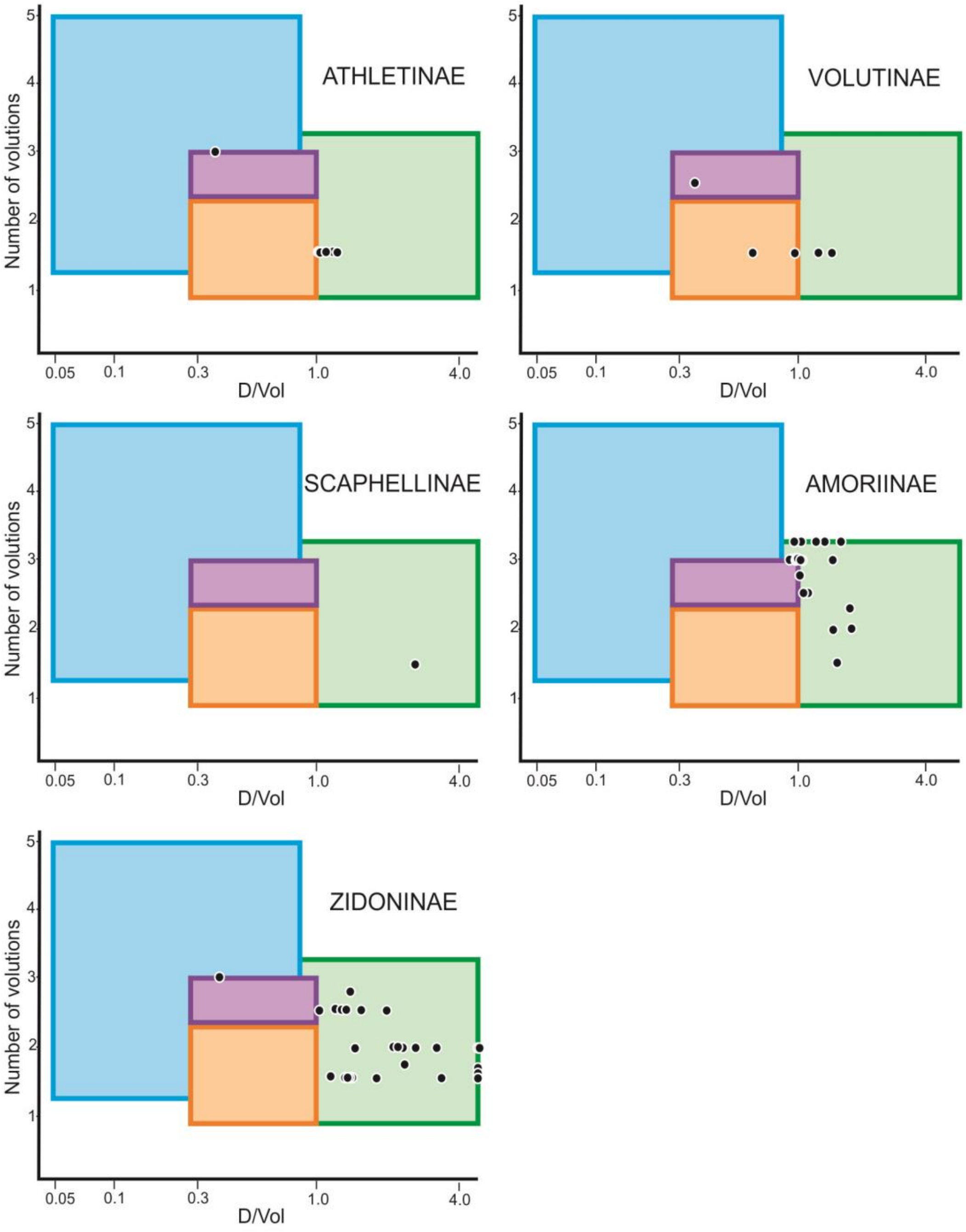


**Figure 5.5** Plot of protoconch measurements for the subfamilies Athletinae, Volutinae, Scaphellinae, Amoriinae and Zidoninae of the family Volutidae. Blue box = planktotrophy, orange box = lecithotrophy, green box = direct development, purple box = planktotrophy or lecithotropy.

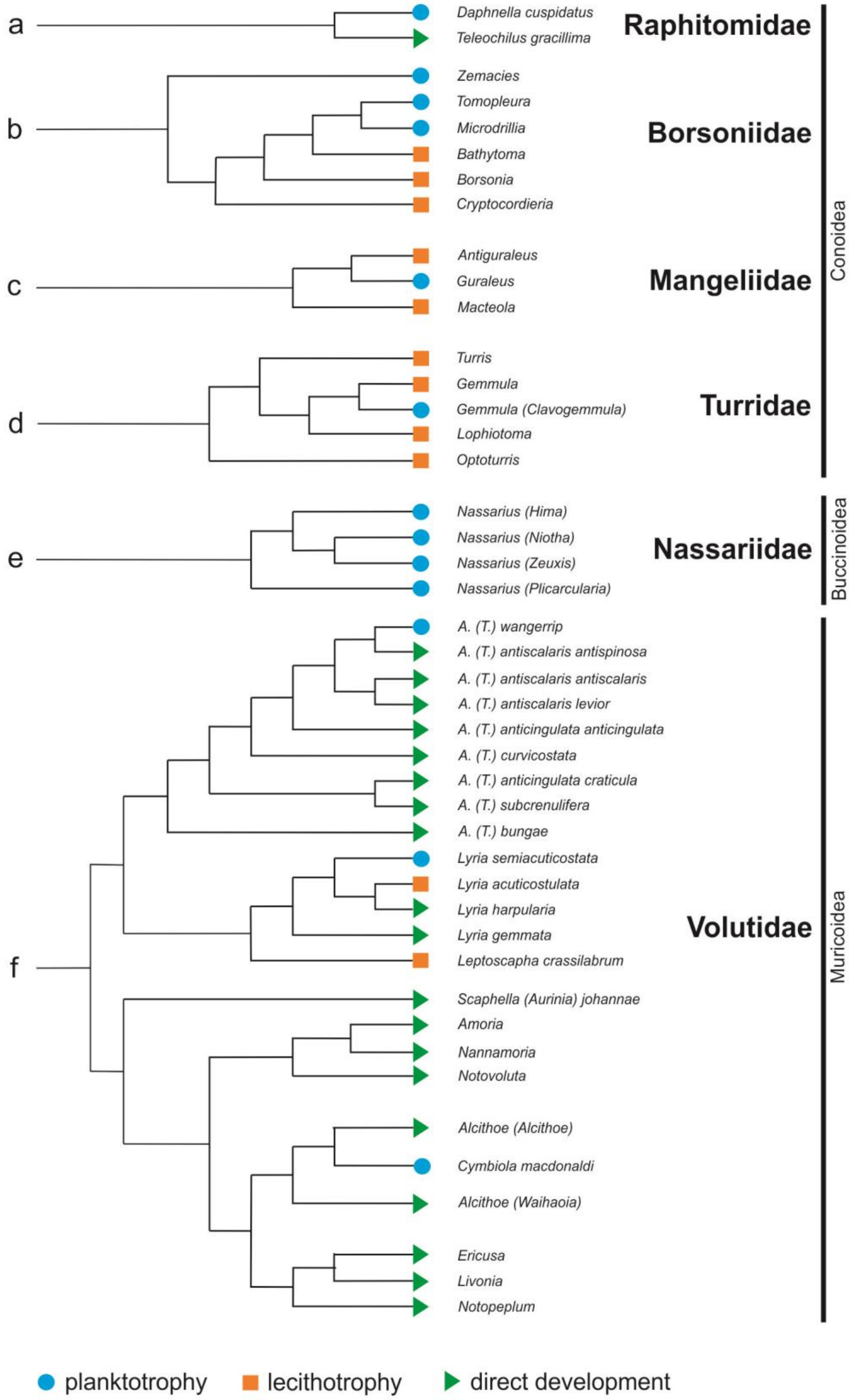


**Figure 5.6** Cladograms of taxa used in this research with larval strategies mapped onto terminal taxa: a) Raphitomidae, b) Borsoniidae, c) Mangeliidae, d) Turridae, e) Nassariidae and f) Volutidae.

## 5.2 RECONSTRUCTION OF ANCESTRAL DEVELOPMENTAL MODE

Having established the distribution of larval strategies in terminal taxa on the phylogenetic trees produced in Chapter 4 (Figure 5.6), a number of methods can be used to reconstruct the ancestral mode of development. The methods used in this thesis are maximum parsimony and maximum-likelihood analysis. The family Nassariidae are excluded from these analyses due to the lack of variation in developmental mode. Since all nassariids in this study have planktotrophic larvae, the ancestral mode of development can be unambiguously determined as planktotrophy.

### **5.2.1** MAXIMUM PARSIMONY ANALYSIS

To reconstruct ancestral developmental mode using maximum parsimony analysis, larval strategies are mapped onto the phylogenetic trees of each family using MacClade 4.08 (Maddison & Maddison, 2005). Outgroups included in these analyses follow those in Chapter 4: *Conus* for the conoidean families Raphitomidae, Borsoniidae, Mangeliidae and Turridae and *Mitra* for the family Volutidae. The type species for both *Conus* and *Mitra* are planktotrophs. Planktotrophy is assigned a character state of 0, lecithotrophy a character state of 1 and direct development a character state of 2. This allows the theoretical prediction that planktotrophy is plesiomorphic and that there is an ordered transformation through lecithotrophy to direct development to be explored. Transitions between the different larval strategies are treated in three ways: unordered, ordered and irreversible. Unordered transitions allow transitions to any larval strategy in any order and direction. Ordered transitions allow changes in larval strategy to occur in any direction but ordered from planktotrophy through lecithotrophy to direct development. Irreversible transitions only allow ordered changes in larval strategy in a forward direction only i.e. from planktotrophy to lecithotrophy to direct development. Where developmental traits are treated as irreversible, planktotrophy will always be considered to be the ancestral developmental mode. Transitions between character states are equally weighted. Maximum parsimony trees for unordered, ordered and irreversible transitions for the families Raphitomidae, Borsoniidae, Mangeliidae and Turridae are presented in Figures 5.7 and 5.8. Maximum parsimony trees for unordered, ordered and irreversible transitions in the family Volutidae are presented in figures 5.9, 5.10 and 5.11.

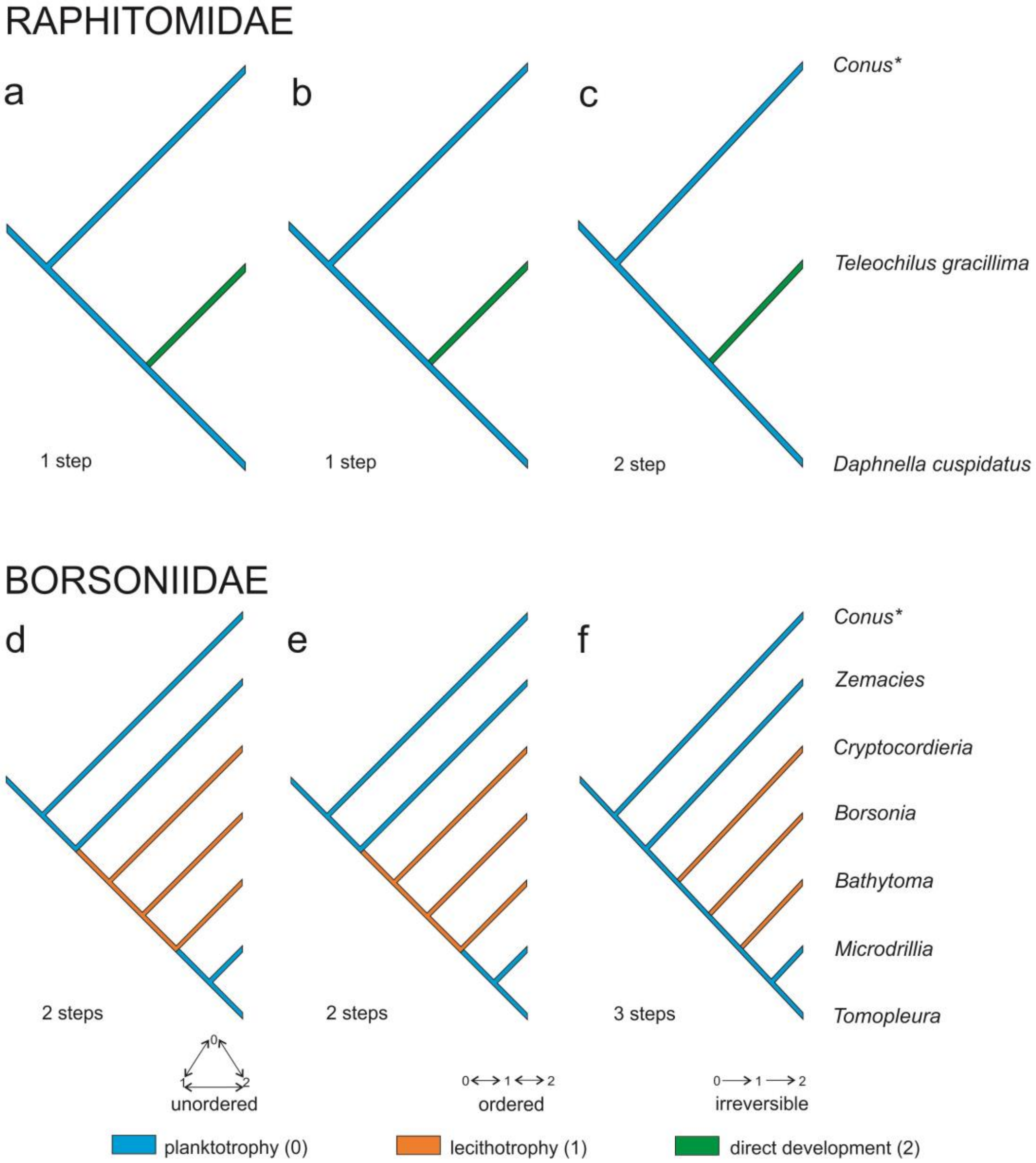


**Figure 5.7** Maximum parsimony reconstruction of ancestral larval strategies of Cenozoic gastropods from the families Raphitomidae and Borsoniidae of southeastern Australia: a) unordered, b) ordered and c) irreversible transitions for the family Raphitomidae; d) unordered, e) ordered and f) irreversible transitions for the family Borsoniidae.

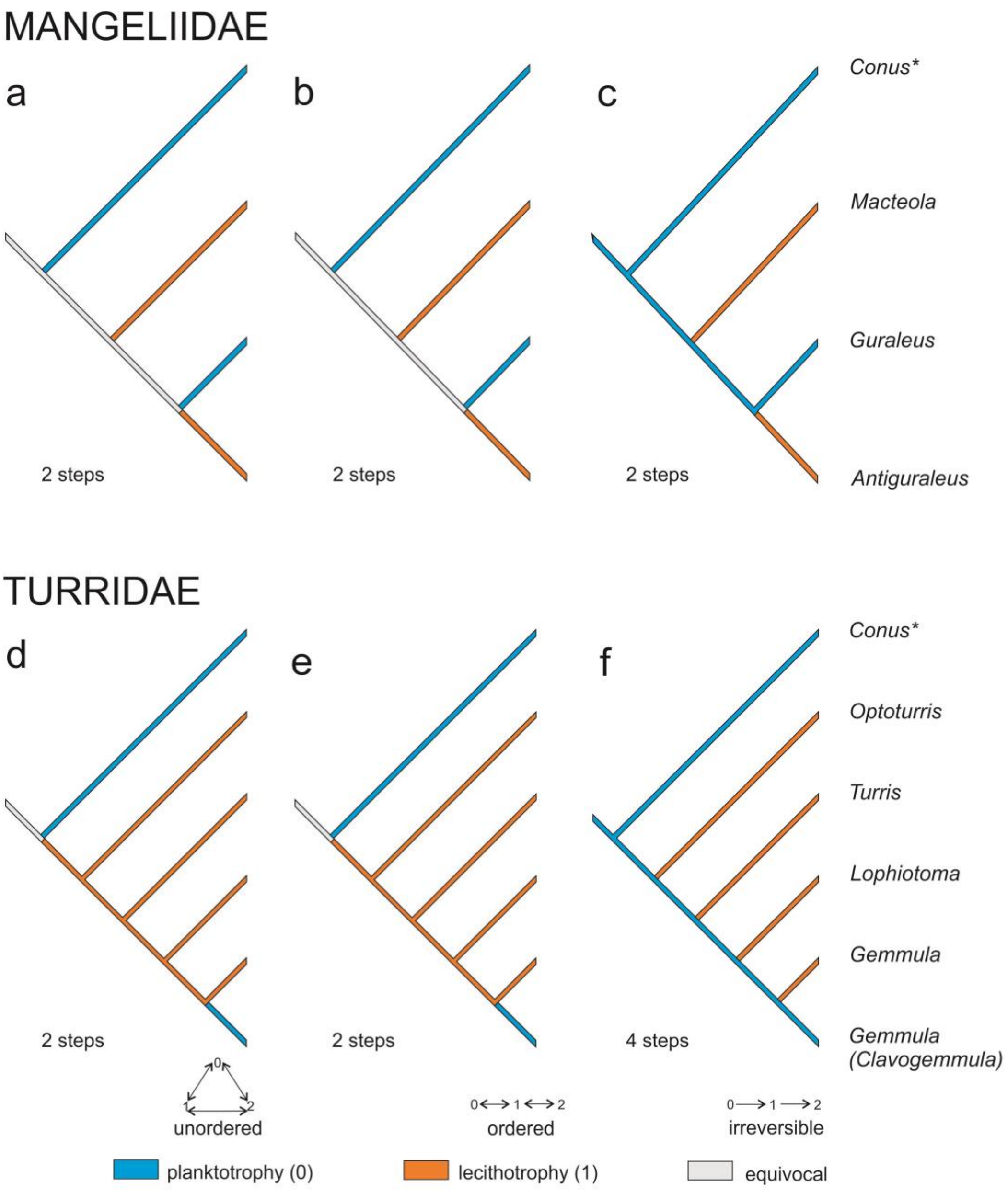


**Figure 5.8** Maximum parsimony reconstruction of ancestral larval strategies of Cenozoic gastropods from the families Mangeliidae and Turridae of southeastern Australia: a) unordered, b) ordered and c) irreversible transitions for the family Mangeliidae; d) unordered, e) ordered and f) irreversible transitions for the family Turridae.

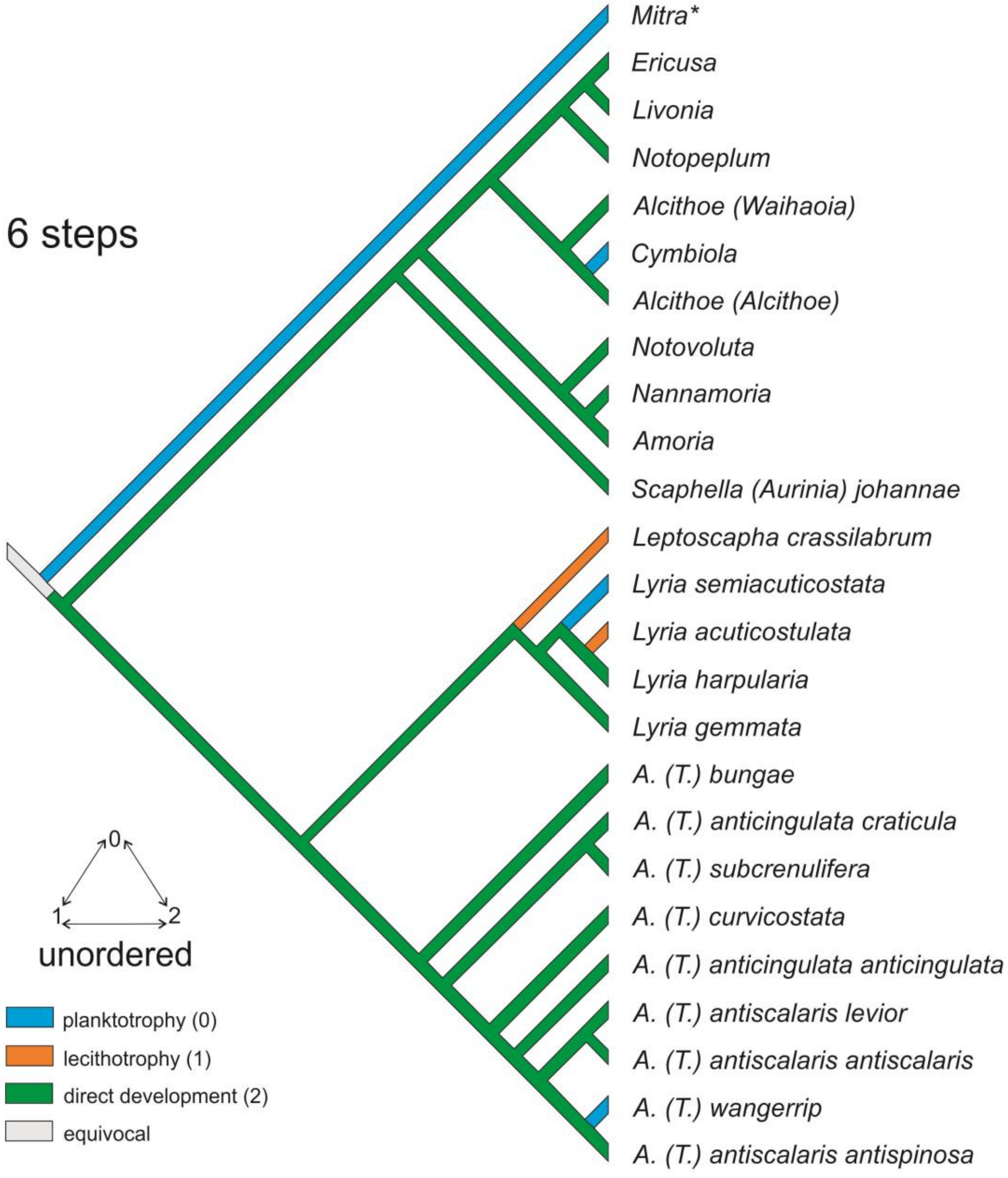


**Figure 5.9** Maximum parsimony reconstruction of ancestral larval strategies of Cenozoic gastropods from the family Volutidae of southeastern Australia where transitions are treated as unordered.

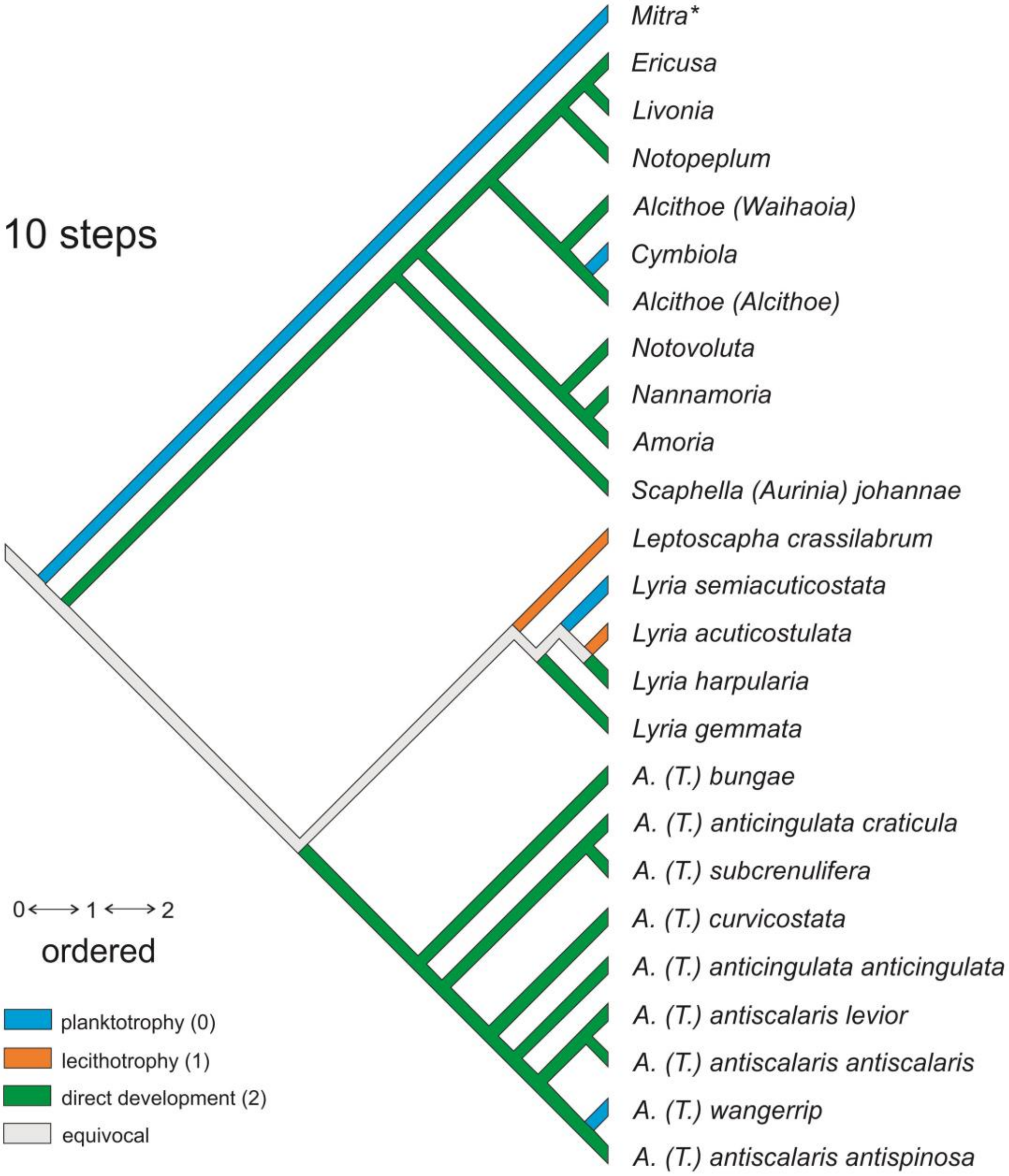


**Figure 5.10** Maximum parsimony reconstruction of ancestral larval strategies of Cenozoic gastropods from the family Volutidae of southeastern Australia where transitions are treated as ordered.

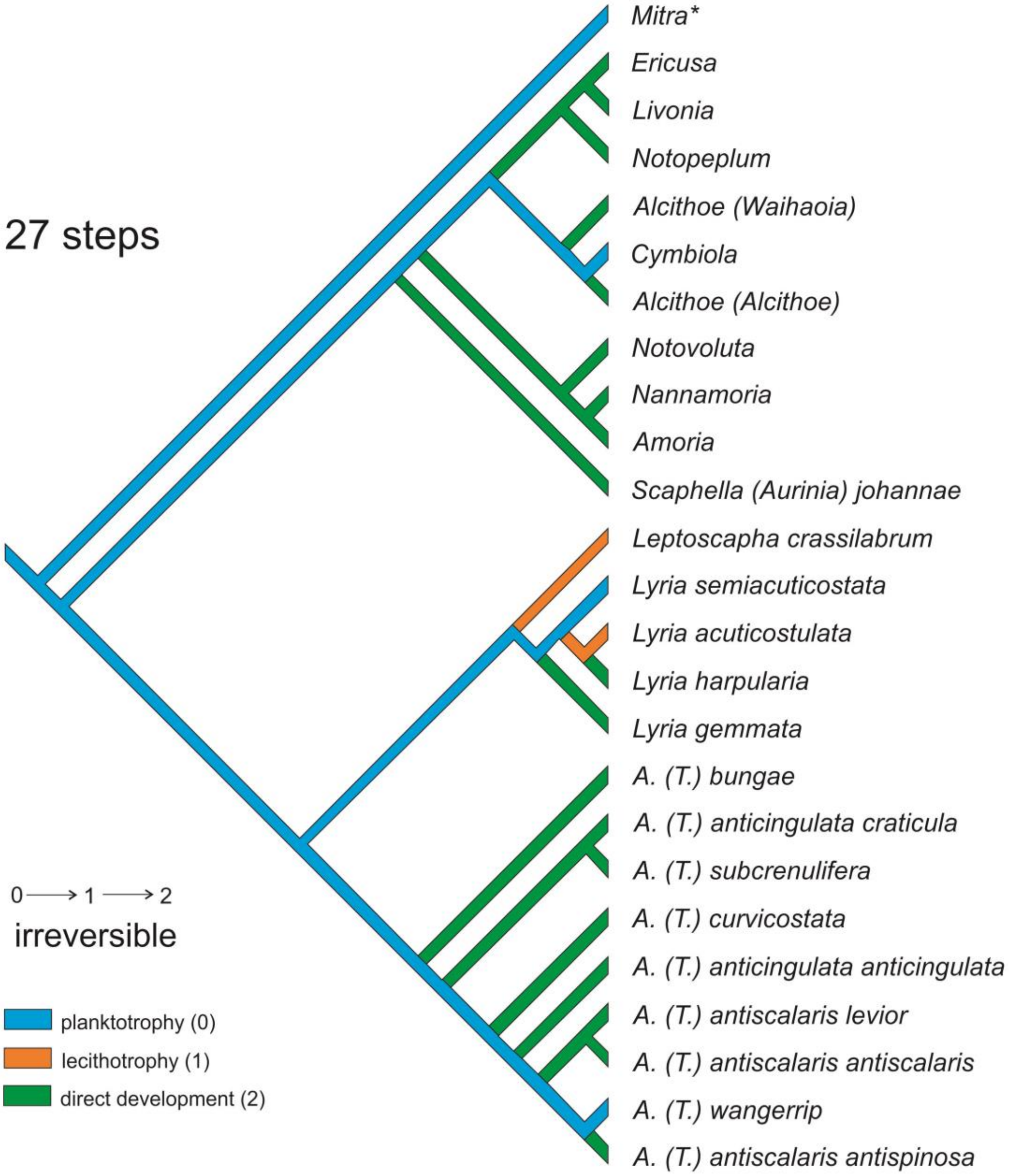


**Figure 5.11** Maximum parsimony reconstruction of ancestral larval strategies of Cenozoic gastropods from the family Volutidae of southeastern Australia where transitions are treated as irreversible.

For each of the conoidean families (Raphitomidae, Borsoniidae, Mangeliidae and Turridae) there are only two larval modes. Consequently, the results will be the same regardless of whether developmental traits are treated as unordered or ordered, although both analyses are presented for completeness. The trees of these families do not represent all species found in southeastern Australia, but due to uncertain taxonomic placement no other taxa can be included in this study (see Chapter 3 for discussion). The tree of the family Volutidae includes all species/genera found in Cenozoic strata of southeastern Australia. The possible ancestral larval strategies for each family are summarised in Table 5.3. Where the trees cannot unequivocally determine the ancestral larval mode, planktotrophy is always possible according to this analysis. For conoidean families this is because there are only two possible larval strategies. Maximum parsimony analysis indicates that lecithotrophy is the most unlikely ancestral larval strategy in the family Volutidae.

| | **Unordered** | **Ordered** | **Irreversible** |
|---|---|---|---|
| **Raphitomidae** | P | P | P |
| **Borsoniidae** | P | P | P |
| **Mangeliidae** | E (P or L) | E (P or L) | P |
| **Turridae** | E (P or L) | E (P or L) | P |
| **Volutidae** | E (P or DD) | E (P or DD) | P |

**Table 5.3** Table showing the possible ancestral larval modes for each family included in this study based on maximum parsimony analysis where characters are treated as unordered, ordered and irreversible. Larval strategies in brackets are the most likely ancestral modes based on the number of steps of each tree. E = Equivocal, P = Planktotrophy, L = Lecithotrophy, DD = Direct Development.

### **5.2.2** MAXIMUM-LIKELIHOOD ANALYSIS

Reconstruction of ancestral modes of development using maximum-likelihood analysis is carried out using Mesquite 2.75 (Maddison & Maddison, 2011). The Mk1 model ("Markov k-state 1 parameter model") is used to assess the proportional support for each larval strategy at all internal nodes by maximising the likelihood with each node fixed in turn to each of the three possible larval strategies (local estimator model of Pagel, 1999). Significant support for a particular character state was established by a likelihood ratio of 7.4:1 or more (Maddison & Maddison, 2011). Outgroups were used to root the trees and are the same as those used in Chapter 4: *Conus* for the conoidean families Raphitomidae, Borsoniidae, Mangeliidae and Turridae and *Mitra* for the family Volutidae. The type species for both *Conus* and *Mitra* are planktotrophs. As for maximum parsimony analysis, planktotrophy, lecithotrophy and direct development were assigned the character states 0, 1 and 2 respectively. Analyses were carried out using equal branch lengths for all trees.

Proportional support of each larval strategy at the basal node of each tree indicates the likely ancestral developmental mode. Maximum-likelihood trees for the families Raphitomidae, Borsoniidae, Mangeliidae and Turridae are presented in Figure 5.12. The maximum-likelihood tree for the family Volutidae is presented in Figure 5.13. The possible ancestral larval strategies and the proportions of support for each at the basal node for each family are summarised in Table 5.4.

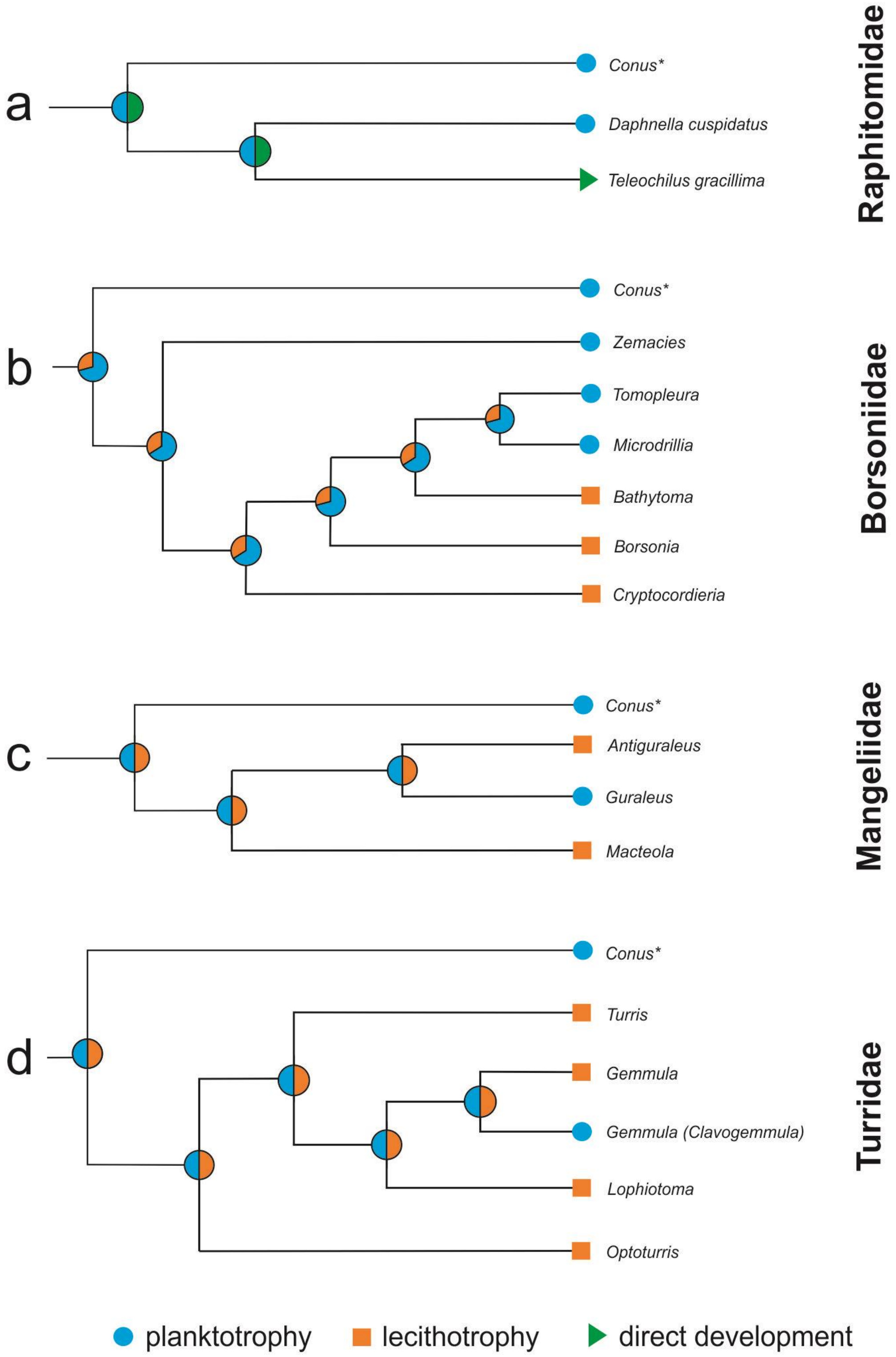


**Figure 5.12** Maximum-likelihood reconstruction of ancestral larval strategies of Cenozoic gastropods from the families Raphitomidae, Borsoniidae, Mangeliidae and Turridae of southeastern Australia. Pie charts indicate relative support for each character state at each node. Ratios of 7.4:1 are considered significant and indicated by an asterisk.

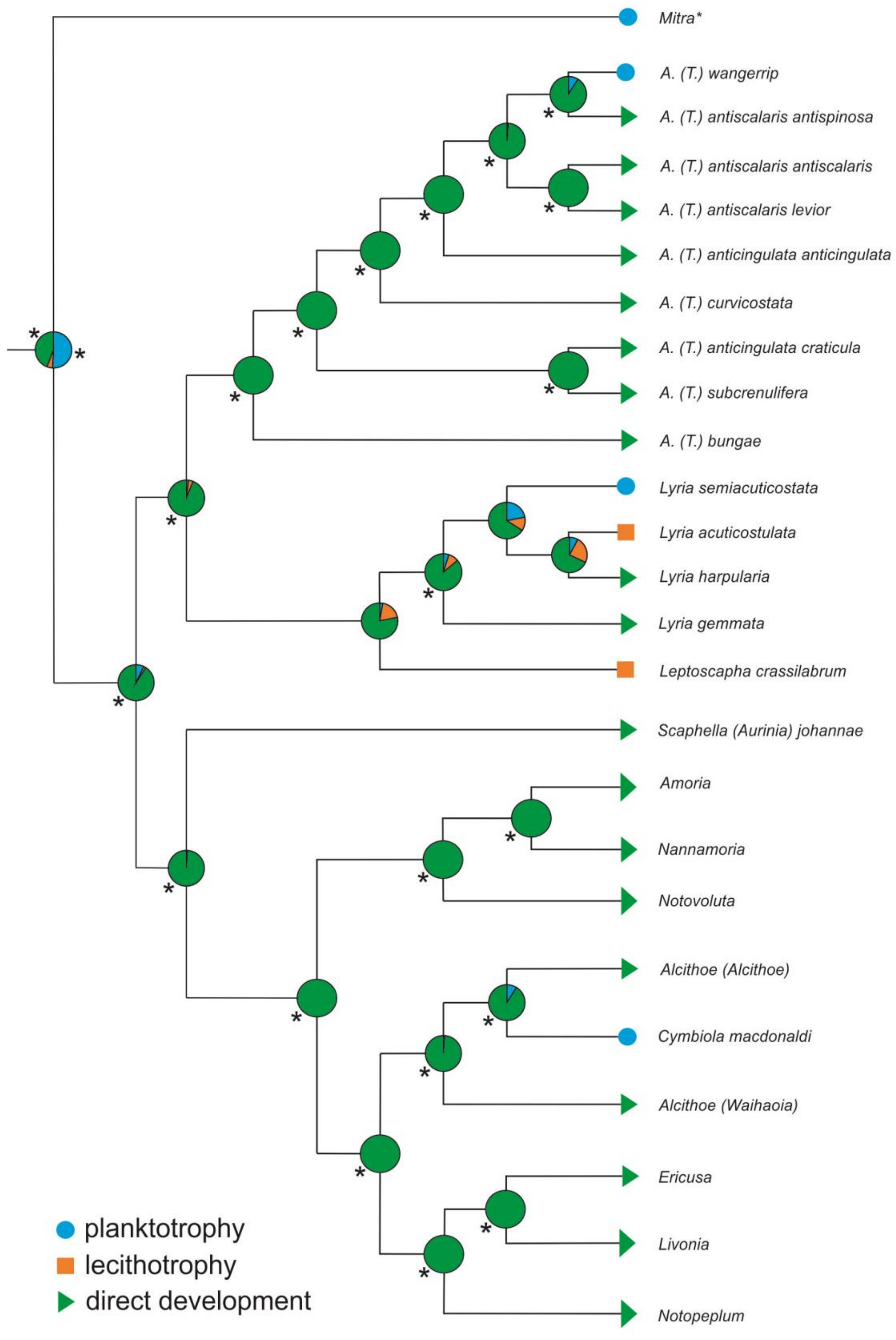


**Figure 5.13** Maximum-likelihood reconstruction of ancestral larval strategies of Cenozoic gastropods from the family Volutidae of southeastern Australia. Pie charts indicate relative support for each character state at each node. Ratios of 7.4:1 are considered significant and indicated by an asterisk.

| | **P** | **L** | **DD** |
|---|---|---|---|
| **Raphitomidae** | 0.5 | - | 0.5 |
| **Borsoniidae** | 0.71 | 0.29 | - |
| **Mangeliidae** | 0.5 | 0.5 | - |
| **Turridae** | 0.5 | 0.5 | - |
| **Volutidae** | 0.51* | 0.05 | 0.44* |

**Table 5.4** Table showing the possible ancestral larval modes for each family included in this study based on maximum-likelihood analysis. Numerical values indicate the proportional support for each character state at the basal node of each tree. Ratios of 7.4:1 are considered significant and indicated by an asterisk. P = Planktotrophy, L = Lecithotrophy, DD = Direct Development.

Maximum-likelihood analysis shows equal support for planktotrophy and lecithtrophy as the ancestral larval mode in the families Mangeliidae (Figure 5.12c) and Turridae (Figure 5.12d). Similarly, planktotrophy and direct development are equally likely ancestral larval strategies in the family Raphitomidae (Figure 5.12a). Analysis of the family Borsoniidae (Figure 5.12b) indicates that planktotrophy is the best supported ancestral character state although this is not considered to be significant (ratio less than 7.4:1). The small datasets for each of the conoidean families is likely to contribute to the equal support of ancestral character states. By including more taxa in these analyses, it may be possible to find the more likely ancestral larval strategy. Both planktotrophy and direct development are indicated as possible ancestral developmental modes in the family Volutidae (Figure 5.13), both with significant support (ratio 7.4:1 or more). Lecithotrophy is considered to be the least likely ancestral mode of development in the Volutidae of southeastern Australia.

The results from both maximum parsimony and maximum-likelihood analysis are almost identical, although the latter indicates the level of uncertainty for each character state. Planktotrophy is always a possible ancestral developmental mode regardless of the method used to reconstruct ancestral larval strategies. A comparison of the results of the two methods is presented in Table 5.5 (using equal weight unordered maximum parsimony).

| | Maximum Parsimony | Maximum-likelihood |
|---|---|---|
| **Raphitomidae** | P | P or D |
| **Borsoniidae** | P | P or L |
| **Mangeliidae** | P or L | P or L |
| **Turridae** | P or L | P or L |
| **Volutidae** | P or DD | P or DD |

**Table 5.5** Comparison of results of ancestral developmental mode reconstruction using maximum parsimony and maximum-likelihood methods.

## 5.3 NUMBER AND ORDER OF CHANGES IN DEVELOPMENTAL MODE

Three approaches are used in this thesis to examine the number and order of switches in larval mode of Cenozoic gastropods from southeastern Australia: maximum parsimony, maximum parsimony sensitivity analysis and maximum-likelihood. The Nassariidae are excluded from these analyses as there is no variation in larval strategy within this family.

### **5.3.1** MAXIMUM PARSIMONY ANALYSIS

For each of the families included in this study, larval strategies are not concentrated to particular clades but are scattered randomly across the trees. Using maximum parsimony analysis (Figures 5.7, 5.8, 5.9, 5.10 and 5.11), the number and order of shifts in larval strategy can be examined when developmental traits are treated as unordered, ordered or irreversible. The number and order of changes in larval strategy for each family when planktotrophy is considered the ancestral larval mode (which is possible for all families) are summarised in Table 5.6. Outgroup taxa used in these phylogenies are not included in the number of changes in developmental mode but just to polarise the tree. If the outgroup is altered (perhaps to something more closely related to the ingroup taxa) then this may alter the number of changes seen on the tree.

| | Unordered | Ordered | Irreversible |
|---|---|---|---|
| **Raphitomidae** | P → DD (1) | P → DD (1) | P → DD (1) |
| **Borsoniidae** | P → L (1)<br>L → P (1) | P → L (1)<br>L → P (1) | P → L (3) |
| **Mangeliidae** | P → L (2) | P → L (2) | P → L (2) |
| **Turridae** | P → L (1)<br>L → P (1) | P → L (1)<br>L → P (1) | P → L (4) |
| **Volutidae** | P → DD (1)<br>DD → L (2)<br>DD → P (3) | P → DD (4)<br>P → L (2)<br>DD → P (2) | P → DD (13)<br>P → L (2) |

**Table 5.6** Table showing the order and number (in brackets) of changes in larval mode for each family when planktotrophy is considered to be the ancestral developmental mode. P = planktotrophy, L = lecithotrophy, DD = direct development.

The results summarised in Table 5.6 suggest that switches from planktotrophy to nonplanktotrophy are possible, as theory predicts. However, the analyses also suggest that reversals from nonplanktotrophy to planktotrophy are also possible when transitions between character states are equally weighted. This is considered theoretically far less likely due to the presumed difficulty in reacquiring the specialised structures required for feeding and mobility in the plankton (e.g. Strathmann, 1978).

Within the family Volutidae, there are no instances of planktotrophic lineages giving rise to lecithotrophic lineages which in turn give rise to direct development. This suggests that ordered transformations are unlikely in this family. It is not possible to assess ordered transformations in any other family included in this study as they do not possess more than two developmental modes.

Maximum parsimony analysis of ancestral larval modes has indicated that lecithotrophy is a possible plesiomorphic developmental mode in the families Mangeliidae and Turridae. The number and order of changes in larval strategy for these families, when lecithotrophy is considered to be the ancestral larval mode, are summarised in Table 5.7. These results suggest only one transition from lecithotrophy to planktotrophy.

| | Unordered | Ordered |
|---|---|---|
| **Mangeliidae** | L → P (1) | L → P (1) |
| **Turridae** | L → P (1) | L → P (1) |

**Table 5.7** Table showing the order and number (in brackets) of changes in larval mode for the families Mangeliidae and Turridae when lecithotrophy is considered to be the ancestral developmental mode. P = planktotrophy, L = lecithotrophy, DD = direct development.

Maximum parsimony analysis of ancestral larval modes has indicated that direct development is as likely to be the plesiomorphic developmental mode as planktotrophy in the family Volutidae. The number and order of changes in larval strategy for this family, when direct development is considered to be the ancestral larval mode, are summarised in Table 5.8. The results indicate that a maximum of three shifts from direct development to planktotrophy, and two from direct development to lecithotrophy occur in the volutes of southeastern Australia.

| | Unordered | Ordered |
|---|---|---|
| **Volutidae** | DD → P (3)<br>DD → L (2) | DD → P (3)<br>DD → L (2) |

**Table 5.8** Table showing the order and number (in brackets) of changes in larval mode for the family Volutidae when direct development is considered to be the ancestral developmental mode. P = planktotrophy, L = lecithotrophy, DD = direct development.

Equally weighted maximum parsimony reconstructions indicate that up to three independent gains of planktotrophy from nonplanktotrophy have occurred in the family Volutidae contradicting the theory of irreversible losses of planktotrophy (Strathmann, 1978). Reconstruction of ancestral larval modes in the star fish family Asterinidae (Hart et al., 1997) also indicated that planktotrophy could be lost and then regained. Two possible theories have been put forward to explain these reversals (Cunningham, 1999). Firstly, these reconstructions may indeed reflect true evolutionary patterns and therefore the prediction of irreversibility is incorrect. Secondly, irreversible losses of planktotrophic larvae may be so frequent that it is possible that parsimony incorrectly reconstructs losses and gains of feeding larvae. However, Cunningham (1999) also noted that rapid evolution does not necessarily suggest that larval feeding cannot be regained once lost.

### **5.3.2** MAXIMUM PARSIMONY SENSITIVITY ANALYSIS

Although maximum parsimony analysis is the most widely used method for reconstructing ancestral character states, it has been noted that acceptance of these reconstructions is dependent on assumptions regarding evolutionary processes (e.g. Sober, 1988; Maddison, 1994; Ree & Donoghue, 1998). These evolutionary assumptions are quantified by a matrix of costs, e.g. the loss or gain of a particular character state (Ree & Donoghue, 1998), referred to as a step matrix (Maddison & Maddison, 1992). Step matrices determine the extent to which transitions in one direction are favoured over transitions in the opposite direction (Ree & Donoghue, 1998). Although the most common approach is to assign equal costs to all character state transitions, Swofford & Maddison (1992) note that this is in itself an assumption about character state evolution. To assess assumptions regarding the directionality of evolutionary change, a quantitative approach referred to as sensitivity analysis is used (Ree & Donoghue, 1998).

Sensitivity analysis uses a graphical approach to assess the sensitivity of character state transitions to cost assumptions. The number of independent losses or gains of a particular character state are inferred from a maximum parsimony tree. The cost of gaining the character state ($C_G$) is compared to the cost of losing the character state ($C_L$). The initial assumption is that the costs of gains or losses are equal. Sensitivity analysis examines how large the ratio of $C_G$:$C_L$ has to be before a node becomes equivocal or more parsimoniously assigned to the alternative character state. Over a whole tree, where $C_G < C_L$ more gains are inferred and where $C_G > C_L$ more losses are inferred.

For this analysis, lecithotrophy and direct development are combined as nonplanktotrophy. The loss and gain of nonplanktotrophy is recorded. The cost of change in one direction is changed by increments of 1.0 whilst the cost of change in the opposite direction is maintained at 1.0. The number of changes is displayed as a continuous line to help visualise this step function. The point at which the lines cross on the x-axis (inflection point) of the cost-change graph indicates the ratio at which the relative frequency of gains versus losses is reversed. Cost-change graphs for the families Volutidae, Borsoniidae, Mangeliidae and

Turridae are presented in Figure 5.14. The families Raphitomidae and Nassariidae are excluded due to limited number of taxa and lack of variation in larval mode respectively.

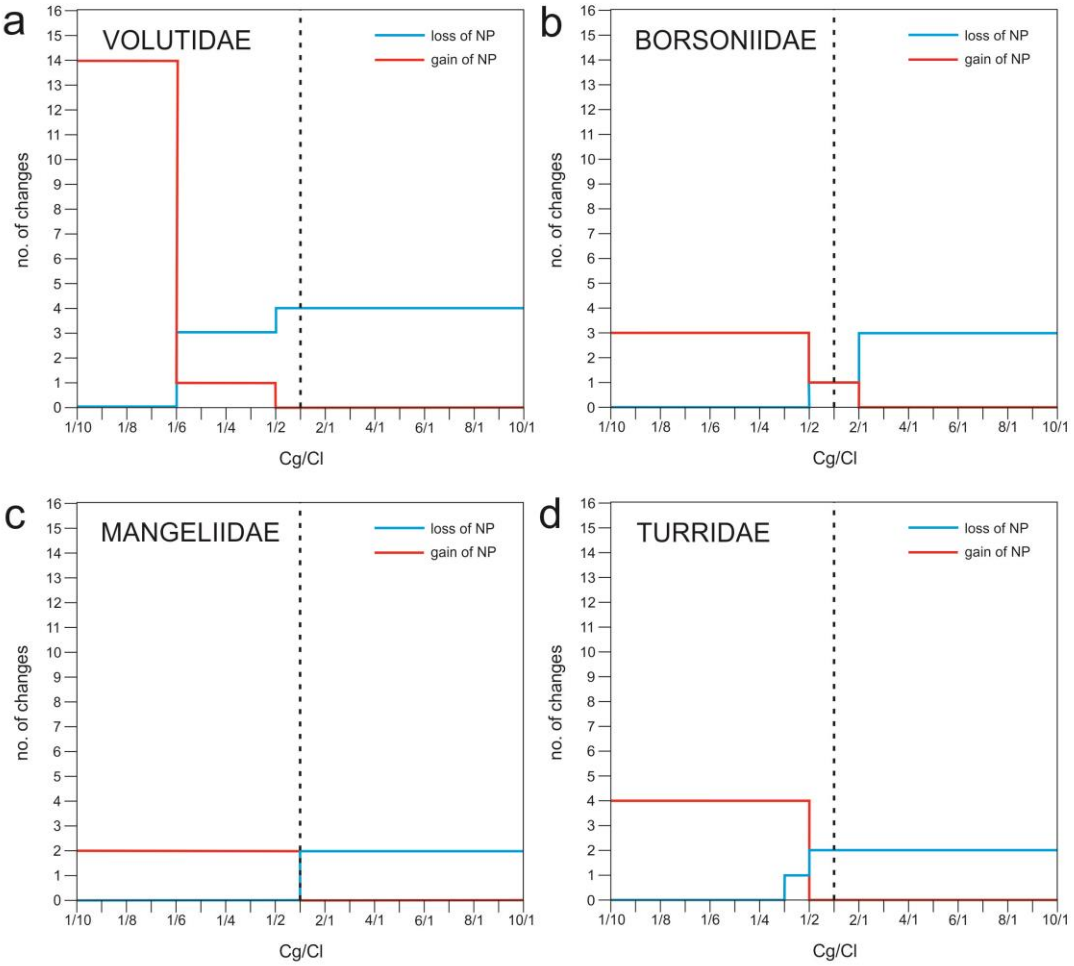


**Figure 5.14** Cost-change graphs for the families Volutidae, Borsoniidae, Mangeliidae and Turridae. Cg = cost of gaining nonplanktotrophy, Cl = cost of losing nonplanktotrophy.

The cost-change graph for the family Volutidae indicates that when $C_G = C_L$ there are more inferred losses (4) than gains (0). The inflection point occurs where the ratio of $C_G/C_L = 1/6$ at which point no switches to planktotrophy (losses) are observed, but instead multiple transitions to nonplanktotrophy (gains) occur. This implies that if a switch from nonplanktotrophy to planktotrophy were six times more difficult than the opposite transition, the pattern of multiple shifts from planktotrophy to nonplanktotrophy (as predicted by Strathmann (1978), Wray (1995) etc) would be observed. A similar pattern is seen in the Turridae where the inflection point occurs where the ratio of $C_G/C_L = 1/2$. The inflection point on the cost-change graphs for the families Borsoniidae and Mangeliidae occur where $C_G = C_L$.

### **5.3.3** MAXIMUM-LIKELIHOOD ANALYSIS

Maximum likelihood analysis (Figures 5.12 and 5.13) concurs with maximum parsimony analysis in establishing the number and order of changes in larval mode but provides extra information regarding the likelihood of a particular larval strategy occurring at any particular node. This provides little extra information for the conoidean families but does suggest that the number and order of changes in larval strategy within the Volutidae is less certain, particularly for the Volutinae clade but also for the Athletinae and Zidoninae clades. The level of uncertainty is not great enough to offer a possibility different to that established by maximum parsimony analysis.

## 5.4 CONGRUENCE OF PHYLOGENY AND STRATIGRAPHY

Three methods are used to test the congruence of phylogeny and stratigraphy and analyse the quality of the fossil record of the gastropods from the Cenozoic of southeastern Australia used in this study: the Stratigraphic Consistency Index (SCI), the Relative Completeness Index (RCI) and the Gap Excess Ratio (GER). The stratigraphic range of the taxa used in this chapter are shown in Figure 5.15. The stratigraphic range and phylogenies of each of these taxa are shown in Figure 5.16. These figures provide the basis for establishing the SCI, RCI and GER for each family. Although these three methods provide a good measure for establishing the congruence of stratigraphy and phylogeny and for assessing the quality of the fossil record, there has been some criticism regarding the SCI and RCI (Siddall, 1996, 1997, 1998; Wills, 1999). Siddall (1996) suggests that the SCI value is biased by the number of nodes of a tree, i.e., larger trees with more clades will have lower SCI values than smaller trees with fewer nodes. Similarly, Wills (1999) suggests that tree topology significantly biases SCI values. Siddall (1998) finds the presumption of the RCI value that all taxa have simultaneous origins “a most disturbing proposition”. Despite these criticisms, these are the most commonly used methods for assessing congruence and the quality of the fossil record, and so are included in this study.

The Stratigraphic Consistency Index examines how well the stratigraphy fits a cladogram using a node-by-node approach (Huelsenbeck, 1994). The method assesses how well each node fits the stratigraphy, starting at the most distal node and comparing it with the node immediately below. The node is considered to be consistent where the stratigraphic ages of the taxa above it are younger than, or equal to it in age (Hitchin & Benton, 1997). The consistency of the root node cannot be calculated and is excluded. The SCI is defined as:

$$\mathrm{SCI} = \frac{\mathrm{C}}{\mathrm{N}}$$

where C = number of stratigraphically consistent nodes and N = number of internal nodes (excluding the root). The closer the SCI is to 1, the more consistent the nodes are considered to be.

The SCI was calculated for each family used in this thesis based on generic level phylogenies. The SCI was also calculated for the subfamilies Volutinae and Athletinae of the family Volutidae based on a species level phylogeny. The results of this analysis are presented in Table 5.9. The results suggest that for most families the nodes are completely or two-thirds consistent with the stratigraphy. With the smaller trees, this may be the result of limited number of taxa and by including all known taxa from the region (which is not possible as part of this study) the result may not be so good. The result for the family Turridae indicates that there is no congruence between the stratigraphy and the phylogeny due to the fact that the oldest genus (*Gemmula (Clavogemmula)* is also one of most distal nodes on the tree (Figure 5.16).

| Family | SCI |
|---|---|
| Raphitomidae | 1.0 |
| Borsoniidae | 1.0 |
| Mangeliidae | 1.0 |
| Turridae | 0 |
| Nassariidae | 0.66 |
| Volutidae | 1.0 |
| Athletinae + Volutinae | 0.66 |

**Table 5.9** SCI values for each family based on genus level phylogenies and the combinations of the volute subfamilies Athletinae and Volutinae based on species level phylogenies.

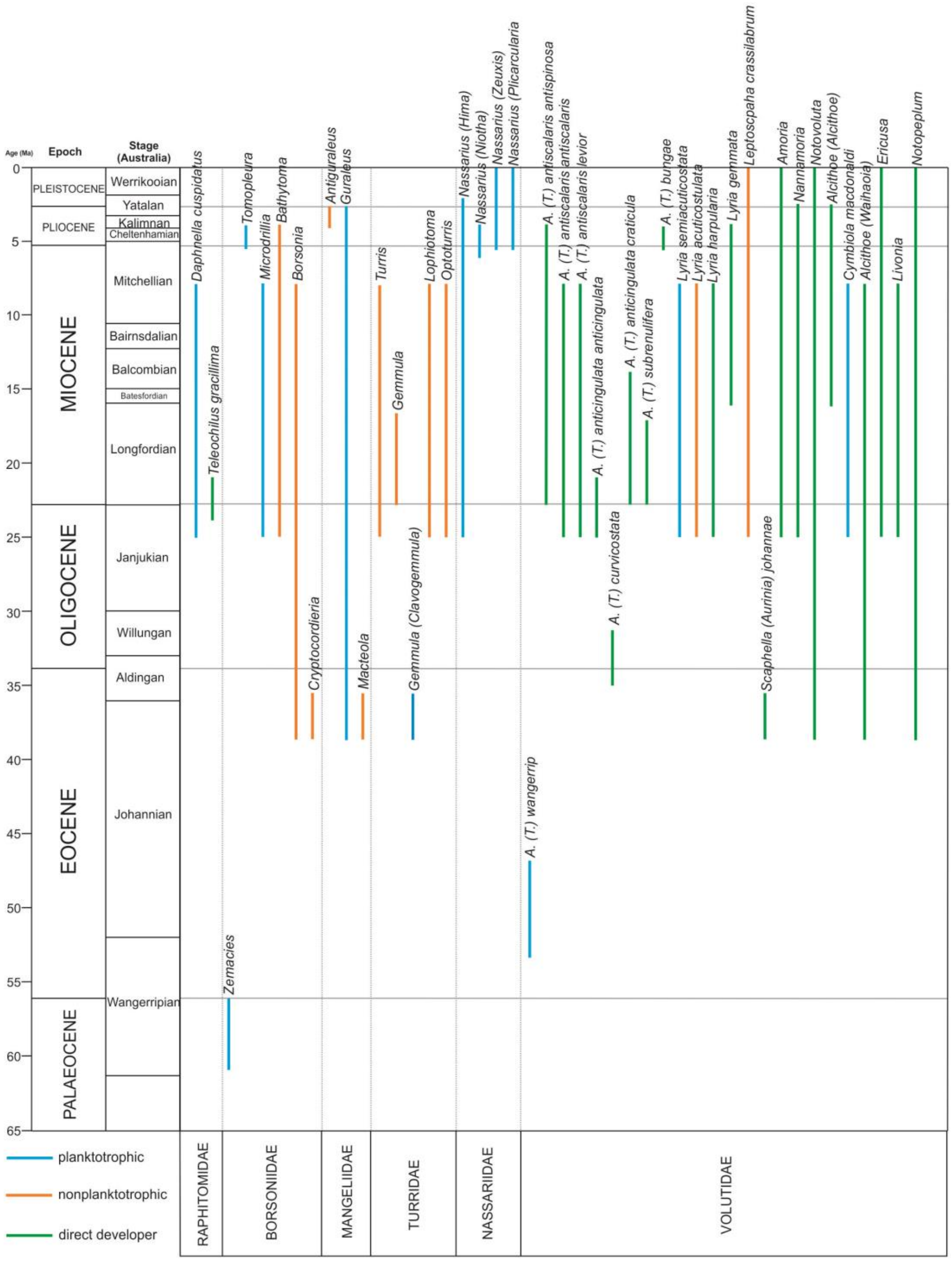


**Figure 5.15** Stratigraphic distribution of Cenozoic gastropods from the families Volutidae, Nassariidae, Raphitomidae, Borsoniidae, Mangeliidae and Turridae from southeastern Australia.

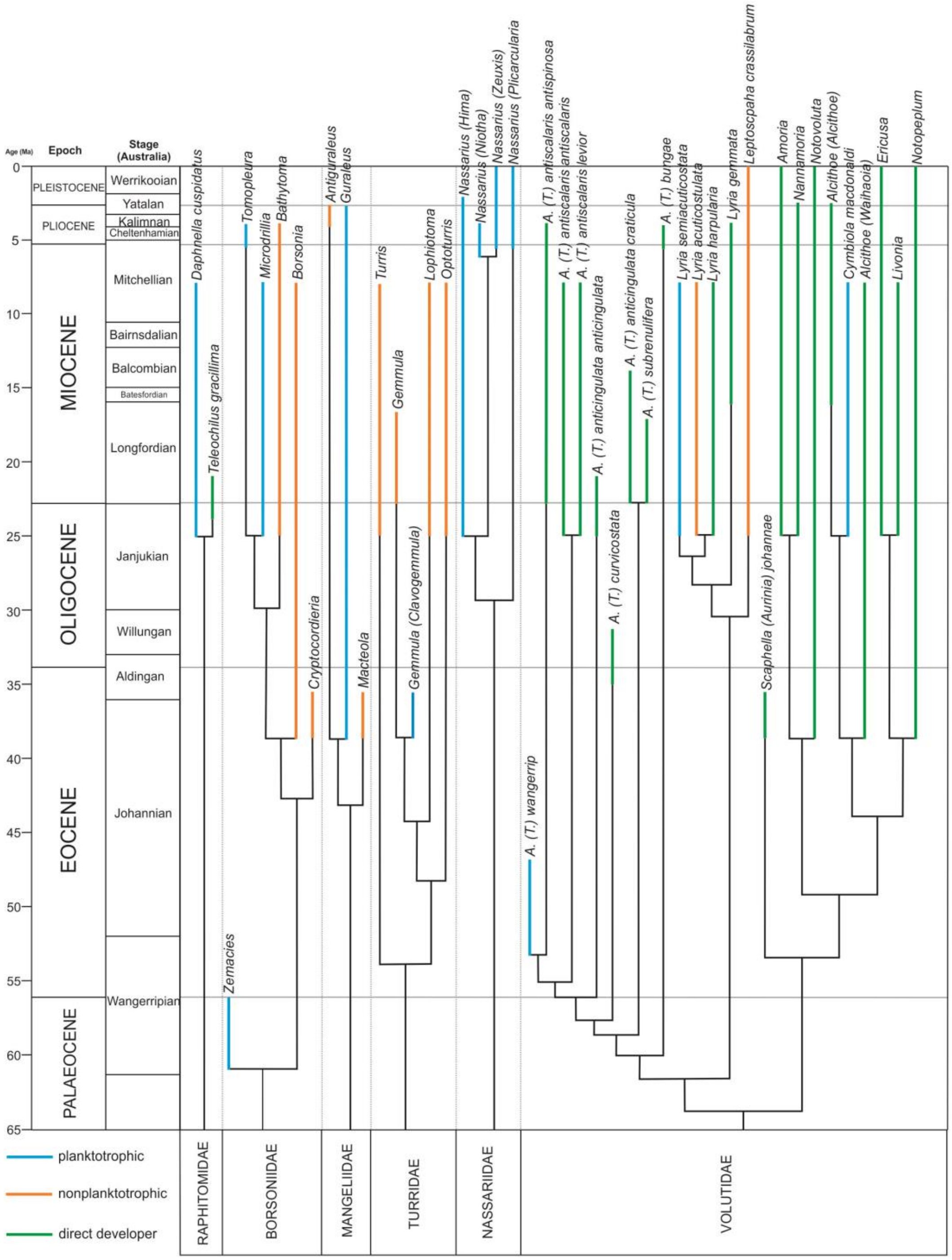


**Figure 5.16** Stratigraphic distribution and phylogenies of Cenozoic gastropods from the families Volutidae, Nassariidae, Raphitomidae, Borsoniidae, Mangeliidae and Turridae from southeastern Australia.

The Relative Completeness Index (RCI) assesses the quality of the fossil record by establishing the relative completeness of the stratigraphic ranges of taxa using ghost ranges (Benton & Hitchin, 1996; Hitchin & Benton, 1997). The stratigraphic range of each taxon is hypothetically extended to the stratigraphic range of its sister taxon. This unseen range is referred to as the Minimum Implied Gap (MIG). The RCI of a tree is calculated as:

$$\mathrm{RCI} = \left(1 - \frac{\Sigma(\mathrm{MIG})}{\Sigma(\mathrm{SLR})}\right) \times 100\%$$

where MIG = the Minimum Implied Gap and SLR = the Simple Range Length for each taxon. Standard time scales are used to establish stratigraphic ranges and no estimate of uncertainty is calculated. Values range from infinitely negative, where the sum of SLR exceeds the expected gap, to 100%, where there are no gaps and the fossil record is considered complete. RCI values are considered to be a maximum and lower values can be achieved by establishing ancestor-descendant relationships (Hitchin & Benton, 1997).

RCI values were calculated for each tree at generic level and for the subfamilies Volutinae and Athletinae at species levels. The results of this analysis are presented in Table 5.10.

| Family | RCI |
|---|---|
| Raphitomidae | 0 |
| Borsoniidae | 29% |
| Mangeliidae | 16% |
| Turridae | 7% |
| Nassariidae | -18% |
| Volutidae | 71% |
| Athletinae + Volutinae | -34% |

**Table 5.10** RCI values for each family based on genus level phylogenies and the combinations of the volute subfamilies Athletinae and Volutinae based on species level phylogenies.

RCI values suggest that the fossil record of the families Borsoniidae, Mangeliidae, Turridae and Volutidae at genus level are relatively complete. However, when the fossil record of the volute subfamilies Volutinae and Athletinae is examined, it is found to be relatively incomplete suggesting that results are somewhat dependent on the taxonomic level used. The fossil record of the families Raphitomidae and Nassariidae are also found to be relatively incomplete. To increase the completeness of the fossil record for these families, more taxa need to be included, either from other regions (e.g. Gulf of the USA, Mediterranean) or based on better taxonomy of these families in southeastern Australia (particularly for conoidean families). The RCI values presented here suggest that there is a strong preservation bias in the fossil record of Cenozoic gastropods from southeastern Australia.

The Gap Excess Ratio is a modification of the RCI that compares the actual ghost ranges (or gaps) of a tree with the minimum and maximum gaps when the topology of the tree is altered to maximise and minimise ghost ranges (Wills, 1999). The absolute ages of first occurrences of taxa are used to measure the fit of observed ages to the order of branching events implied by a cladogram (Finarelli & Clyde, 2002). The GER is defined as:

$$\mathrm{GER} = 1 - \frac{(\mathrm{MIG} - \mathrm{G_{min}})}{(\mathrm{G_{max}} - \mathrm{G_{min}})}$$

where MIG = minimum implied gap, $G_{min}$ = sum of minimum possible ghost ranges, $G_{max}$ = sum of maximum possible ghost ranges. Values range from 0 to 1 where 0 is MIG = $G_{max}$, the worst possible fit and 1 is MIG = $G_{min}$, the best possible fit (Wills, 1999).

GER values were calculated for each tree at generic level and for the subfamilies Volutinae and Athletinae at species levels. The results of this analysis are presented in Table 5.11.

| Family | GER |
|---|---|
| Raphitomidae | 0 |
| Borsoniidae | 1.0 |
| Mangeliidae | N/C |
| Turridae | 0 |
| Nassariidae | 0.49 |
| Volutidae | 0.79 |
| Athletinae + Volutinae | 0.47 |

**Table 5.11** GER values for each family based on genus level phylogenies and the combinations of the volute subfamilies Athletinae and Volutinae based on species level phylogenies. N/C = Not calculable.

GER values for the family Borsoniidae indicate the best possible fit whilst values for the families Raphitomidae and Turridae indicate the worst possible fit. GER was not calculable for the family Mangeliidae due to the fact that MIG, $G_{min}$ and $G_{max}$ are all equal. Increasing the number of taxa included in the Mangeliidae cladogram may resolve this issue. Values for the families Volutidae and Nassariidae indicate a relatively good fit, although when the subfamilies Volutinae and Athletinae are looked at separately, based on a species level tree, the fit is poorer than that for the Volutidae at genus level.

Contrasting results between these analyses are not unexpected. RCI analyses at species or genus level indicate a less complete fossil record than analyses at higher taxonomic levels due to short species durations (Benton et al., 2000; Jeffery & Emlet, 2003). If gaps are randomly distributed then it is possible that the correct pattern of species durations is presented even where there are significant gaps in the fossil record (Foote, 1997). If the fossil record is calculated to be incomplete but clades are shown to occur in the correct order then it is likely that there is a significant preservation bias (Jeffery & Emlet, 2003). The data presented here suggests that there is a preservation bias in the fossil record of gastropods from Cenozoic southeastern Australia that may limit our understanding of the spatial and temporal distribution of larval strategies.

## 5.5 TIMING OF CHANGES IN DEVELOPMENTAL MODE

The timing of changes in developmental mode of gastropods is a research area yet to be fully explored. This is probably due to the relatively few studies examining larval strategies in fossil taxa and the difficulties in resolving robust phylogenies on which to map switches in larval mode through geological time.

Studies on echinoids from the latest Cretaceous have shown that there are coordinated shifts to nonplanktotrophy over a relatively short period of time (Jeffery, 1997; Cunningham & Jeffery Abt, 2009). These near-synchronous changes in developmental mode are suggested to have been influenced by instability in nutrient availability at this time. If nutrient supply becomes unstable it is reasonable to suggest that non-feeding larval strategies are more advantageous and therefore coordinated shifts to nonplanktotrophy might be likely. Evidence from recent echinoderms living in areas of unstable nutrient supply (e.g. Pearse &

Cameron, 1991) are shown to either synchronise their reproductive cycles to coincide with nutrient blooms, or acquire nonplanktotrophic development in order to be independent of nutrient supply. These studies indicate that external factors relating to the ability to feed is a likely factor influencing shifts in larval mode.

Similar studies on fossil gastropods are yet to be undertaken. In order to examine the timing of switches in developmental mode in Cenozoic gastropods from southeastern Australia, cladograms are mapped onto the stratigraphic ranges of the taxa used in this study. Having established the relationship between taxa through geological time it is possible to indicate changes in larval strategy on branches of the cladograms (Figure 5.16). It should be noted that the nodes on these trees are not calibrated and therefore do not correlate to a specific point in time. As a result, although switches are marked on Figure 5.17 at particular points, it is possible that they occurred higher or lower on the tree but still along the same branch.

This analysis indicates that switches in larval strategies are not confined to a particular period of time and are not coordinated. For most of these families switches may have occurred at any point between the Palaeocene and Late Oligocene. For the family Mangeliidae this is extended to the Early Pliocene. Because it is not possible to constrain switches to a particular point in time, it is impossible to examine whether nutrient supply, or other external factors, influenced changes in developmental mode.

Having examined the quality of the fossil record and the congruence of stratigraphy and phylogenies it is likely that a preservation bias has resulted in large gaps in the fossil record of Cenozoic gastropods from southeastern Australia. Gaps in the fossil record could be due to a collection bias (i.e. not every specimen has been discovered) or could be the result of loss of specimens within the strata. This would result in inaccurate stratigraphic ranges and the possibility of large numbers of missing taxa from each family which makes determining the exact point at which switches occurred extremely difficult. Interestingly, less preservation bias is seen in echinoids from the same time and region and from observations in the field it would appear that there is also less of a preservation bias in bivalves from the Cenozoic strata of southeastern Australia

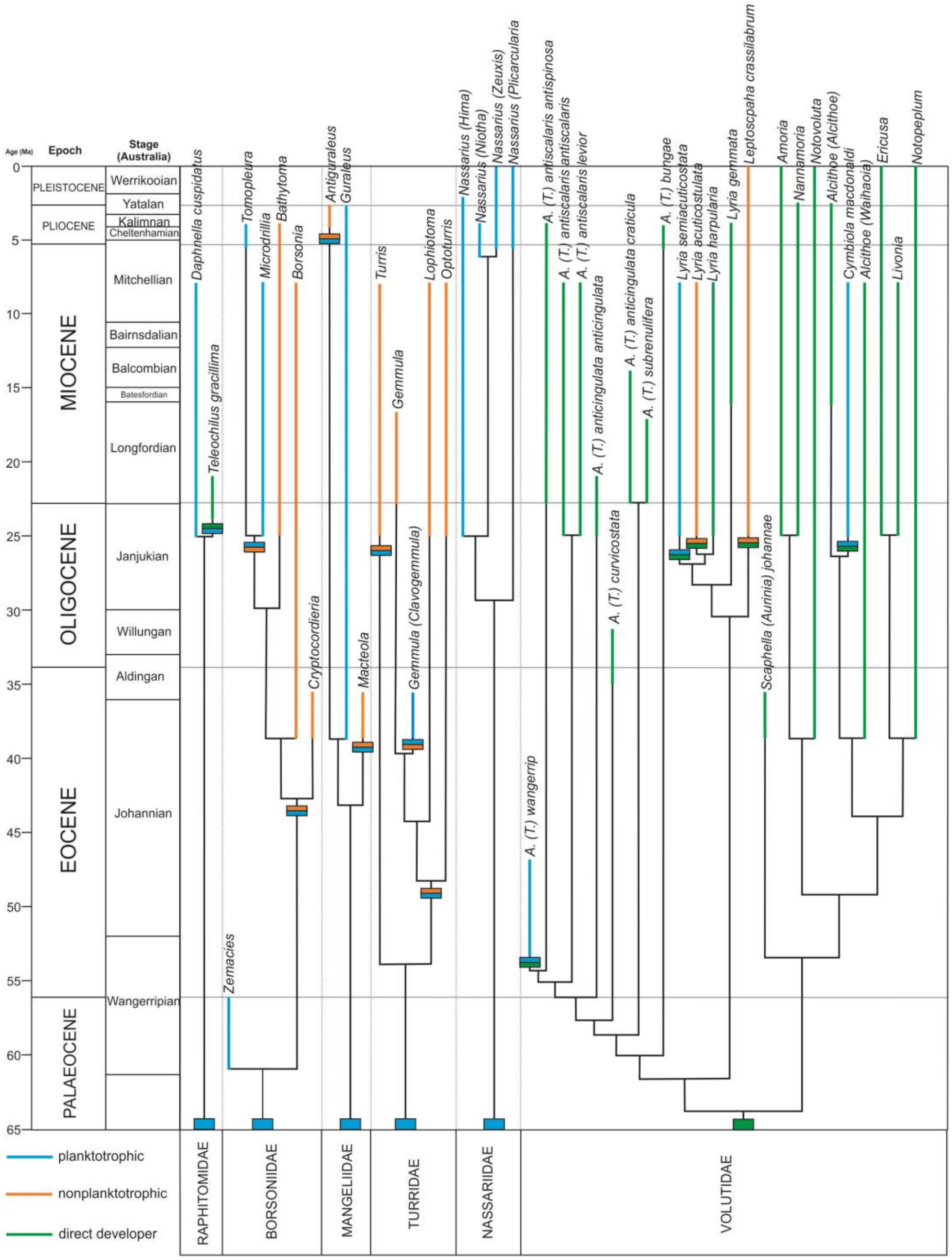


**Figure 5.17** Stratigraphic ranges and phylogenies for each family with switches in larval mode indicated by coloured boxes. The boxes indicate the initial larval strategy (bottom colour) and the larval strategy the switch has been made to (top colour). Blue = planktotrophy, orange = lecithotrophy, green = direct development.

## CHAPTER 6

# MACROEVOLUTIONARY CONSEQUENCES OF LARVAL STRATEGIES

Theory predicts that different larval strategies have different macroevolutionary consequences, and this prediction is the focus of a number of published studies (see Chapter 1 for review of the literature). The gastropod adult body plan severely hampers mobility, often resulting in narrow environmental tolerances during this life stage. As a result, the larval stage, which often includes a planktic phase, provides the optimum opportunity for dispersal. Dispersal potential is arguably the major factor influencing geographic distribution, stratigraphic range and speciation rates. As different larval strategies have different potential for dispersal, it is logical that they will also exhibit different geographic and stratigraphic distributions and speciation rates. This chapter examines the link between larval strategy and these three macroevolutionary factors using non-phylogenetic methods and examines speciation events using phylogenetic methods.

Species with planktotrophic larvae are predicted to have greater dispersal abilities than lecithotrophic species due to their longer pelagic phase, resulting in wider geographic distributions (e.g. Shuto, 1974; Scheltema, 1977, 1978, 1979; Ó Foighil, 1989; Emlet, 1995). Species with direct developing larvae do not undergo a pelagic phase and as a result are predicted to have the narrowest geographic distributions. Geographic range is likely to be linked to species longevity because widely distributed species are less vulnerable to local catastrophes. If this prediction holds true then it is also logical to assume that planktotrophic species will exhibit lower speciation rates than lecithotrophic and direct developing taxa due to their reduced vulnerability to localised extinction events.  Despite these predictions this topic remains relatively untested when examining changes through geological time. The predicted macroevolutionary consequences of different larval strategies is summarised in Table 6.1.

| | Geographic distribution | Species longevity | Speciation rate |
|---|---|---|---|
| **Planktotrophic** | Wide | Long | Low |
| **Lecithotrophy** | Narrow | Short | High |
| **Direct development** | Very narrow | Very short | Very high |

**Table 6.1 P**redicted macroevolutionary consequences for species with planktotrophic, lecithotrophic and direct developing larvae.

Studies on living gastropods from the Indo-Pacific region have shown that species with planktotrophic larvae have greater dispersal abilities and as a result wider geographic distributions than nonplanktotrophic species (Shuto, 1974). Similar patterns are seen in species of the slipper limpet *Crepidula* in the waters of the Atlantic and Gulf Coast of USA (Collin, 2001) and in gastropod families in Polynesia and the Western Pacific (Scheltema and Williams, 1983). Prosobranch gastropods with direct developing larvae from southeastern Australia are shown to inhabit relatively closed local populations which evolve independently from one another (Hoskin, 1997). Planktic species of the family Volutidae from the Neogene of the Gulf Coast of USA have wide geographic distributions even during periods of regression when delta building is taking place, indicating that oceanic barriers of this type do not affect the dispersal patterns of planktic larvae (Hansen, 1980). It is worth noting that Hansen (1980) uses geographic units of ~75km to calculate geographic distributions rather than exact ranges, which may result in overestimations of geographic range. Late Cretaceous gastropods from the Atlantic Coast Plain show a statistically significant difference in geographic range between planktotrophs and nonplanktotrophs (Jablonski, 1986; Jablonski and Hunt, 2006). These studies support the hypothesis that geographic range is greater in species with a long planktic period than those with a short or absent planktic period. However, a small number of studies on gastropods contradict these results. Poor correlation between planktonic period and geographic range is seen in species from the family Cypraeidae but this is thought to be the result of estimation error, intraspecific variation and inappropriate taxonomic scale which can obscure macroecological patterns (Paulay and Meyer, 2006). Similarly, the brooding species *Littorina saxtilis* is more widespread than the closely related planktonic species *Littorina littorea* in the northern Atlantic but observations are scattered and more data are required to corroborate these results (Johannesson, 1988).

Species longevity of planktotrophic species is shown to be longer than that seen in nonplanktotrophic species in a number of studies (e.g. Hansen, 1978, 1980; Jablonski, 1982, 1986; Gili & Martinell, 1994) providing support for theoretical models that greater ability to disperse will increase geographical and stratigraphical ranges by reducing vulnerability to local catastrophes (e.g. Shuto, 1974; Scheltema, 1977; Jablonski & Lutz, 1983). Data on species longevity are somewhat lacking in the literature, perhaps as a result of gaps in the fossil record. Nassarid fossils from Neogene sediments of the Mediterranean and North East Atlantic coasts show a strong correlation between larval mode and species longevity (Gili and Martinell, 1994). Studies on Tertiary neogastropods from the Gulf Coast of the USA show comparable results (Hansen, 1978, 1980). Cretaceous fossil prosobranch and shelled opisthobranch species from the Gulf Coast and Atlantic Coast Plain of North America indicated that species with planktotrophic larvae show significant frequencies of overlapping stratigraphic range whilst species with nonplanktotrophic larvae have significant frequencies of abutting species durations (Jablonski, 1986). These results strongly support the hypothesis that planktotrophic species with greater dispersal abilities show greater species stratigraphic durations. By contrast, Cenozoic gastropod species from the families Architectonicidae, Cymatiidae, Tonnidae and Volutidae in Polynesia and the western Pacific islands do not strongly support the argument that temporal longevity is related to mode of development (Scheltema and Williams, 1983).

Examination of speciation rates has received very little attention within the Gastropoda and is an area requiring attention. Nonplanktotrophic species are predicted to be less able to maintain gene flow between geographically isolated populations resulting in increased speciation events (Shuto, 1974). Electrophoretic and biochemical studies on living populations of marine invertebrates support the prediction that planktotrophic species exhibit low levels of genetic differentiation compared to nonplanktotrophic species suggesting that speciation rates are higher in the latter (e.g. Wium-Andersen, 1970; Gooch et al., 1972; Berger, 1973; Snyder and Gooch, 1973; Gooch, 1975; Campbell, 1978; Crisp, 1978; Grassle & Grassle, 1978; Siebnaller, 1978; Wilkins et al., 1978; Black & Johnson, 1979; Buroker et al., 1979a, b; Ward & Warwick, 1980). Significant genetic differentiation seen within living populations of nonplanktotrophic *Crepidula* gastropods compared with limited variation in planktotrophic populations of the same genus along the Gulf and Atlantic Coasts of North America corroborates this prediction (Collin, 2001). By contrast, Cretaceous gastropods from the Gulf Coast and Atlantic Coastal Plain show a significant inverse relationship between geographic range and speciation rate but show only a weak inverse relation between geographic range and total number of species originating within a genus (Jablonski & Roy, 2003). Neither the total number of species produced through time nor the number of species within a single time interval is found to be a positively correlated with the geographic range of species in a clade (Jablonski & Roy, 2003).

The link between larval strategies and macroevolutionary trends is yet to be explored in Cenozoic gastropods from southeastern Australia, but one study has used fossil temnopleurid echinoids from this region to test predictions. The study indicates that geographic and stratigraphic distributions were greater in planktotrophic taxa than nonplanktotrophic taxa but that this difference was not statistically significant (Jeffery & Emlet, 2003). Analysis of speciation rates revealed significantly higher rates in nonplanktotrophic taxa than planktotrophic taxa, as hypothesised.

## 6.1 MATERIALS AND METHODS

The dataset comprises the 104 species examined in Chapter 3, whose larval strategies have been unambiguously determined. Although, for at least four of these families, more species are present in the Cenozoic deposits of southeastern Australia, only those that can be confidently assigned to particular families are included. The species included in these analyses, their larval strategies and geographic and stratigraphic distributions are presented in Appendix 3. The dataset is initially treated as a whole, although the dataset for each family is also considered.

### **6.1.1** GEOGRAPHIC DISTRIBUTION

Geographic range for each species was determined by calculating the straight-line distance between the two most distant localities at which the species was found. Locality data for each species was established from field observations, data in published literature and data from museum specimens. The greatest distance between localities for each species was calculated using the spherical geometry (Haversine formula, Robusto, 1957) and was based on the Earth's radius equalling 6371km. Data for each locality used in this study are presented in Appendix 1 and localities associated with each species are outlined under the species descriptions in Chapter 3. As localities used in this study are situated in a restricted area along a passive margin, it is concluded that positions are relatively unchanged since time of deposition and therefore palaeogeographic reconstructions of the southeastern Australian coastline are not required. Due to large gaps in the fossil record in this region it is not possible to limit geographic range to age-equivalent strata. Issues relating to geographically migrating populations are discussed in the results section of this chapter. As it was not possible to visit every locality from which specimens were recovered, the longitude and latitude of each locality were ascertained using online mapping tools (e.g. Google Maps) to avoid inconsistencies in the locality data.

### **6.1.2** SPECIES LONGEVITY

The stratigraphic range of each species was collated from field observations, museum specimens and unambiguous records in the literature. Stratigraphic ranges for each species are available in Chapter 3 under each species' description. Species longevity is calculated as the difference between the first and last occurrence of each species. The age of the first occurrence corresponds to the date of the lower boundary of the first formation in which the species occurs. The age of the last occurrence corresponds to the date of the upper boundary of the last formation in which the species occurs. These ranges may include periods of time in which no gastropods were recovered from the sediments of southeastern Australia (i.e. ghost ranges). The temporal resolution of the formations included in this study is discussed in Chapter 2. Errors in stratigraphic ranges occur due to the inability to date specific gastropod-bearing horizons within formations and therefore ranges may be overestimated.

### **6.1.3** SPECIATION RATES

Analysis of speciation rates based on only the species included in this study is clearly flawed due to the large numbers of missing taxa (particularly in the conoidean families). Speciation rates are estimated for generic lineages using occurrence data of each species included within each genus. Speciation rates are calculated by the number of species divided by the sum of species duration. This calculation provides per species per million year speciation rates. Overestimations or underestimations of species durations may lead to erroneous results. Until more accurate dates can be established for each species (e.g. higher resolution dating of horizons within formations), this method is considered to provide a good estimate of speciation rates for the families considered in this research.

### **6.1.4** SPECIATION EVENTS

Speciation events are calculated for each family using phylogenies produced in Chapter 4. The ancestral mode of development at each internal node of the trees is determined and the numbers of speciation events involving ancestors of each developmental mode are tabulated. Separate calculations are made for reversible and irreversible transitions between different larval modes. Speciation events are calculated at species level, inferring the extra speciation events from genus level trees (i.e. speciation events are extrapolated from genus level phylogenetic analyses). This approach assumes the topology of the tree does not change when more taxa are included and therefore the distribution of larval strategies does not change. If a robust species level tree could be produced it would be useful to check these analyses.

### **6.1.5** COMPARATIVE ANALYSIS

To assess the relationship between larval mode and various species level traits, Mann Whitney *U*-tests were carried out. This test examines the statistical significance of differences between two datasets. This test assumes that species level traits evolved independently from one another (i.e not inheritable) and is a non-phylogenetic approach. Mann Whitney *U*-tests were only carried out when all taxa were combined in a single analysis as the sample sizes of individual families are too small to provide reliable results. Three larval modes are considered in this chapter (planktotrophy, lecithotrophy and direct development) and therefore Mann Whitney *U*-tests were carried out in four ways for geographic range, species longevity and speciation rates. Initially, lecithotrophy and direct development are combined so that planktotrophy can be tested against nonplanktotrophy. Three further analyses test planktotrophy against lecithotrophy, planktotrophy against direct development and lecithotrophy against direct development. Analysis is carried out as a 1-tailed test and results are considered significant at 5% or less.

Comparative analysis by independent contrasts was not performed due to the fact that phylogenies include both genera and species and the approach requires species level phylogenies. If robust species level phylogenies could be produced then it would be possible to conduct comparative analysis by independent contrasts (as in Jeffery & Emlet, 2003).

## 6.2 RESULTS

Results for each analysis are shown for all taxa and for each individual family except in the case of speciation events where the dataset is not considered as a whole due to the lack of a robust tree which includes all taxa.

### **6.2.1** GEOGRAPHIC DISTRIBUTION

The distribution of geographic range according to larval mode is presented graphically for all taxa in Figure 6.1. When all taxa are considered together the median values of planktotrophy, lecithotrophy and direct development are 277km, 10km and 256km respectively. As expected, there is a significant difference between the median values of geographic range of planktotrophs and lecithotrophs. However, direct developers appear to have much wider geographic distributions than theory predicts. The difference in geographic range between planktotrophs and lecithotrophs (P = 0.01) and lecithotrophs and direct developers ($P = 0.02$) is considered to be statistically significant as determined by Mann Whitney *U*-tests (Table 6.2). The difference in geographic range between planktotrophs and direct developers is not found to be statistically significant ($P = 0.19$). When lecithotrophy and direct development are combined the difference is also not considered statistically significant ($P = 0.09$).

The significant difference between the geographic ranges of planktotrophs and lecithotrophs supports the theory that larvae with a longer planktic period will have wider distributions. The non-significant difference between planktotrophy and direct development suggests that this may not always be the case. The majority of direct developing taxa included in this study have geographic ranges of less than 200km indicating that those species with wide geographic distributions may be exceptions rather than the rule. In addition, it is possible that direct developers with very wide geographic ranges may include taxa with wide morphological variation that could be interpreted as several species. If this is the case then the geographic distribution of these species could be overestimated. However, the taxonomy of each family has been carefully examined and the comprehensive taxonomic revision in Chapter 3 indicates that this is very unlikely.

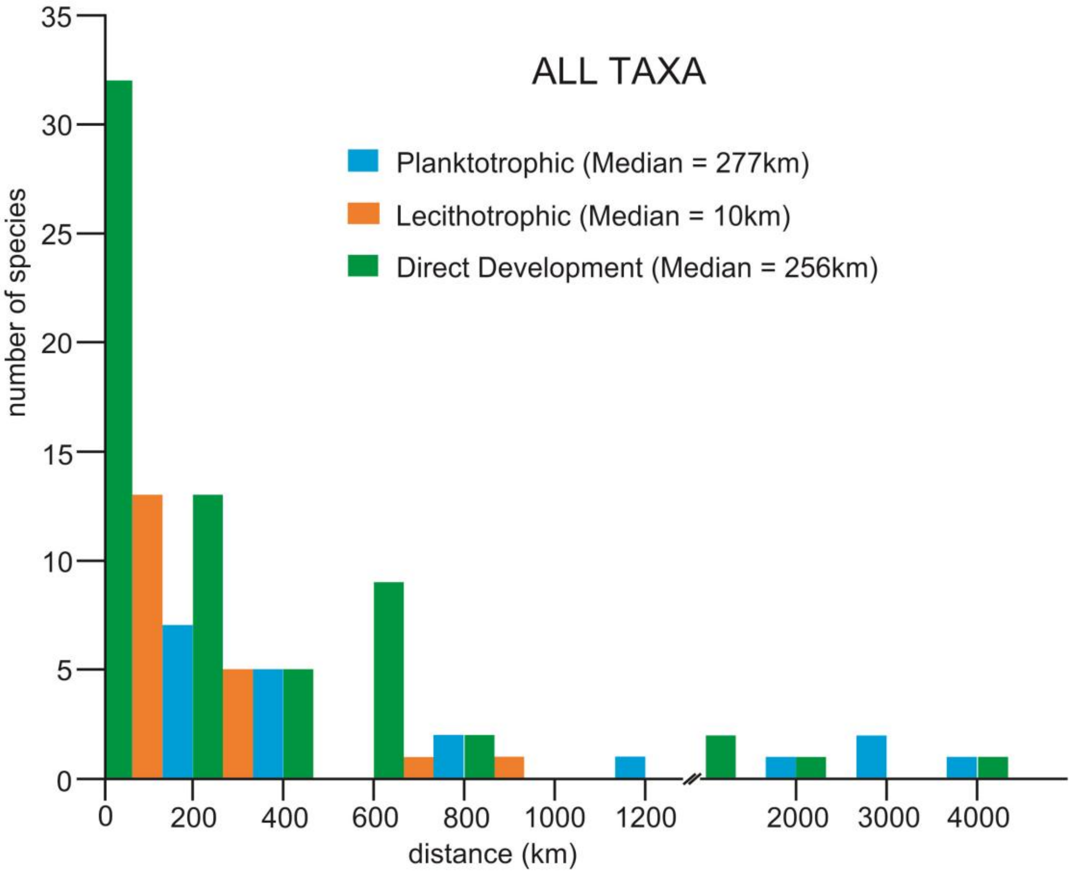


**Figure 6.1** Distribution of geographic ranges of all taxa included in this study according to larval mode.

| Larval strategies | $N_1$ | $N_2$ | *U*-statistic | *P*-value |
|---|---|---|---|---|
| P:NP | 19 | 85 | 967.0 | 0.09 |
| P:L | 19 | 20 | 268.0 | 0.01 |
| P:DD | 19 | 65 | 699.0 | 0.19 |
| L:DD | 20 | 65 | 840.0 | 0.02 |

**Table 6.2** Statistical results of comparison of larval mode and geographic range conducted with the Mann Whitney *U*-test.

When each family is considered individually results are variable. The distribution of geographic range according to larval mode for each family is presented in Figure 6.2. Median values for the family Volutidae indicate that there is no correlation between larval mode and geographic range. Lecithotrophic taxa have the highest median value in this family. As the family Nassariidae only includes planktotrophic taxa no comparison can be made within this family. However, the median geographic range of the nassariids is 1735km, which is significantly higher than that seen in any other family. Median values for the family Raphitomidae could not be calculated due to there being too few taxa but both planktotrophic and direct developing taxa in this family have relatively narrow geographic distributions not exceeding 50km. Both the Mangeliidae and Borsoniidae have median geographic range values that support the suggestion that planktotrophic taxa have wider distributions than lecithotrophic taxa, although the relatively small sample size of these families must be taken into consideration. Geographic ranges of taxa in the family Turridae contradict predictions with lecithotrophs having much wider distributions than planktotrophs. However, this dataset only includes one planktotroph and therefore is unlikely to be a true reflection of distributions in this family.

Two issues need to be considered when examining the geographic range of Cenozoic gastropods from southeastern Australia. The first is the issue of a preservation bias within the gastropod fossil record of this region. The distribution of accessible fossil gastropod-bearing outcrops in southeastern Australia will influence the quality of the data collected. Gastropod fossils from Cenozoic deposits of this region are generally concentrated at thin horizons and there is evidence of major gaps in the fossil record which could be due to the exclusion of whole species or the exclusion of particular instances of each species. As a result, the data are unlikely to include all taxa from each family, even those considered complete, such as the Volutidae and the Nassariidae. The second issue is the possibility of geographic migration of taxa through time. The data presented here encompasses the geographic distributions of taxa throughout the Cenozoic and is not specific to age-equivalent strata. It is therefore possible that wider distributions may be the result of migration. Unfortunately it is not possible to accurately calculate geographic range for taxa within age-equivalent strata due to preservation biases, since most of these fossil-rich horizons are also geographically restricted.

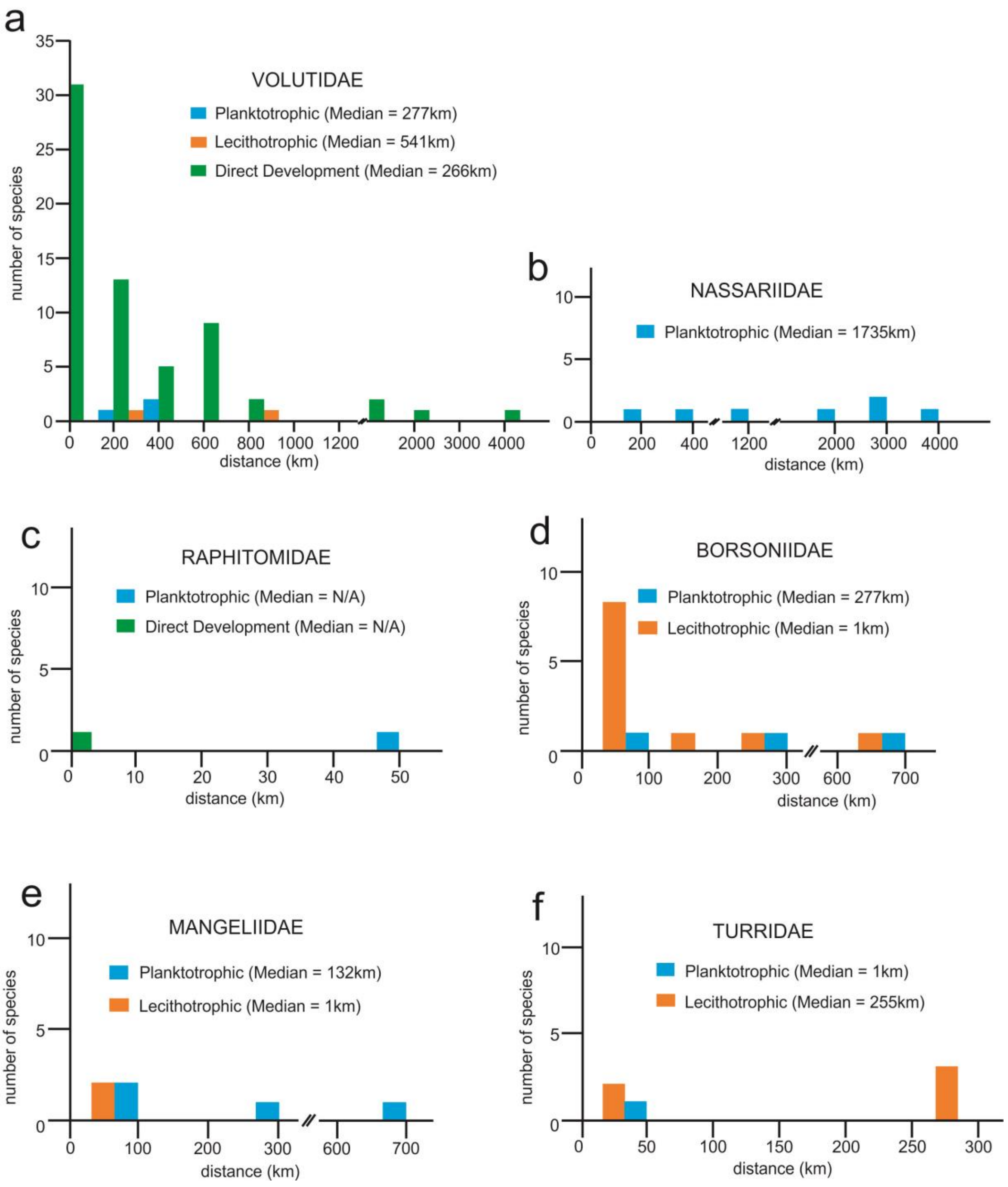


**Figure 6.2** Distribution of geographic ranges of each family included in this study according to larval mode. a) Volutidae, b) Nassariidae, c) Raphitomidae, d) Borsoniidae, e) Mangeliidae and f) Turridae.

### **6.2.2** SPECIES LONGEVITY

The distribution of species longevity according to larval mode is presented graphically for all taxa in Figure 6.3. When all taxa are considered together the median values of planktotrophy, lecithotrophy and direct development are 5 million years, 10 million years, and 7 million years respectively. The difference between these values is small and does not support the hypothesis that planktotrophic taxa have longer species durations than nonplanktotrophic taxa. A Mann Whitney *U*-test (Table 6.3) indicates that the difference between planktotrophic and nonplanktotrophic species durations is not significant ($P = 0.16$).

| Larval strategies | $N_1$ | $N_2$ | *U*-statistic | *P*-value |
|---|---|---|---|---|
| P:NP | 19 | 85 | 928.0 | 0.16 |
| P:L | 19 | 20 | 222.0 | 0.19 |
| P:DD | 19 | 65 | 706.0 | 0.18 |
| L:DD | 20 | 65 | 693.5 | 0.33 |

**Table 6.3** Statistical results of comparison of larval mode and species longevity conducted with the Mann Whitney U-test.

The difference in species longevity between planktotrophs and lecithotrophs (P = 0.19) and lecithotrophs and direct developers ($P = 0.18$) is not considered to be statistically significant based on Mann Whitney *U*-tests. The difference in species longevity between planktotrophs and direct developers is also not found to be statistically significant ($P = 0.33$). Overall, these results indicate that there is no significant difference in species longevity of different larval modes in Cenozoic gastropods from southeastern Australia.

When each family is considered individually results are similar. The distribution of geographic range according to larval mode for each family is presented in Figure 6.4. Within the family Volutidae, lecithotrophs have the highest median value of species duration and direct development the shortest. Comparison between the family Nassariidae and other families indicate that nassariid planktotrophic taxa have short species durations compared to planktotrophs in other families. Median values of species longevity indicate that there is no correlation between larval mode and species longevity in the families Mangeliidae and Borsoniidae. Species longevity appears to be longer for planktotrophs than nonplanktotrophs in the Raphitomidae but there is a severe paucity of data on which to base this conclusion. The family Turridae indicates lecithotrophic taxa have longer species durations than planktotrophs but again, the small sample size may skew results.

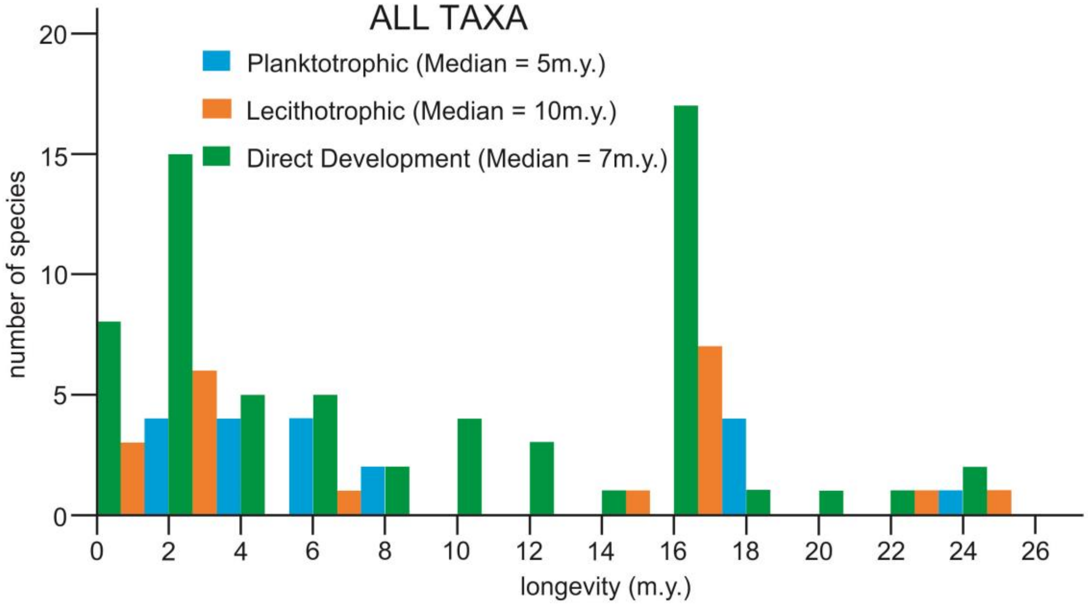


**Figure 6.3** Distribution of species durations of all taxa included in this study according to larval mode.

Due to the preservation biases previously discussed, it is likely that the data presented in this study do not reflect true patterns of species longevity in Cenozoic gastropods from southeastern Australia. The gaps in the fossil record highlighted previously may have a significant impact on the observed first and last occurrences of species which will ultimately cause underestimates of species durations. On the other hand, the fossil gastropods in this study are often concentrated to thin horizons within formations which cannot be accurately dated. Consequently, the duration of the whole formation is used which will result in overestimates of species durations.

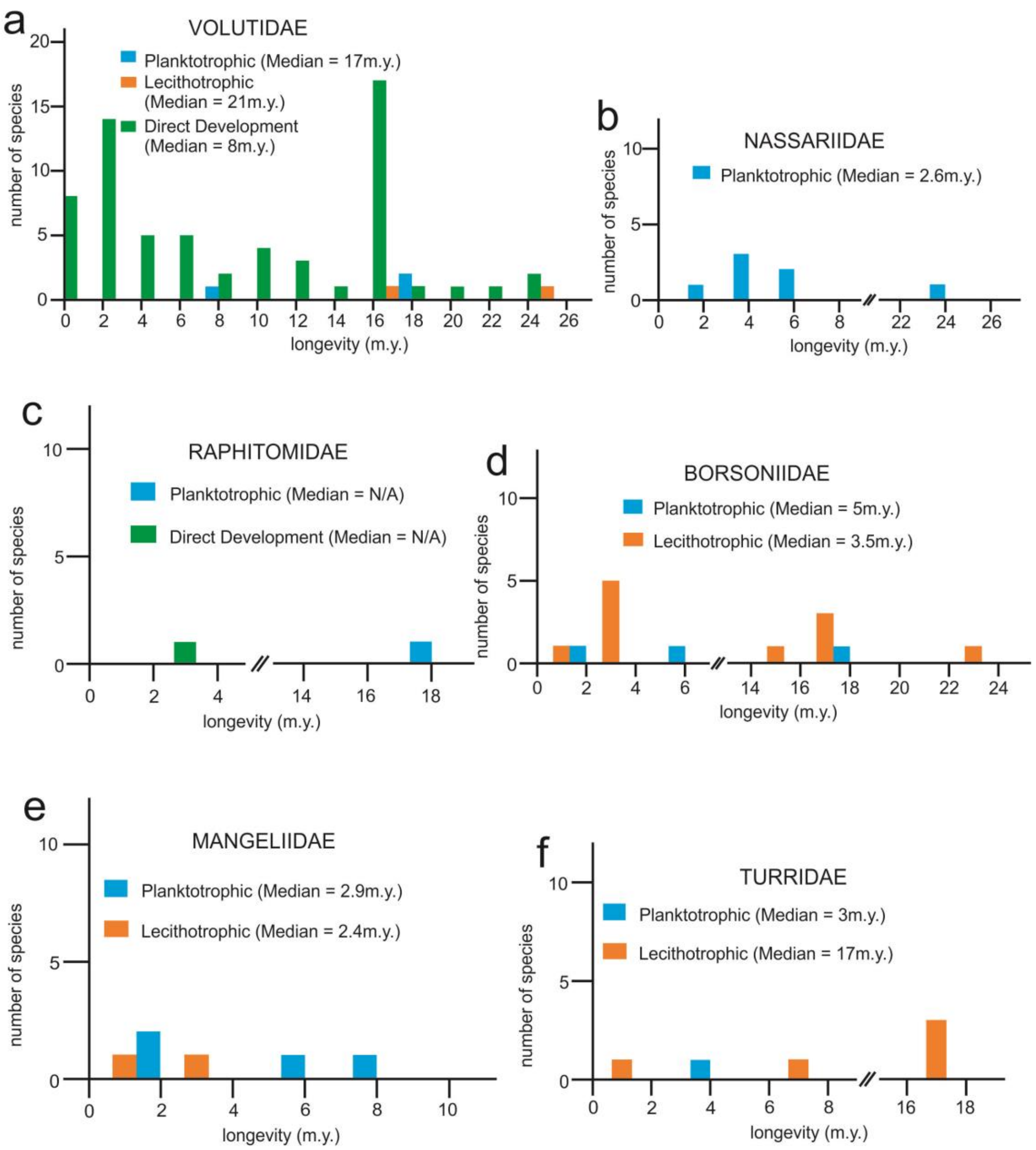


**Figure 6.4** Distribution of species duration of each family included in this study according to larval mode. a) Volutidae, b) Nassariidae, c) Raphitomidae, d) Borsoniidae, e) Mangeliidae and f) Turridae.

### **6.2.3** SPECIATION RATES

The distribution of speciation rates according to larval mode is presented graphically for all taxa in Figure 6.5. When all taxa are considered together, the median values of speciation rates for planktotrophy, lecithotrophy and direct development are 0.18, 0.11 and 0.11 species per million years respectively. Interestingly, the highest speciation rates are seen in planktotrophic genera and the lowest in direct developing genera which contradicts the predicted result. A Mann Whitney *U*-test (Table 6.4) indicates that there is no significant difference in speciation rates between planktotrophic and nonplanktotrophic taxa ($P$ = 0.35). The difference between speciation rates of planktotrophs and lecithotrophs is also found to be insignificant ($P$ = 0.32). Similarly, where the difference should be the greatest, between planktotrophs and direct developers, the difference is the most statistically insignificant ($P$ = 0.41). A Mann Whitney *U*-test also found the difference between speciation rates of lecithotrophs and direct developers to be statistically insignificant ($P$ = 0.26). The data for all taxa included in this study do not support the hypothesis that planktotrophic species with a prolonged planktic period will have lower speciation rates than nonplanktotrophic species with a reduced or absent planktic period due to decresed vulnerability to local catastrophes. The data suggest that for most generic lineages speciation rate is not significantly correlated to larval strategy.

Similar results are seen when each family is examined individually. Speciation rates according to larval mode for each family are presented in Figures 6.6 and 6.7. In the family Volutidae the highest median speciation rates are seen in direct developers and the lowest in lecithotrophs (although there is little difference between lecithotrophs and planktotrophs). Whilst the difference is not particularly significant, the result does somewhat support the hypothesis that higher speciation rates will occur in nonplanktotrophic lineages. Similarly, the highest median value in the family Mangeliidae is seen in the lecithotrophs. On the other hand, both the turrids and borsoniids indicate that planktotrophy has the highest median speciation rate when compared to the lecithotrophs. When the Nassariidae planktotrophic taxa are compared to planktotrophic taxa from other families, it seems this family has fairly high speciation rates. As in other analyses, the Raphitomidae cannot really be considered due to the fact that it only contains one planktotroph and one direct developer. As speciation rates are calculated using stratigraphic ranges and number of species it is likely that these values do not reflect true patterns in the fossil record since missing taxa and inaccurate stratigraphic ranges may have skewed the data needed to calculate speciation rates accurately.

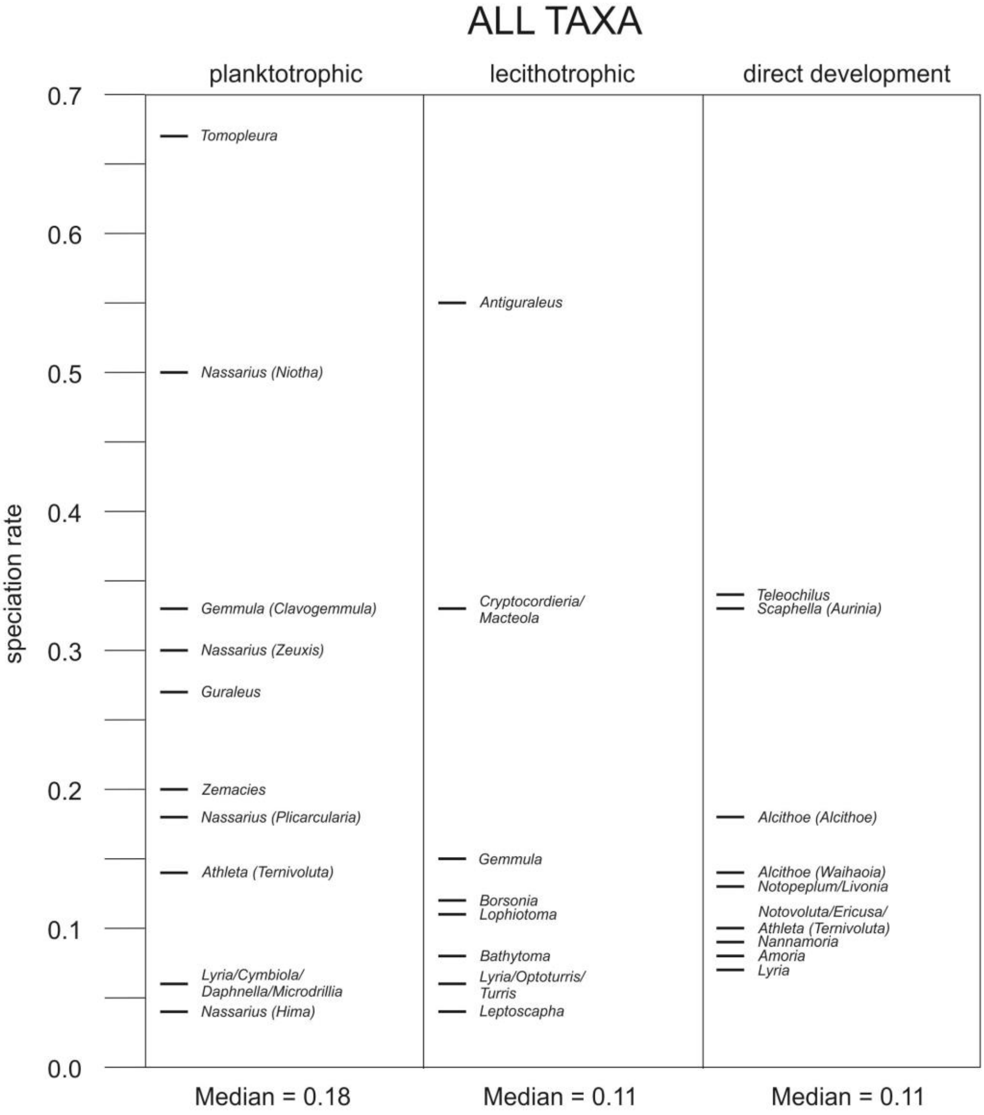


**Figure 6.5** Distribution of speciation rates of all genera included in this study according to larval mode.

| Larval strategies | $N_1$ | $N_2$ | *U*-statistic | *P*-value |
|---|---|---|---|---|
| P:NP | 13 | 23 | 162.0 | 0.35 |
| P:L | 13 | 11 | 79.5 | 0.32 |
| P:DD | 13 | 12 | 82.5 | 0.41 |
| L:DD | 11 | 12 | 76.5 | 0.26 |

**Table 6.4** Statistical results of comparison of larval mode and speciation rates conducted with the Mann Whitney U-test.

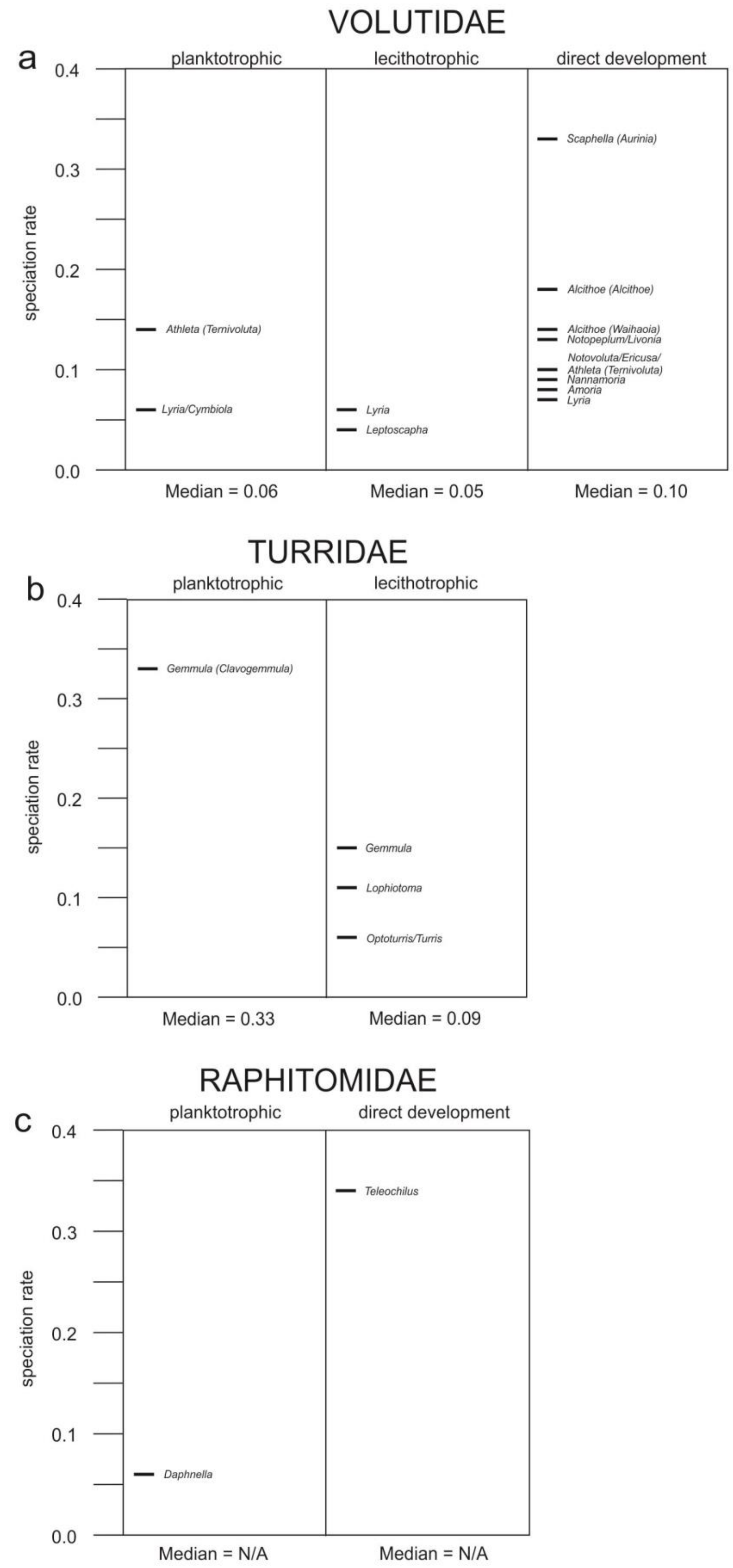


**Figure 6.6** Distribution of speciation rates of the families a) Volutidae, b) Turridae and c) Raphitomidae included in this study according to larval mode.

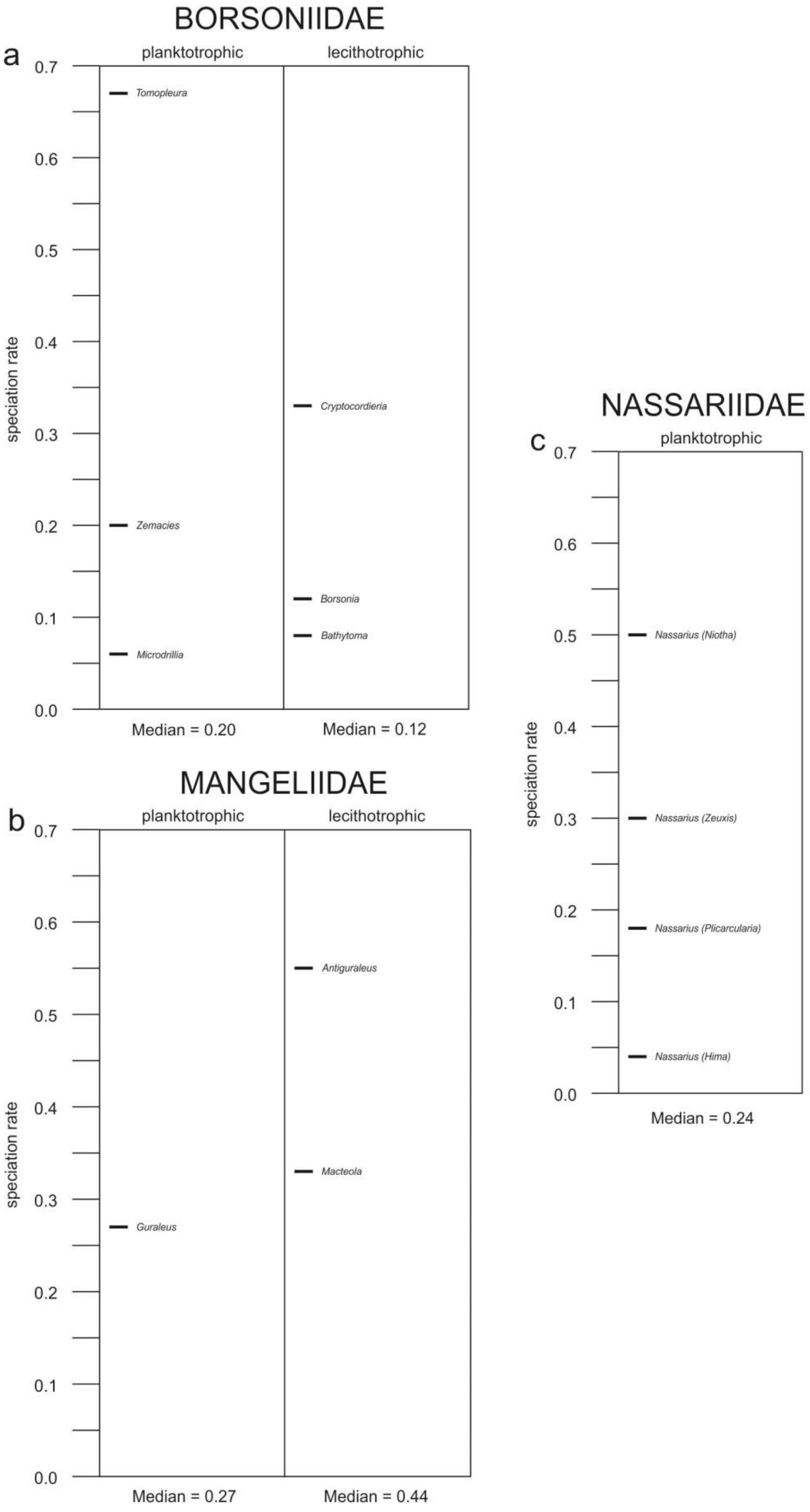


**Figure 6.7** Distribution of speciation rates of the families a) Borsoniidae, b) Mangeliidae and c) Nassariidae included in this study according to larval mode.

### **6.2.4** SPECIATION EVENTS

The number of speciation events associated with planktotrophic, lecithotrophic and direct developing ancestors is shown for each family based on irreversible and reversible transformations in Figures 6.8, 6.9, 6.10 and 6.11.

The phylogenetic tree of the Volutidae includes a mix of both genera and species. In order to calculate speciation events the number of taxa assigned to each genus was included in calculations based on the assumption that by including these species the topology of the tree would not be altered. There are 69 species of volute included in this analysis and thus 68 speciation events each represented by an internal node of the tree. Of these 68 speciation events 16 occurred in planktotrophic ancestral taxa, one in a lecithotrophic taxon and 51 in direct developing taxa when transitions are treated as irreversible (Figure 6.8). By comparison, when transitions are treated as reversible all 68 speciation events occurred in direct developing ancestral taxa (Figure 6.9). These results indicate that more speciation events have occurred in direct developing ancestors than lecithotrophic or planktotrophic ancestors, regardless of whether transitions are reversible or irreversible.

The phylogenetic tree of the Nassariidae is based on genus level analysis. In order to calculate speciation events the number of species assigned to each genus was included in calculations. All seven taxa included in this family are planktotrophic and therefore regardless of whether transitions are irreversible or reversible all six possible speciation events occurred in planktotrophic taxa (Figure 6.10, 6.11). Similarly, the small dataset of the family Raphitomidae reveals that the single speciation event must occur in a planktotrophic ancestral taxon (Figure 6.9, 6.11).

The phylogenetic tree of the family Borsoniidae is based on genus level analysis. In order to calculate speciation events the number of species assigned to each genus was included in calculations based on the assumption that by including these species the topology of the tree would not be altered. There are 14 species of borsoniid included in this analysis and thus 13 speciation events each represented by an internal node of the tree. Of these 13 speciation events five occurred in planktotrophic ancestral taxa and eight in lecithotrophic taxa when transitions are treated as irreversible (Figure 6.10). By comparison, when transitions are treated as reversible two speciation events occurred in planktotrophic ancestral taxa and 11 in lecithotrophic ancestral taxa (Figure 6.11). These results indicate that more speciation events have occurred in lecithotrophic ancestors than planktotrophic ancestors, regardless of whether transitions are reversible or irreversible.

The phylogenetic tree of the Mangeliidae is based on genus level analysis. Calculation of speciation events includes all species assigned to each genus based on the assumption that by including these species the topology of the tree would not be altered. There are six species included in this analysis and therefore five speciation events each represented by an internal node of the tree. All five speciation events occurred in planktotrophic ancestral taxa when transitions are treated as irreversible (Figure 6.10). By treating transitions as reversible two outcomes are possible depending on whether the ancestral larval mode of the whole tree is considered planktotrophic or lecithotrophic. If the basal node of the tree is considered to be planktotrophic then the result is the same as that revealed by irreversible transitions (Figure 6.11). If the basal node of the tree is lecithotrophic then two speciation events occur in planktotrophic ancestral taxa and three in lecithotrophic ancestral taxa (Figure 6.11).

| | Family | Planktotrophic | Lecithotrophic | Direct development |
|---|---|---|---|---|
| **IRREVERSIBLE** | Volutidae | 16 | 1 | 51 |
| | Nassariidae | 6 | 0 | 0 |
| | Raphitomidae | 1 | 0 | 0 |
| | Borsoniidae | 5 | 8 | 0 |
| | Mangeliidae | 5 | 0 | 0 |
| | Turridae | 4 | 1 | 0 |
| **REVERSIBLE** | Volutidae | 0 | 0 | 68 |
| | Nassariidae | 6 | 0 | 0 |
| | Raphitomidae | 1 | 0 | 0 |
| | Borsoniidae | 2 | 11 | 0 |
| | Mangeliidae | 2 or 5 | 3 or 0 | 0 |
| | Turridae | 0 | 5 | 0 |

**Table 6.5** Number of speciation events occurring in ancestral taxa of each larval strategy for each family.

The phylogenetic tree of the Turridae is based on genus level analysis. In order to calculate speciation events the number of species assigned to each genus was included in calculations based on the assumption that by including these species the topology of the tree would not be altered. There are six species of turrid included in this analysis and as a result five speciation events each represented by an internal node of the tree. When transitions are treated as irreversible, four speciation events are found to have occurred in planktotrophic ancestral taxa and one in a lecithotrophic taxon (Figure 6.10). If transitions are treated as reversible, all five speciation events occurred in lecithotrophic ancestral taxa (Figure 6.11).

The number of speciation events occurring in ancestral taxa of each larval strategy for each family is summarised in Table 6.5. The results do not suggest that more speciation events occur in a particular larval strategy than any other. However, most speciation events occur in direct developers in the family Volutidae, in lecithotrophs in the family Borsoniidae and in planktotrophs in the family Nassariidae and Raphitomidae regardless of whether transitions are considered reversible or irreversible. In the families Mangeliidae and Turridae, the results differ when transitions are treated as reversible or irreversible.

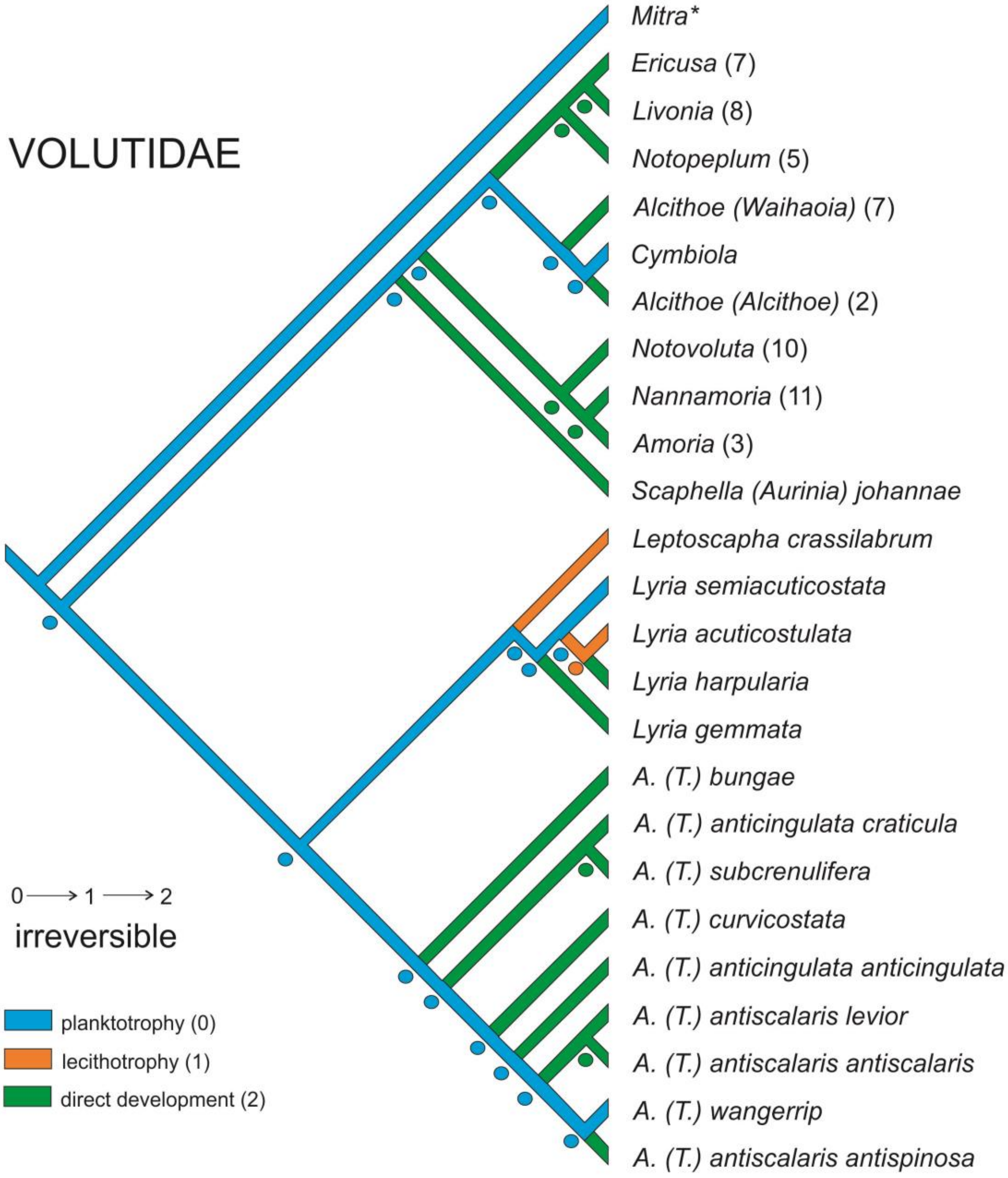


**Figure 6.8** Speciation events in the family Volutidae for planktotrophs, lecithotrophs and direct developers based on irreversible transitions.

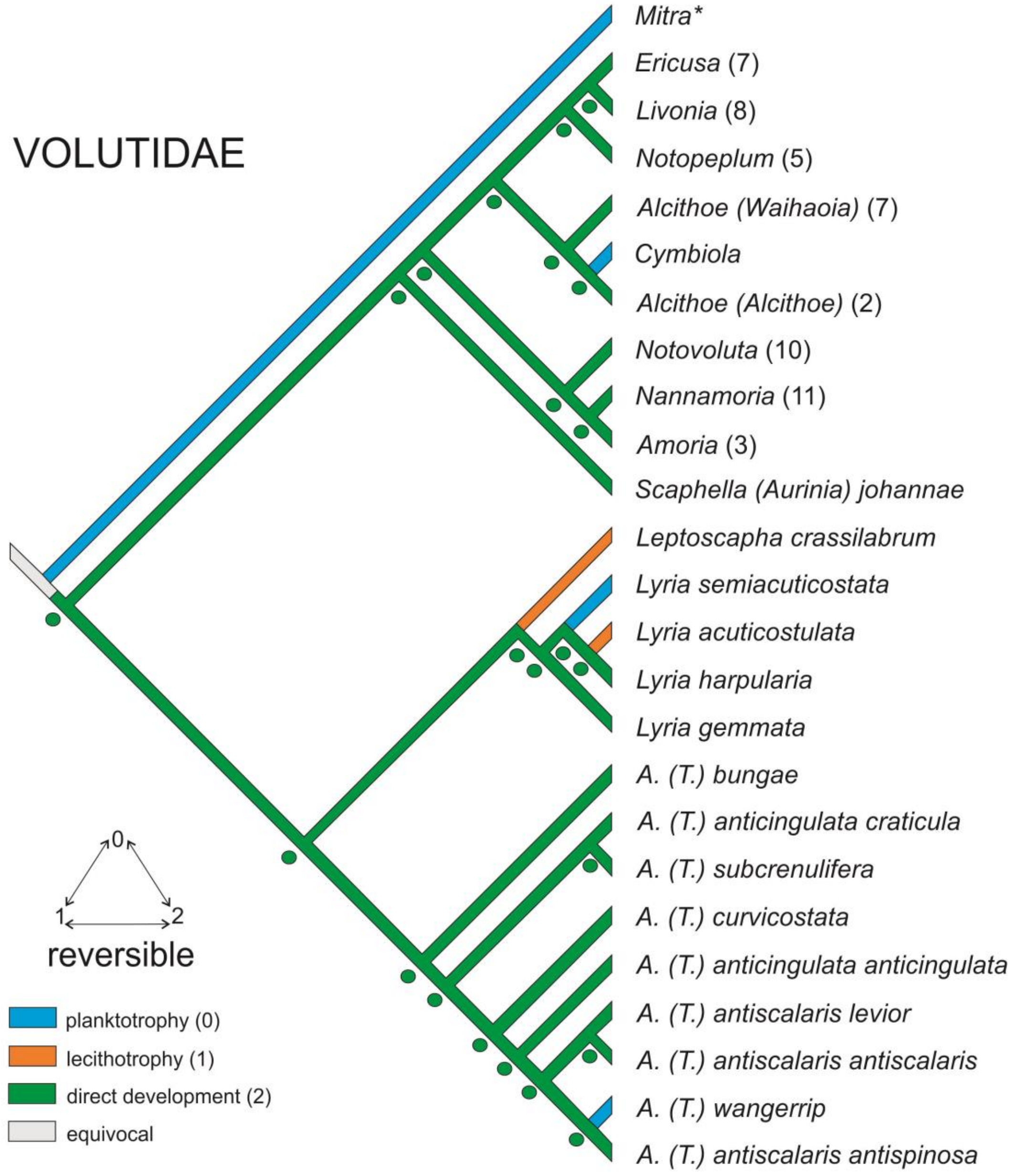


**Figure 6.9** Speciation events in the family Volutidae for planktotrophs, lecithotrophs and direct developers based on reversible transitions.

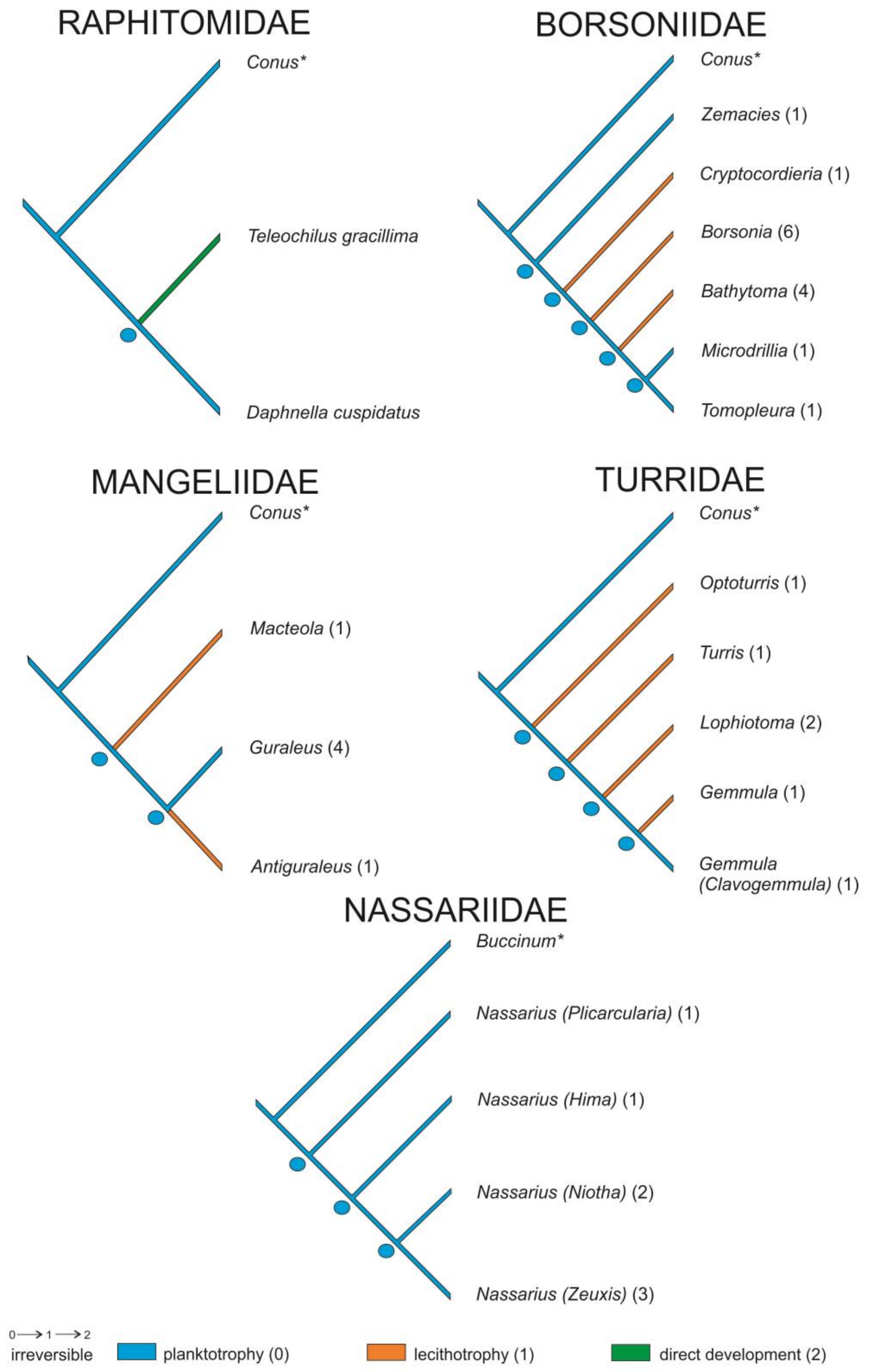


**Figure 6.10** Speciation events in the families Nassariidae, Raphitomidae, Borsoniidae, Mangeliidae and Turridae for planktotrophs, lecithotrophs and direct developers based on irreversible transitions.

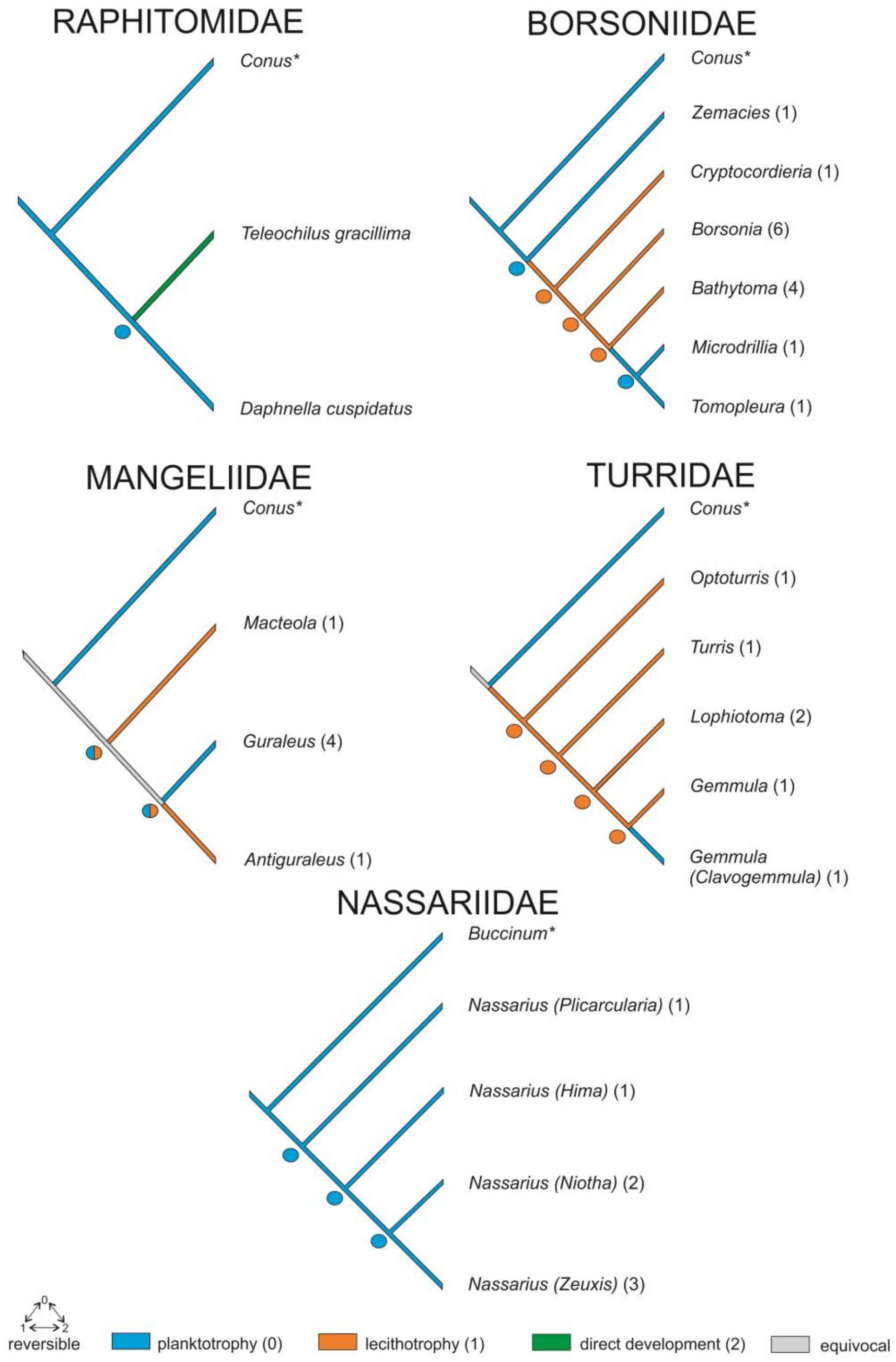


**Figure 6.11** Speciation events in the families Nassariidae, Raphitomidae, Borsoniidae, Mangeliidae and Turridae for planktotrophs, lecithotrophs and direct developers based on reversible transitions.

## 6.3 SUMMARY

Theory predicts that planktotrophy is associated with wide geographic distributions, long species durations and low speciation rates and nonplanktotrophy with narrow geographic distributions, short species durations and high speciation rates. The analysis carried out in this chapter suggests that these macroevolutionary consequences are not exhibited in Cenozoic gastropods from southeastern Australia, as they are for temnopleurid echinoids from the same time and region (Jeffery & Emlet, 2003) and similar families along the Gulf Coast of the USA during the Cenozoic (Hansen, 1980). If the results of this research reflect true patterns in the gastropod fossil record then it can be surmised that there is no link between larval strategy and macroevolution in gastropods from southeastern Australia. Whilst it is possible that these results reflect true patterns for these taxa in this region, it seems more likely that preservation biases have greatly affected the temporal and spatial distribution of these taxa. Geographic distribution data may also be affected by the possibility of migrating populations through time. The only way to resolve these problems is to increase the regional dataset by finding taxa in localities not already visited. However, the collection of gastropods from this region has been a point of interest for many collectors for over a hundred years suggesting that the likelihood of finding new localities and more specimens is very unlikely. Therefore, it might be more sensible to expand the datasets over larger regions or to compile a global dataset for each family. Whilst this is not within the scope of this study it is certainly an area that would benefit from attention in the future. To overcome the problem relating to migrating populations, geographic distribution would need to be collected for specific time intervals. Again, the problem lies in the major gaps occurring in the fossil record and the only possible resolution is to expand the datasets to larger regions or to compile a global dataset for each family. Interestingly, these major gaps in the fossil record are not as apparent in echinoids (Jeffery & Emlet, 2003) or bivalves (from observations in the field) from the Cenozoic strata of southeastern Australia.

# CHAPTER 7

# CONCLUSIONS AND FUTURE WORK

The aim of this research was to examine the evolution of larval strategies in gastropods from the Cenozoic sediments of southeastern Australia. In order to do this a taxonomic revision of six families was undertaken and phylogenetic analysis used to determine the relationships between taxa. Phylogenetic methods were used to map changes in larval strategies through geological time and to determine the ancestral mode of development. Non-phylogenetic methods were used to examine the macroevolutionary consequences of different modes of larval development and test widely held assumptions. This chapter discusses the results of the analyses carried out in this study and examines the difficulties encountered, with suggestions for improvements and future studies.

As discussed in detail in Chapter 1, the published literature on larval strategies and their evolutionary trends suggests a number of general “rules”. Theory predicts that planktotrophic larvae will exhibit wider geographic distributions, longer species durations and lower speciation rates than nonplanktotrophic species as a result of greater dispersal ability. However, acceptance of these predictions is based on limited data. This research sought to examine the macroevolutionary consequences of larval strategies in fossil marine invertebrates using Cenozoic gastropods from southeastern Australia as an example (Chapter 6). Equally, very little in known about the evolution of larval strategies through geological time. Although planktotrophy is considered to the likeliest primitive condition, there is relatively little published literature examining this in detail. This research has examined the order and timing of switches in larval strategy in fossil gastropods from southeastern Australia, with the aim of increasing our understanding of the evolution of developmental mode (Chapter 5).

## 7.1 TAXONOMY

A taxonomic revision of 104 species belonging to six families was carried out to establish distinct species and correctly assign them to genera and families. The taxonomic revision of the family Volutidae included 69 species assigned to 13 genera and closely follows the taxonomic revisions by Darragh (1971, 1988). The taxonomic revision of the family Nassariidae included seven species assigned to four subgenera of the genus *Nassarius* and closely follows the taxonomic revision of Cernohorsky (1981). The four remaining families (Raphitomidae, Borsoniidae, Mangeliidae and Turridae) have traditionally been considered as subfamilies of the family Turridae. Recent advances in the classification of conoideans by Bouchet et al. (2011) have promoted these subfamilies to family status based on molecular phylogenies by Puillandre et al. (2011), and anatomical and morphological data. This study has followed the generic assignment of Bouchet et al. (2011). Two species belonging to two genera were assigned to the family Raphitomidae. The Borsoniidae includes 14 species belonging to six genera. Six species in three genera were assigned to the family Mangeliidae and the Turridae included six species from five genera.

The taxonomic revision of the families Volutidae and Nassariidae are considered to be complete and include all known species from the Cenozoic strata of southeastern Australia. However, the taxonomic revision of the other four families presented in this thesis is considered to be incomplete. The classification set out by Bouchet et al. (2011) is based on living taxa only and problems arose in trying to assign fossil genera to families due to the lack of anatomical characters. This was mostly due to the conchological variability in family descriptions outlined by Bouchet et al. (2011). Although data for more “turrids” was collected, they were not included in this research because they could not be confidently assigned to families.

There is a great deal of scope for taxonomic studies of Cenozoic gastropods from southeastern Australia that were not included as part of this thesis. For the families Raphitomidae, Borsoniidae, Mangeliidae and Turridae, a comprehensive regional taxonomic revision is desperately needed. The classification framework adopted in this study is relatively new and as a result is yet to be used in regional studies. As molecular and anatomical data are not available in fossil specimens, a taxonomic revision would require more definitive conchological characters for each family. There is also the opportunity to examine the taxonomy of families not included in this study, such as cowries, mitrids and turritellids, which are found in abundance in southeastern Australian strata. Whilst this study has sought to resolve the regional taxonomy of gastropods as best as possible, the global taxonomy stills requires a great deal of attention. Of the families examined here only the Nassariidae has been examined on a global scale (Cernohorsky, 1984). If the global taxonomy of each of these families can be established then there is scope to examine global trends in the evolution of larval modes.

A final point regarding taxonomy concerns the occurrence of moulds in the strata of southeastern Australia. Whilst the majority of gastropod specimens from this region are exceptionally well preserved, they are confined to specific horizons. Outside of these horizons, only moulds could be found and unfortunately if they cannot be successfully identified then they cannot be used for research of this kind. As methods advance it is hoped that gaps in the fossil record of southeastern Australia can be closed by identification of moulds.

## 7.2 PHYLOGENETIC ANALYSES

Phylogenetic analysis was carried out for all six families included in this research. The decision to use genus or species level analysis was based on variation in larval mode. Where more than one larval mode presented itself within a single genus, species level analysis was carried out. All other analyses were carried out at genus level. Subfamily level analysis was carried out for the Volutidae (the only family with subfamilial divisions). Characters were based on shell morphology only (except for the Nassariidae) due to the lack of anatomical data for fossil taxa. Composite trees were created to show the relationships between subfamilies and families.

Most of the cladograms produced by these analyses were not very robust with low bootstrap and Bremer support values which is commonly the case in species level phylogenetic analyses. Phylogenetic analysis of gastropod fossils is often viewed as problematic (e.g. Harasewych, 1984; Emberton, 1995; Frýda, 1999; Wagner, 2001). The major problem encountered in this study concerned characters and character states. It proved very difficult to establish distinct characters with distinct character states and as a result the number of available characters was quite limited. Problems also arose, due to large numbers of uninformative characters limiting the number of taxa that could be analysed at any one time (hence the creation of composite trees). Missing taxa, either as a result of preservation biases or due to exclusion (see section 7.1), may also have resulted in less robust trees. Whilst little can be done to eliminate problems with gaps in the fossil record, it might still be possible to use taxa that are yet to be successfully identified through taxonomic revisions. Traditionally, phylogenetic analysis follows taxonomic revision. However, there is still scope to produce phylogenetic trees in cases of taxonomic dispute, if each taxon is considered a distinct taxonomic unit allowing for taxonomy to follow phylogenetic analysis.

Ideally, robust species level analyses would be carried out in order to examine evolutionary trends at high resolution. This is clearly not possible in gastropods at this time. However, there are some potential solutions relating to missing taxa and character definition. To reduce the number of missing taxa, analyses of global datasets could be carried out. Whilst this would produce results at a lower resolution it would perhaps provide a better indication of relationships between taxa at higher taxonomic levels. Similarly, if the regional taxonomy of conoidean families can be improved then this would significantly reduce the number of taxa which were lost to this study. In truth, the best way to improve phylogenetic analyses of gastropods is to increase the quality and number of characters that can be used. The need for innovative approaches to character definition is being investigated by a few researchers. The use of geometric morphometric data has been explored in *Conus* taxa (Smith & Hendricks, 2013) whilst the separation of juvenile and adult characters has also been investigated (Papadopoulos et al., 2004).

## 7.3 ORDER AND TIMING OF CHANGES IN LARVAL MODE

In order to examine the evolution of larval mode, a large dataset of developmental mode data was produced. Developmental mode was inferred from the protoconchs of the gastropod specimens used in the taxonomic revision. Phylogenetic analyses were used in this research to reconstruct ancestral modes of development and provide insight into the order and timing of switches in larval strategies. Reconstructions of ancestral developmental modes were carried out using maximum parsimony and maximum-likelihood methods. Planktotrophy is considered to be the most likely ancestral larval mode in gastropods by many researchers (e.g. Hansen, 1982; Lieberman et al., 1993; Duda & Palumbi, 1999; Fedosov & Puillandre, 2012). The analyses carried out in this study reveal that the ancestral mode of development cannot be unequivocally determined. This may in part be due to the small datasets of some of the families (i.e. conoidean families) but may also be a result of poorly resolved trees. Examination of switches in larval mode using maximum parsimony and maximum-likelihood analyses indicated that transitions may not be irreversible as predicted (Strathmann, 1978). Many researchers suggest regaining specialised structures associated with planktotrophy is too difficult to achieve and therefore reversals are extremely unlikely. However, sensitivity analysis carried out as part of this study indicates that reversals may not be as difficult as previously thought. The results suggested that in the family Volutidae switches from nonplanktotrophy to planktotrophy is only six times harder than switches in the other direction. The timing of switches in larval mode was mapped onto cladograms correlated to the stratigraphy of the region but revealed no coordinated shifts at precise points in time. As a result it is not possible to investigate the possible external factors driving switches, as has been done for echinoids (e.g. Jeffery, 1997).

Much of the work on the order and timing of switches requires congruence between phylogenies and stratigraphy and limited gaps in the fossil record. Three methods were used to assess these issues: the Stratigraphic Consistency Index, the Relative Completeness Index and the Gap Excess Ratio. Whilst most of the trees were stratigraphically congruent suggesting that the branching order was broadly correct, large gaps in the fossil record were revealed. However, these large gaps in the fossil record were not unexpected due to preservation in specific horizons. The issue of missing taxa, either from preservation biases or excluded taxa, suggests that evolutionary patterns seen in this research may not entirely reflect true patterns through geological time. In particular, missing taxa and missing occurrences of taxa results in inaccurate data for the temporal and spatial distribution of species.

In order to improve our understanding of larval mode evolution, a number of further studies could be carried out. Taxa excluded due to uncertain taxonomic placement could be included and the analyses repeated in the hope that more data will provide more robust results and reduce issues relating to gaps in the fossil record. The same analyses could also be carried out for global datasets of individual families, similar to work undertaken on echinoids (e.g. Jeffery & Emlet, 2003). Our understanding of larval mode evolution may also be improved by looking into different groups, such as bivalves where fossil larval mode can be inferred, or in other regions of the world, such as the Gulf Coast of the USA and the Paris Basin where a range of developmental modes have been recorded in a number of taxonomic groups. Work of this kind has been carried out for temnopleurid echinoids in southeastern Australia (Jeffery & Emlet, 2003) but more studies are needed in a variety of groups to build the bigger picture.

A final suggestion for further work involves expanding this type of research beyond the Cenozoic and into the Mesozoic and Palaeozoic, not just in gastropods but also in other groups of marine invertebrate. The evolution of larval strategies in spatangoid echinoids during the Late Cretaceous has already been examined (Cunningham & Jeffery Abt, 2009) and provides a comparable dataset for future research. This may offer interesting insights into the ancestral larval mode as well as extending our understanding of evolutionary trends further back in geological time.

## 7.4 MACROEVOLUTIONARY CONSEQUENCES OF LARVAL STRATEGIES

The penultimate chapter of this thesis explored the macroevolutionary consequences of larval strategies and compared these results with those predicted in the literature. The analyses indicated that gastropods in southeastern Australia exhibit very little difference in geographic and stratigraphic range between different larval strategies. Therefore, the prediction that planktotrophic taxa will exhibit wider geographic ranges and longer species duration is not supported by this study. Speciation rates are predicted to be higher in nonplanktotrophs than planktotrophs but again, the analyses carried out in this research do not find any difference between different larval modes. Similar studies on gastropods from the Gulf Coast of the USA have shown more support for predicted results (Hansen, 1980).

It is likely that two main factors have affected the results of the analysis in this study. Firstly, the exclusion of taxa that could not be assigned to particular families has reduced the size of the dataset. Secondly, preservation biases, as indicated by SCI, RCI and GER values, are likely to have affected our interpretation of spatial and temporal distributions of taxa.

There are a number of further studies that could be carried out to advance our understanding of the links between macroevolution and larval mode in gastropods. The analysis could be repeated including taxa previously excluded due to uncertain taxonomic placement. If all the taxa are analysed together then their taxonomic placement is not necessarily an issue, only that their larval mode has been correctly inferred. The second proposal is to examine these patterns on global datasets of individual families, which would require well established taxonomies. This may reduce issues relating to preservation biases but there may be problems in correlating the stratigraphy for different global regions. Other potential studies include carrying out the analyses on bivalves from southeastern Australia and comparing the results to those patterns seen in gastropods and echinoids of this area. Similarly, analyses could be carried out on echinoids from the Gulf Coast of the USA and compared to studies on gastropods and bivalves already carried out in that region.

In conclusion, whilst the results of this study do not necessarily support hypotheses laid out in the literature nor do they absolutely contradict theory either. It is clear that preservation biases influenced the results of analyses carried out in this research. However, there is still a great deal of scope for further studies to be carried out both in southeastern Australia and elsewhere in the world, using gastropods and other groups.

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# APPENDIX 1 – LOCALITY DATA

| LOCALITY NUMBER | LOCALITY DESCIPTION | LATITUDE, LONGITUDE | FORMATION NAME | FORMATION AGE | REFERENCE |
|---|---|---|---|---|---|
| **VIC001** | G.S.V locality "Aw7", Rivernook, black silt beneath an outcrop of indurated siltstone, 1 mile southeast of Point Ronald, Princetown, Victoria | **-38.71597°, +143.16847°** | Dilwyn Formation | Johannian (E. Eocene) 53.5-46.5Ma | Darragh, 1971 |
| **VIC002** | G.S.V. locality "Aw1", northwest outcrop, 0.6 miles north of Point Flinders, Victoria | **-38.84403°, +143.49347°** | Glen Aire Clay | Aldingan - Willunhgan (L. Eocene - E. Oligocene) 35-31.5Ma | Darragh, 1971 |
| **VIC003** | G.S.V. locality "Aw4", Aire coast, 1.1 miles northwest of the mouth of the Aire River, Victoria | **-38.79557°, +143.444538°** | Glen Aire Clay | Aldingan - Willunhgan (L. Eocene - E. Oligocene) 35-31.5Ma | Darragh, 1971 |
| **VIC004** | G.S.V. locality "Ad22", Bird Rock cliffs, strata approximately 17-37ft below cap of Bird Rock, Victoria | **-38.34681°, +144.31097°** | Jan Juc Marl | Janjukian (L. Oligocene) 25-23Ma | Darragh, 1971 |
| **VIC005** | Bird Rock Cliffs, Torquay, Victoria | **-38.34681°, +144.31097°** | Jan Juc Marl | Janjukian (L. Oligocene) 25-23Ma | Darragh, 1971 |
| **VIC006** | Bed "B100", clay immediately beneath the Point Addis Limestone, southwest side of Bells Headland, Victoria | **-38.37042°, +144.28152°** | Jan Juc Marl | Janjukian (L. Oligocene) 25-23Ma | Darragh, 1971 |
| **VIC007** | Left bank of Barwon River, 3.5 miles south of Birregurra, Victoria | **-38.387326°, +143.770823°** | Jan Juc Marl | Janjukian (L. Oligocene) 25-23Ma | Darragh, 1971 |

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|---|---|---|---|---|---|
| **VIC008** | Cliff section at southwest end of Jan Juc Beach, approximately 100 yards northeast of Bird Rock, Torquay, Victoria | **-38.35103°, +144.300785°** | Puebla Formation | Longfordian - Balcombian (E. - M. Miocene) 23-14Ma | Darragh, 1971 |
| **VIC009** | Left bank, Barwon River, Birregurra, Victoria | **-38.341858°, +143.790264°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC010** | 70ft in well at J. Keyte's farm, 3 miles east of Mount Arapiles, Victoria | **-36.755141°, +141.790441°** | Unknown | - | Darragh, 1971 |
| **VIC011** | Slip on south bank of Lake Costin, 0.3 miles west of Horden Vale-Red Hill Road, Horden Vale, Victoria | **-38.780099°, +143.484771°** | Fishing Point Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC012** | Cliff 100ft above Lake Craven, Aire River, 0.25 miles northwest of Red Hill, Horden Vale, Victoria | **-38.788345°, +143.481617°** | Fishing Point Marl | Longfordian (E. Miocene) 23-17Ma | Darragh, 1971 |
| **VIC013** | G.S.V. locality "Ad14", Section 24, Block 1, Parish of Moolap, 1.5 miles north of Curlewis Railway crossing, Victoria | **-38.161691°, +144.515877°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971, 1988 |
| **VIC014** | Belmont Shaft, Victoria | **-38.18003°, +144.34282°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971, 1988 |
| **VIC015** | "Bed 7", G.S.V. "Fc 20", 60ft up section, Amphitheatre, Leigh River, Victoria | **-38.097078°, +144.05827°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |

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|---|---|---|---|---|---|
| **VIC016** | Cutting, Cobden-Lavers Hill Road, 0.8 miles south of Kennedys Creek, Victoria | **-38.546152°, +143.249531°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC017** | “Chapple’s locality”, landslips on Latrobe Creek, 0.75 miles northwest of Princetown, Victoria | **-38.68216°, +143.151169°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC018** | Cutting on Princetown-Simpson Road, 1.7 miles south of Melrose Road, Victoria | **-38.642484°, +143.133659°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC019** | Cutting on Bornung Road, at top of hill, 1.3 miles north of Coriemungle, Victoria | **-38.519564°, +143.079243°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC020** | Limestone Creek, Glenelg River, Victoria | **-37.76653°, +141.20569°** | Whalers Bluff Formation | Mitchellian - Yatalan (L. Miocene - Pliocene) 6-3Ma | Darragh, 1971 |
| **VIC021** | 20-30ft above Lake Craven, southeast side of Fischers Point, Horden Vale, Victoria | **-38.791724°, +143.479986°** | Fishing Point Marl | Longfordian (E. Miocene) 23-17Ma | Darragh, 1971 |
| **VIC022** | Fossil Beach, Balcombe Bay, 1.5 miles south of Mornington, Victoria† | **-38.24208°, +145.02763°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC023** | 200 yards south of Grices Creek, Victoria | **-38.18736°, +145.09903°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |

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| **VIC024** | Dennant Creek, approximately 50 yards from older volcanics, Victoria | **-38.186995°, +145.084258°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC025** | Cliff section to south of Manyung Rocks and north of sewer pipe and jetty, "bed 10Ba", Victoria | **-38.19374°, +145.067854°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC026** | Downstream section, Grices Creek, beds "8 Ba-g", Victoria | **-38.164998°, +145.099912°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC027** | Southeastern trunk sewer between Braeside shaft and shaft at corner of Boundary and Centre Dandenong Roads, Dingley, Victoria | **-37.9826°, +145.116477°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC028** | Altona Bay Coal Shaft, Victoria | **-37.89014°, +144.84042°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC029** | Red Hill, Shelford-Inverleigh Road, Victoria | **-38.05179°, +143.98928°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971, 1988 |
| **VIC030** | Left bank, Native Hut Creek, southwest of Glenleigh, Victoria | **-38.03514°, +144.05347°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC031** | Right bank, Native Hut Creek, 100 yards south of Hamilton Highway, Victoria | **-38.095153°, +144.103332°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |

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|---|---|---|---|---|---|
| **VIC032** | Junction of Native Hut Creek and Barwon River, Victoria | **38.110519°, +144.139595°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC033** | Left bank, Barwon River, Section 2B, Parish of Murgheboluc, Victoria | **38.110519°, +144.139595** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC034** | Left bank, Barwon River, near junction with Bruces Creek, Section 4A, Parish of Murgheboluc, Victoria | **38.02486°, +144.14514°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1971 |
| **VIC035** | Cliff at north west end of Gibson Beach, Princetown, Victoria | **-38.66875°, +143.11041°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC036** | Cliff immediately beneath limestone on track to V.A.L. quarry, Curdies, Victoria | **38.44468°, +142.94374°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC037** | Cutting, Timboon-Port Campbell Road, 100yards from Timboon shops, Victoria | **38.485005°, +142.981653°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC038** | Clifton Bank, Muddy Creek, Yulecart, Hamilton, Victoria | **-37.74160°, +141.93473°** | Muddy Creek Marl | Balcombian - Bairnsdalian (M. Miocene) 15-11Ma | Darragh, 1971 |
| **VIC039** | Grange Burn, 0.75 mile above Henty’s House, Hamilton, Victoria | **-37.72776°, +141.93871°** | Muddy Creek Marl | Balcombian - Bairnsdalian (M. Miocene) 15-11Ma | Darragh, 1971 |

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|---|---|---|---|---|---|
| **VIC040** | G.S.V. locality Aw10, cliff at Rutledge Beach, Princetown, Victoria | **-38.63070°, +143.06013°** | Port Campbell Limestone | Batesfordian - Mitchellian (M.- L. Miocene) 16-6Ma | Darragh, 1971 |
| **VIC041** | North west shore of Lake Bullen Merri, Camperdown, Victoria | **-38.242259°, +143.092203°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC042** | Well at Wiridgil, Camperdown, Victoria | **-38.23333°, +143.21667°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1971 |
| **VIC043** | Bed of Spring Creek, 0.5 mile north east of Spring Creek Homestead, Minhamite, Victoria | **-38.01667°, +142.41667°** | Port Campbell Limestone | Batesfordian - Mitchellian (M.- L. Miocene) 16-6Ma | Darragh, 1971 |
| **VIC044** | Rose Hill, near Bairnsdale, Victoria | **-37.813581°, +147.594109°** | Tambo River Formation | Mitchellian (L. Miocene) 10-5.5Ma | Darragh, 1971 |
| **VIC045** | Sample 1, 66-120ft, Bore 12, Parish of Stradbroke, Victoria | **-38.278821°, +147.0401°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1971 |
| **VIC046** | Cutting on Princes Highway, left bank, Bunga Creek, Lakes Entrance, Victoria | **-37.853068°, +148.036351°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1971 |
| **VIC047** | Ritchies cutting, Scrivenor Road, right bank, Mississippi Creek, G.S.V. locality Fl., Victoria | **-37.838462°, +147.951293°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1971 |

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|---|---|---|---|---|---|
| **VIC048** | Lake Bunga crossing, Victoria | **-37.864995°, +148.04384°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1971 |
| **VIC049** | Lowest shell bed, cutting on Nyerimalang Road, approximately 12ft above and Meringa Creek, Victoria | **-37.87134°, +147.92695°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1971 |
| **VIC050** | Bluff on west side of North Arm, south of Hunter Gully, Lakes Entrance, Victoria | **-37.873092°, +147.978716°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1971 |
| **VIC051** | Just below high tide level on east side of North Arm, on point at end of Ferndale Parade, Lakes Entrance, Victoria | **-37.87465°, +147.988093°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1971 |
| **VIC052** | Mallacoota Inlet, Victoria | **-37.56125°, +149.76598°** | Recent | - | Cernohorsky, 1981 |
| **VIC053** | Port Melbourne, Victoria | **-37.82896°, +144.91061°** | Recent | - | Cernohorsky, 1981 |
| **VIC054** | Altona, Victoria | **-37.869471°, +144.830246°** | Recent | - | Cernohorsky, 1981 |
| **VIC055** | North Arm, Lakes Entrance, Victoria | **-37.86625°, +147.98125°** | Recent | - | Cernohorsky, 1981 |

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| **VIC056** | Port Phillip, Victoria | **-38.10736°, +144.89125°** | Recent | - | Cernohorsky, 1981 |
| **VIC057** | Off Rhyll, Westport, Victoria | **-38.47779°, +145.27985°** | Recent | - | Cernohorsky, 1981 |
| **VIC058** | Hobson's Bay, Victoria | **-37.85486°, +144.93597°** | Recent | - | Cernohorsky, 1981 |
| **VIC059** | Gippsland, Victoria | **-38.13430°, +147.46902°** | Formation unknown | Pliocene | Reath, 1925; Cernohorsky, 1981 |
| **VIC060** | Muddy Creek, near Hamilton, Victoria | **-37.74160°, +141.93473°** | Grange Burn Formation | Mitchellian - Kalimnan (L. Miocene - Pliocene) 6-4Ma | Cernohorsky, 1981 |
| **VIC061** | Grange Burn, near Hamilton Victoria | **-37.72776°, +141.93871°** | Grange Burn Formation | Mitchellian - Kalimnan (L. Miocene - Pliocene) 6-4Ma | Cernohorsky, 1981 |
| **VIC062** | South west side of Bunga Creek, Upper Jemmy's Point, East of Lakes Entrance, Victoria | **-37.848541°, +148.031182°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Cernohorsky, 1981 |
| **VIC063** | Sorrento Bore, Mornington Peninsula, Victoria | **-38.34376°, +144.74300°** | Formation unknown | Pliocene | Cernohorsky, 1981 |

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|---|---|---|---|---|---|
| **VIC064** | Point Welshpool, Victoria | **-38.6899°, +146.48676°** | Recent | - | Cernohorsky, 1981 |
| **VIC065** | Wilson’s Promontory, Victoria | **-38.97073°, +146.3687°** | Recent | - | Cernohorsky, 1981 |
| **VIC066** | Newhaven, Victoria | **-38.51688°, +145.33388°** | Recent | - | Cernohorsky, 1981 |
| **VIC067** | Western Port, Victoria | **-38.32042°, +145.25098°** | Recent | - | Cernohorsky, 1981 |
| **VIC068** | Cowes, Victoria | **-38.46955°, +145.23848°** | Recent | - | Cernohorsky, 1981 |
| **VIC069** | Phillip Island, Victoria | **-38.47319°, +145.22792°** | Recent | - | Cernohorsky, 1981 |
| **VIC070** | Point Leo, Victoria | **-38.42403°, +145.07903°** | Recent | - | Cernohorsky, 1981 |
| **VIC071** | Sandringham, Victoria | **-37.95249°, +145.01231°** | Recent | - | Cernohorsky, 1981 |

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| **VIC072** | Melbourne, Victoria | **-38.37111°, +144.91533°** | Recent | - | Cernohorsky, 1981 |
| **VIC073** | Rosebud, Victoria | **-37.8243°, +144.97398°** | Recent | - | Cernohorsky, 1981 |
| **VIC074** | Sorrento, Victoria | **-38.34376°, +144.74300°** | Recent | - | Cernohorsky, 1981 |
| **VIC075** | Port Fairy, Victoria | **-38.3308°, +142.17635°** | Recent | - | Cernohorsky, 1981 |
| **VIC076** | Portland Bay, Victoria | **-38.32903°, +141.63625°** | Recent | - | Cernohorsky, 1981 |
| **VIC077** | Moine River mouth, Victoria | **-38.23764°, +142.23541°** | Formation unknown | Pleistocene | Cernohorsky, 1981 |
| **VIC078** | Mallee Bore No. 8, Victoria | **-34.326103°, +142.371983 °** | Formation unknown | Pleistocene | Cernohorsky, 1981 |
| **VIC079** | Fyansford, Victoria | **-38.12399°, +144.28987 °** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Cernohorsky, 1981 |

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|---|---|---|---|---|---|
| **VIC080** | Schnapper Point, Port Phillip Bay, Victoria | **-38.21236°, +145.03209°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Cernohorsky, 1981 |
| **VIC081** | Gellibrand, Victoria | **-38.52819°, +143.54529°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Cernohorsky, 1981 |
| **VIC082** | South east end of Gibson Beach, Princetown, Victoria | **-38.67172°, +143.11482°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Cernohorsky, 1981 |
| **VIC083** | Altona, Victoria | **-37.869471°, +144.830246°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Cernohorsky, 1981 |
| **VIC084** | Mount Eliza, Victoria | **-38.19379°, +145.09488°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Cernohorsky, 1981 |
| **VIC085** | Mornington, Victoria | **-38.22779°, +145.06226°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Cernohorsky, 1981 |
| **VIC086** | Moorabool River near Lethbridge, Victora. | **-37.959358°, +144.159765°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |
| **VIC087** | Cutting on Steens Road, 2.1km north of Cooriemungle Road, Cooriemungle, Victoria | **38.510968°, +143.080101°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1988 |

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| **VIC088** | Clay overburden, just above limestone, Australian Cement Quarry, right bank of Moorabool River, Batesford, Victoria | **-38.112139°, +144.29615°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |
| **VIC089** | Cliff on left bank of Leigh River at "Farrells", Allotment 44, Parish of Carrah, Victoria | **-38.103375°, +144.06301°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |
| **VIC090** | 0-2m above water on right bank, Moorabool River, NNW of Farm, Victoria | **38.129155°, +144.288769°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |
| **VIC091** | BCIII, dark gritty clay, in washout 2, forked gully nearest mouth of Johanna River, Johanna, Victoria | **. -38.765712°, +143.389456°** | Browns Creek Clay | Johannian - Aldingan (L. Eocene) 38.5-35.5Ma | Darragh, 1988 |
| **VIC092** | BCI, 9.6m dark clay with Turritella below green sand in washout 1 nearest mouth of Browns Creek, Johanna, Victoria | **-38.757863°, +143.377343°** | Browns Creek Clay | Johannian - Aldingan (L. Eocene) 38.5-35.5Ma | Darragh, 1988 |
| **VIC093** | Cliff section Addiscot Beach, beds B109-107, SW of small gully, clay overlying Demons Bluff Formation, Torquay, Victoria | **-38.390446°, +144.252462°** | Jan Juc Marl | Janjukian (L. Oligocene) 25-23Ma | Darragh, 1988 |
| **VIC094** | Bed of Warrambine Creek, immediately downstream from Winchelsea-Inverleigh Road bridge, Victoria | **-38.151078°, +144.006107°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |
| **VIC095** | 0-4m above high water mark in cliff east of Kalimna Jetty, Kalimna, Victoria | **-37.882568°, +147.965262°** | Jemmys Point Formation | Mirchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1988 |

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| **VIC096** | Loose shells in Glenelg River derived from slips at Roscoes Cliff, Victoria | **-38.052387°, +140.997026°** | Whalers Bluff Formation | Mitchellian - Yatalan (L. Miocene - Pliocene) 6-3Ma | Darragh, 1988 |
| **VIC097** | 19m, sheft at Wurdiboluc, Victoria | **-38.301582°, +144.042639°** | Jan Juc Marl | Janjukian (L. Oligocene) 25-23Ma | Darragh, 1988 |
| **VIC098** | Approximately G.S.V. locality Ad28, Orphanage Hill, Fyansford, Victoria | **-38.141716°, +144.310166°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |
| **VIC099** | Williams Road cutting, Cowleys Creek, Victoria | **-38.482496°, +143.060189°** | Formation unknown | - | Darragh, 1988 |
| **VIC100** | Dam on Lot 393 (A. Smith) in 2nd gully north east of house, tributary of Tomahawk Creek, Victoria | **-38.450635°, +143.416431°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1988 |
| **VIC101** | 55m in bore on R. Hardy's property, Dalmore, Victoria | **-38.199424°, +145.418128°** | Formation unknown | - | Darragh, 1988 |
| **VIC102** | G.S.V. loc. F2, floor and sides of tramway cutting north of Scrivenors Road, Mississippi Creek, Victoria | **-37.837971°, +147.950885°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1988 |
| **VIC103** | Sands exposed in sewer tunnel, 12.2m below wright Street, Bentleigh, between Centre Road and Beech Street, Victoria | **-37.915391°, +145.030003°** | Black Rock Sandstone | Mitchellian - Cheltenhamian (L. Miocene - M. Pliocene) 6-4Ma | Darragh, 1988 |

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| **VIC104** | Shelly clay at base of cliff at high tide mark opposite Dogtooth Beacon between Deauville Street and Hutchinson Avenue, Beaumaris, Victoria | **-37.988942°, +145.047297°** | Black Rock Sandstone | Mitchellian - Cheltenhamian (L. Miocene - M. Pliocene) 6-4Ma | Darragh, 1988 |
| **VIC105** | Upper quarry, Bellevue, left bank, Mitchell River, Victoria | **-37.64966°, +147.338348°** | Formation unknown | - | Darragh, 1988 |
| **VIC106** | Outcrop in road ditch, 20m west of Lakes Entrance Development No. 1 oil bore, right bank of Bunga Creek, Victoria | **-37.848541°, +148.031182°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1988 |
| **VIC107** | Cutting on Princes Highway, north east side of Bunga Creek, bed 6g, uppermost shell bed, Victoria | **-37.852729°, +148.036737°** | Jemmys Point Formation | Mitchellian - Kalimnan (Pliocene) 5.5-4Ma | Darragh, 1988 |
| **VIC108** | G.S.V. locality Ad12, shore platform, north east corner section 23, block 1, Parish of Moolap, Victoria | **-38.130962°, +144.428909°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |
| **VIC109** | Left bank of Leigh River, about 30m above river, prominent limestone bands, south of small gully, Victoria | **-38.108054°, +144.063785°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |
| **VIC110** | Left bank of Glenelg River, just above water level at south end of Devils Den, Myaring, Victoria | **-37.77292°, +141.236115°** | Port Campbell Limestone | Batesfordian - Mitchellian (M.- L. Miocene) 16-6Ma | Darragh, 1988 |
| **VIC111** | 1-3m above river in cliff, left bank of Leigh River, due north of Inverleigh, Victoria | **-38.09696°, +144.057283°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |

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| **VIC112** | Leigh River at Inverleigh Bridge, Victoria | **-38.099983°, +144.062583°** | Fyansford Formation | Janjukian - Mitchellian (L. Oligocene - L Miocene) 25-8Ma | Darragh, 1988 |
| **VIC113** | Cliff 5km north west of Point Ronald, Princetown, Victoria | **-38.678542°, +143.12027°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Darragh, 1988 |
| **VIC114** | BCIII, dark gritty clay, 16m above greensand in washout 1 nearest mouth of Browns Creek, Johanna, Victoria | **-38.757863°, +143.377343°** | Browns Creek Clay | Johannian - Aldingan (L. Eocene) 38.5-35.5Ma | Darragh, 1988 |
| **VIC115** | Upper beds, Spring Creek, Victoria | **-38.342114°, +144.317513°** | Formation unknown | - | Powell, 1944 |
| **VIC116** | Clifton Beach, Princetown, Victoria | **+38.6779°, -143.124°** | Gellibrand Marl | Longfordian (E. Miocene) 23-16.5Ma | Powell, 1944 |
| **VIC117** | Mallee Bore No. 6, Victoria | **-34.326103°, +142.371983°** | Formation unknown | Pliocene | Powell, 1944 |
| **VIC118** | Southeast side of Dilwyn Cove, north side of Bell Point, 6km southeast of Princetown, from boulders on beach derived from 0.5m grey (weathered) sandstone about 15m above beach, Victoria | **-38.739222°, +143.191338°** | Pebble Point Formation | Wangerripian (L. Palaeocene) 61-56Ma | Darragh, 1997 |
| **VIC119** | Sorrento Bore, Mornington Peninsula, Victoria | **-38.34376°, +144.74300°** | Formation unknown | Miocene | Powell, 1944 |

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| **TAS001** | Lowermost part of cliff section between Fossil Bluff and Table Cape, north of Wynyard, Tasmania | **-40.950344°, +145.730209°** | Freestone Cove Sandstone | Longfordian (E. Miocene) 23.9-23Ma | Darragh, 1971, 1988 |
| **TAS002** | Upper part of cliff section between Fossil Bluff and Table Cape, north of Wynyard, Tasmania | **-40.950344°, +145.730209°** | Fossil Bluff Sandstone | Longfordian (E. Miocene) 2.9-23Ma | Darragh, 1971 |
| **TAS003** | Swan Point, Tasmania | **-41.25°, +146.97°** | Recent | - | Cernohorsky, 1981 |
| **TAS004** | Tamar River, Tasmania | **41.24772°, +146.95766°** | Recent | - | Cernohorsky, 1981 |
| **TAS005** | Taroona, Tasmania | **-42.94°, +147.34°** | Recent | - | Cernohorsky, 1981 |
| **TAS006** | Margate, Tasmania | **-43.02814°, +147.26256°** | Recent | - | Cernohorsky, 1981 |
| **TAS007** | Tinderbox, Tasmania | **-43.05°, +147.33°** | Recent | - | Cernohorsky, 1981 |
| **TAS008** | Fisher Island, Bass Strait, Tasmania | **-40.218°, +148-238°** | Recent | - | Cernohorsky, 1981 |

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| **TAS009** | Thunder and Lightning Bay, Barren Island, Tasmania | **-42.816°, +147.531°** | Recent | - | Cernohorsky, 1981 |
| **TAS010** | Circular Head, Tasmania | **-40.768°, +145.307°** | Recent | - | Cernohorsky, 1981 |
| **TAS011** | West side of Cape Portland, Tasmania | **-40.741°, +147.937°** | Recent | - | Cernohorsky, 1981 |
| **TAS012** | Stanley, Tasmania | **-40.763°, +145.291°** | Recent | - | Cernohorsky, 1981 |
| **TAS013** | Green’s Beach, Tasmania | **-41.084°, +146.751°** | Recent | - | Cernohorsky, 1981 |
| **TAS014** | Near mouth of River Inglis, Wynyard, Tasmania | **-41.064°, +145.609°** | Recent | - | Cernohorsky, 1981 |
| **TAS015** | Samphire Island, Near Flinders Island, Tasmania | **-47.771°, +147.459°** | Recent | - | Cernohorsky, 1981 |
| **TAS016** | Long Point, Flinders Island, Tasmania | **-40.100°, +147.952°** | Recent | - | Cernohorsky, 1981 |

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| **TAS017** | Coles Bay, Tasmania | **-42.134°, +148.292°** | Recent | - | Cernohorsky, 1981 |
| **TAS018** | Oyster Bay, Maria Island, Tasmania | **-42.685°, +148.021°** | Recent | - | Cernohorsky, 1981 |
| **TAS019** | Marion Bay. Tasmania | **-42.807°, 1470894°** | Recent | - | Cernohorsky, 1981 |
| **TAS020** | Bream Creek, Tasmania, | **-42.748°, +147.843°** | Recent | - | Cernohorsky, 1981 |
| **TAS021** | Hobart, Tasmania | **-42.882°, +147.323°** | Recent | - | Cernohorsky, 1981 |
| **TAS022** | Pittwater, Tasmania | **-42.815°, +147.514°** | Recent | - | Cernohorsky, 1981 |
| **TAS023** | Sandy Bay, Tasmania | **-42.908°, +147.344°** | Recent | - | Cernohorsky, 1981 |
| **TAS024** | Eaglehawk Neck, Tasmania | **-43.017°, +147.925°** | Recent | - | Cernohorsky, 1981 |

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| **TAS025** | Rockeby, Tasmania | **-42.900°, +147.442°** | Recent | - | Cernohorsky, 1981 |
| **TAS026** | Pirate’s Bay, Tasmania | **-43.023°, +147.934°** | Recent | - | Cernohorsky, 1981 |
| **TAS027** | Simmonds Bay in Barnes Bay, Tasmania | **-43.130°, +147.358°** | Recent | - | Cernohorsky, 1981 |
| **TAS028** | Bruny Island, Tasmania | **-43.297°, +147.285°** | Recent | - | Cernohorsky, 1981 |
| **TAS029** | Bridport, south of Bruny Island, Tasmania | **-40.995°, +147.388°** | Recent | - | Cernohorsky, 1981 |
| **TAS030** | Bay of Islands, south Bruny Island, Tasmania | **-43.414°, +147.360°** | Recent | - | Cernohorsky, 1981 |
| **TAS031** | Cooks Beach, Tasmania | **-42.225°, +147.270°** | Recent | - | Cernohorsky, 1981 |
| **TAS032** | White Beach, Tasmania | **-43.120°, +147.735°** | Recent | - | Cernohorsky, 1981 |

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| **TAS033** | West Ulverstone, Tasmania | **-41.147°, 146.160°** | Recent | | Cernohorsky, 1981 |
| **TAS034** | Dam on Block 22 (Lees), Furneaux Estate Section A, 11km ENE of junction of No. 4 and No. 3 Roads, Flinders Island, Tasmania | **-40.102235°, +148.289337°** | Cameron Inlet Formation | Kalimnan - Yatalan (L. Pliocene) 3.5-2.5Ma | Darragh, 1988 |
| **TAS035** | North Patriarch Drain, Block 6, 1.1km east of Link Road, Memana, Flinders Island, Tasmania | **-39.999856°, +148.111204°** | Cameron Inlet Formation | Kalimnan - Yatalan (L. Pliocene) 3.5-2.5Ma | Darragh, 1988 |
| **TAS036** | Dam (64) on block 22 Furneaux Estate Section A, 4.3km east-north-east of junction of No. 4 and No. 3 Roads, Flinders Island, Tasmania | **-39.999856°, +148.111204°** | Cameron Inlet Formation | Kalimnan - Yatalan (L. Pliocene) 3.5-2.5Ma | Darragh, 1988 |
| **TAS037** | TAS037 Dam (58) on lot 47, Furneaux Estate Section B, 1.3km due east of junction of No. 3 and No. 7 Roads, Flinders Island, Tasmania | **-39.999856°, +148.111204°** | Cameron Inlet Formation | Kalimnan - Yatalan (L. Pliocene) 3.5-2.5Ma | Darragh, 1988 |
| **TAS038** | Dam (5) on lot 82, Furneaux Estate Section D, 2.6km north-north-east of junction of No. 11 and No. 2A Roads, Flinders Island, Tasmania | **-39.999856°, +148.111204°** | Memana Formation | Yatalan - Werrikooian (E. Pleistocene) 2.5-1.5Ma | Darragh, 1988 |
| **TAS039** | Dam (6) on lot 88, Furneaux Estate Section D, 2.4km east-north-east of junction of No. 11 and No. 2A Roads, Flinders Island, Tasmania | **-39.999856°, +148.111204°** | Memana Formation | Yatalan - Werrikooian (E. Pleistocene) 2.5-1.5Ma | Darragh, 1988 |
| **SA001** | Left bank, Murray River, gully, 3 miles south of Morgan – Cadell Road, South Australia | **-34.081686°, +139.68996°** | Cadell Formation | Batesfordian (M. Miocene) 15.5-15Ma | Darragh, 1971 |

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| **SA002** | Well sinking, Murray Desert, Mindarie, South Australia | **-34.81404°, +140.21797°** | Bookpurnong Formation | Mitchellian (L> Miocene) 7.2-6.5Ma | Darragh, 1971 |
| **SA003** | Adelaide, South Australia | **-34.92866°, +138.59863°** | Recent | - | Cernohorsky, 1981 |
| **SA004** | Arno Bay, South Australia | **-33.91407°, +136.58919°** | Recent | - | Cernohorsky, 1981 |
| **SA005** | Larg's North Beach circa 19km north of Adelaide, South Australia | **-34.81471°, + 138.48988°** | Recent | - | Cernohorsky, 1981 |
| **SA006** | Port Adelaide River, South Australia | **. -34.76178°, +138.51012°** | Recent | - | Cernohorsky, 1981 |
| **SA007** | Larg's Bay, St. Vincent Gulf, South Australia | **-34.81041°, +138.48351** | Recent | - | Cernohorsky, 1981 |
| **SA008** | Outer Harbour, Adelaide, South Australia | **-34.77319°, +138.49873°** | Recent | - | Cernohorsky, 1981 |
| **SA009** | Beachport, South Australia | **-37.480593°, +140.012501°** | Recent | - | Cernohorsky, 1981 |

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| **SA010** | Glenelg, South Australia | **-34.982°, +138.516°** | Recent | - | Cernohorsky, 1981 |
| **SA011** | Holdfast Bay, South Australia | **-34.971°, +138.507°** | Recent | - | Cernohorsky, 1981 |
| **SA012** | Aldinga, South Australia | **-35.326°, +138.423°** | Recent | - | Cernohorsky, 1981 |
| **SA013** | Port Milacowie, South Australia | **-34.831°, +137.421°** | Recent | - | Cernohorsky, 1981 |
| **SA014** | Henley Beach, South Australia | **-34.916°, +138.500°** | Recent | - | Cernohorsky, 1981 |
| **SA015** | Approximately 3km south of Normanville, south of Adelaide. | **-35.443°, +138.321°** | Recent | - | Cernohorsky, 1981 |
| **SA016** | Rocky Point, Kangaroo Island, South Australia | **. -35.798°, +137.834°** | Recent | - | Cernohorsky, 1981 |
| **SA017** | Point Collinson, Gascoyne Beach, South Australia | **-32.541°, +133.894°** | Recent | - | Cernohorsky, 1981 |

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| **SA018** | Penneshaw, north east Kangaroo Island, South Australia | **-35.720°, +137.941** | Recent | - | Cernohorsky, 1981 |
| **SA019** | Port Vincent, South Australia | **-34.778°, +137.858°** | Recent | - | Cernohorsky, 1981 |
| **SA020** | Port Augusta, South Australia | **-32.503°, +137.764°** | Recent | - | Cernohorsky, 1981 |
| **SA021** | Tickera, via Kadina, South Australia | **-33.787°, +137.710°** | Recent | - | Cernohorsky, 1981 |
| **SA022** | North of Stansbury, Yorke's Peninsula, South Australia | **-34.910°, +137.797°** | Recent | - | Cernohorsky, 1981 |
| **SA023** | Pondalowie Bay, Yorke's Peninsula, South Australia | **-35.227°, +136.841°** | Recent | - | Cernohorsky, 1981 |
| **SA024** | Tumby Bay, South Australia | **-34.371°, +136.135°** | Recent | - | Cernohorsky, 1981 |
| **SA025** | Port Lincoln, South Australia | **-34.739°, +135.930°** | Recent | - | Cernohorsky, 1981 |

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| **SA026** | Near Striking Creek, Port Lincoln, South Australia | **-34.739°, +135.930°** | Recent | - | Cernohorsky, 1981 |
| **SA027** | Point Brown, Smoky Bay, South Australia | **-32.542°, +133.851°** | Recent | - | Cernohorsky, 1981 |
| **SA028** | St. Peters Island, south of Ceduna, South Australia | **-32.286°, +133.578°** | Recent | - | Cernohorsky, 1981 |
| **SA029** | Semaphore, South Australia | **-34.837°, +133.485°** | Recent | - | Cernohorsky, 1981 |
| **SA030** | Hindmarsh Bore, South Australia | **-34.904778°, +138.570701°** | Recent | - | Cernohorsky, 1981 |
| **SA031** | Weymouth Bore, Adelaide, South Australia | **-34.8°, +138.7°** | Dry Creek Sands | Kalimnan - Yatalan (Pliocene) 4.4-2.59Ma | Ludbrook, 1958; Cernohorsky, 1981 |
| **SA032** | Abbatoir's Bore, Adelaide, South Australia | **-34.83333°, +138.60972°** | Dry Creek Sands | Kalimnan - Yatalan (Pliocene) 4.4-2.59Ma | Ludbrook, 1958; Cernohorsky, 1982 |
| **SA033** | Hallett's Cove, South Australia | **-35.084377°, +138.492622°** | Hallett Cove Sandstone | Cheltanhamian - Yatalan (Pliocene - Pleistocene) 5.0-2.4Ma | Cernohorsky, 1981 |

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| **SA034** | Lower 6.5m of cliff on south side of Blanche Point, Port Willunga, South Australia | **-35.246951°, +138.461766°** | Blanche Point Marl | Johannian - Aldingan (L. Eocene) 37.8-34Ma | Darragh, 1988 |
| **SA035** | Adelaide Bore, Kent Town Waterworks, Adelaide, South Australia | **-34.928621°, +138.599959°** | Blanche Point Marl | Johannian - Aldingan (L. Eocene) 37.8-34Ma | Darragh, 1988 |
| **SA036** | 25m, bore 240 (G. Heading), Section 261, Hd of Yatala, Klemzig, South Australia | **-34.882376°, +138.636591°** | Blanche Point Marl | Johannian - Aldingan (L. Eocene) 37.8-34Ma | Darragh, 1988 |
| **SA037** | Ardrossan, South Australia | **-34.42307° +137.917428°** | Blanche Point Marl | Johannian - Aldingan (L. Eocene) 37.8-34Ma | Darragh, 1988 |
| **SA038** | 15m coal bore, Moorlands, South Australia | **-35.295784°, +139.641168°** | Buccleuch Group | Johannian - Janjukian (L. Eocene - M. Oligocene) 38-28Ma | Darragh, 1988 |
| **SA039** | 73m, Mundys Well, Canegrass Station, via Kooringa, South Australia | **-33.595959°, +140.025696°** | Formation unknown | - | Darragh, 1988 |
| **SA040** | Newland Head, off Backstairs Passage, South Australia | **-35.692995°, +138.508759°** | Recent | - | Darragh, 1988 |
| **SA041** | Yatala Shoal, South Australia | **. -35.75°, +138.166667°** | Recent | - | Darragh, 1988 |

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| **SA042** | Backstairs Passage, South Australia | **-35.688554°, +138.072018°** | Recent | - | Darragh, 1988 |
| **SA043** | Shell sand, Gleesons, Landing, Daly Head, Yorke Peninsula, South Australia | **- 34.992879°, +136.976166°** | Recent | - | Darragh, 1988 |
| **SA044** | Observation Bore A, Virginia, Head of Munno Para sec 3036, 63.7-66.1m, South Australia | **-34.666316°, +138.560411°** | Bookpurnong Beds | Mitchellian (L. Miocene) 7.2-6.5Ma | Darragh, 1988 |
| **SA045** | Kooyonga bore no. 1, 1932, Hd of Adelaide, Sec. 2028, 119-146m, South Australia | **-34.92866°, +138.59863°** | Bookpurnong Beds | Mitchellian (L. Miocene) 7.2-6.5Ma | Darragh, 1988 |
| **SA046** | F. Virgin bore. Mar 1958, Hd of Munno Para Sec. 3224 103-107m, South Australia | **. -34.732127°, +138.583435°** | Bookpurnong Beds | Mitchellian (L. Miocene) 7.2-6.5Ma | Darragh, 1988 |
| **SA047** | DeRuro bore, Waterloo Corner, Hd of Munno Para, Sec. 4259, 73.2-74.7m, South Australia | **-34.732127°, +138.583435°** | Bookpurnong Beds | Mitchellian (L. Miocene) 7.2-6.5Ma | Darragh, 1988 |
| **SA048** | Jones bore, 1934, Bolivar, Hd of Port Adelaide, Sec. 3502, 106m, South Australia | **-34.751487°, +138.587813°** | Bookpurnong Beds | Mitchellian (L. Miocene) 7.2-6.5Ma | Darragh, 1988 |
| **SA049** | Cliff base, 0.5 miles north of Port Willunga, South Australia | **-35.251367°, +138.463097°** | Blanche Point Formation | Johannian - Aldingan (L. Eocene) 37.8-34Ma | Long, 1981 |

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| **QLD001** | Palleranda Beach and Strand, Townsville, Queensland | **-19.19747°, +146.77460°** | Recent | - | Cernohorsky, 1981 |
| **QLD002** | Mouth of Funnel Creek, Sarina, Queensland | **-22.3°, +148.95°** | Recent | - | Cernohorsky, 1981 |
| **QLD003** | Heron Island, Queensland | **-23.44291° +151.91539°** | Recent | - | Cernohorsky, 1981 |
| **QLD004** | Calliope River estuary, Port Curtis, Queensland | **-23.82877°, +151.21951°** | Recent | - | Cernohorsky, 1981 |
| **QLD005** | Yeppoon, Queensland | **-23.12528°, +150.76778°** | Recent | - | Cernohorsky, 1981 |
| **QLD006** | Point Vernon, Hervey Bay, Queensland | **-25.28961°, +152.83091°** | Recent | - | Cernohorsky, 1981 |
| **QLD007** | Eli Creek, Hervey Bay, Queensland | **-25.28961°, +152.83091°** | Recent | - | Cernohorsky, 1981 |
| **QLD008** | Pialba, Hervey Bay, Queensland | **-25.28961°, +152.83091°** | Recent | - | Cernohorsky, 1981 |

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| **QLD009** | Urangan, Queensland | **-25.23333°, +152.86667°** | Recent | - | Cernohorsky, 1981 |
| **QLD010** | Tin Can Bay, NE of Gympie, Queensland | **-25.91646°, +153.00584°** | Recent | - | Cernohorsky, 1981 |
| **QLD011** | Noosa Inlet, Queensland | **-26.38507°, +153.07578°** | Recent | - | Cernohorsky, 1981 |
| **QLD012** | Maroochydore, Queensland | **-28.65667°, +153.08444°** | Recent | - | Cernohorsky, 1981 |
| **QLD013** | Caloundra, Queensland | **-26.79709°, +153.13771°** | Recent | - | Cernohorsky, 1981 |
| **QLD014** | Sangate, Moreton Bay, Queensland | **-27.29°, +153.25945°** | Recent | - | Cernohorsky, 1981 |
| **QLD015** | Cleveland, Moreton Bay, Queensland | **-27.29°, +153.25945°** | Recent | - | Cernohorsky, 1981 |
| **QLD016** | Scarborough, Moreton Bay, Queensland | **-27.29°, +153.25945°** | Recent | - | Cernohorsky, 1981 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| **QLD017** | Stradbroke Island, Moreton Bay, Queensland | **-27.29°, +153.25945°** | Recent | - | Cernohorsky, 1981 |
| **QLD018** | 3.2km SE of Redland Bat Jetty, Moreton Bay, Queensland 4m. | **-27.29°, +153.25945°** | Recent | - | Cernohorsky, 1981 |
| **QLD019** | Southport, Queensland | **-27.97361°, +153.40471°** | Recent | - | Cernohorsky, 1981 |
| **QLD020** | Coolangatta, Queensland | **-28.16673°, +153.53746°** | Recent | - | Cernohorsky, 1981 |
| **QLD021** | Cape Moretone, Queensland | **-27.028321°, +153.467954°** | Recent | - | Darragh, 1988 |
| **NSW001** | Off Tweed's Head, New South Wales | **-28.17352°, +153.54305°** | Recent | - | Cernohorsky, 1981 |
| **NSW002** | Ballina Beach, New South Wales | **-28.88095°, +153.55874°** | Recent | - | Cernohorsky, 1981 |
| **NSW003** | Newcastle, New South Wales | **-32.92779°, +151.78448°** | Recent | - | Cernohorsky, 1981 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| **NSW004** | Angourie, New South Wales | **-29.4181°, +153.3596°** | Recent | - | Cernohorsky, 1981 |
| **NSW005** | Smith's Lake, S of Forster, New South Wales | **-32.3818°, +152.50121°** | Recent | - | Cernohorsky, 1981 |
| **NSW006** | Mereweather Beach, Newcastle, New South Wales | **-32.94875°, +151.75713°** | Recent | - | Cernohorsky, 1981 |
| **NSW007** | Norah Head, New South Wales | **-33.2818°, +151.58459°** | Recent | - | Cernohorsky, 1981 |
| **NSW008** | Wangi Point, Lake Macquarie, New South Wales | **-33.0818°, +151.1679°** | Recent | - | Cernohorsky, 1981 |
| **NSW009** | Towoon, near The Entrance, New South Wales | **-33.36186°, +151.49824°** | Recent | - | Cernohorsky, 1981 |
| **NSW010** | Prickly Point, Hawkesbury River, New South Wales – 11m | **-33.5152°, +151.17619°** | Recent | - | Cernohorsky, 1981 |
| **NSW011** | Pittwater, Broken Bay, New South Wales | **-33.5485°, +151.3512°** | Recent | - | Cernohorsky, 1981 |

| | | | | | |
|---|---|---|---|---|---|
| **NSW012** | Pittwater Basin, New South Wales | **-33.5485°, +151.3512°** | Recent | - | Cernohorsky, 1981 |
| **NSW013** | Palm Beach, New South Wales | **-33.5985°, +151.3262°** | Recent | - | Cernohorsky, 1981 |
| **NSW014** | Narrabeen Lake, New South Wales | **-33.71247°, +151.28457°** | Recent | - | Cernohorsky, 1981 |
| **NSW015** | Long Reef, Collaroy, New South Wales | **-33.7318°, +151.3179°** | Recent | - | Cernohorsky, 1981 |
| **NSW016** | Lane Cove River, New South Wales | **-33.7485°, +151.0929°** | Recent | - | Cernohorsky, 1981 |
| **NSW017** | Parramatta River, Port Jackson, New South Wales | **33.8318°, +151.1012°** | Recent | - | Cernohorsky, 1981 |
| **NSW018** | Port Jackson, New South Wales – 4m | **-33.8318°, +151.2679°** | Recent | - | Cernohorsky, 1981 |
| **NSW019** | Off Mort’s Dock, Balmain, New South Wales – 7m | **-33.84247°, +151.17154°** | Recent | - | Cernohorsky, 1981 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| **NSW020** | Queenscliff Lagoon, Sydney, New South Wales | **-3378335°, +151.28001°** | Recent | - | Cernohorsky, 1981 |
| **NSW021** | Willoughby Bay, Middle Harbour, Sydney, New South Wales | **-33.8152°, +151.2179°** | Recent | - | Cernohorsky, 1981 |
| **NSW022** | Botany Bay, New South Wales – 6m | **-33.9818°, +151.1846°** | Recent | - | Cernohorsky, 1981 |
| **NSW023** | Gunnamatta Bay, Port Hacking, New South Wales | **-34.0652°, +151.1512°** | Recent | - | Cernohorsky, 1981 |
| **NSW024** | Port Kembla, New South Wales | **-34.4818°, +150.9012°** | Recent | - | Cernohorsky, 1981 |
| **NSW025** | Kelly's Bay, Lake Illawarra, New South Wales | **-34.54027°, +150.86458°** | Recent | - | Cernohorsky, 1981 |
| **NSW026** | Hare Bay, Jervis Bay, New South Wales | **-35.0152°, +150.7679°** | Recent | - | Cernohorsky, 1981 |
| **NSW027** | Burrill Lake, near Ulladulla, New South Wales | **-35.3652°, +150.4346°** | Recent | - | Cernohorsky, 1981 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| **NSW028** | Sussex Inlet, New South Wales | **-35.1652°, +150.6012°** | Recent | - | Cernohorsky, 1981 |
| **NSW029** | Pambula Lake, New South Wales | **-36.9652°, +149.9012°** | Recent | - | Cernohorsky, 1981 |
| **NSW030** | Budgewoi Beach, New South Wales | **-33.236378°, +151.571761°** | Recent | - | Cernohorsky, 1981 |
| **NSW031** | Cooks River, New South Wales | **-33.9152°, +151.1346°** | Recent | - | Cernohorsky, 1981 |
| **NSW032** | Wollanga, New South Wales – 100m | **-36.36941°, +150.07218°** | Recent | - | Cernohorsky, 1981 |
| **NSW033** | Merimbula Estuary, New South Wales | **-36.892664°, +149.92012°** | Recent | - | Cernohorsky, 1981 |
| **NSW034** | Wagonga River, New South Wales | **-36.2152°, +150.1012°** | Recent | - | Cernohorsky, 1981 |
| **NSW035** | Richmond River Beach, New South Wales | **-29.87911° +153.56585°** | Recent | - | Cernohorsky, 1981 |

| | | | | | |
|---|---|---|---|---|---|
| **NSW036** | Wooli, New South Wales | **-29.86161°, +153.26772°** | Recent | - | Cernohorsky, 1981 |
| **NSW037** | Well sinking, Murray Desert, Tareena, New South Wales | **-33.970413°, +141.038017°** | Bookpurnong Beds | Mitchellian (L. Miocene) 7.2-6.5Ma | Darragh, 1988 |
| **WA001** | Penguin Island, Western Australia | **-32.30545°, +115.9607°** | Recent | - | Cernohorsky, 1981 |
| **WA002** | Oyster Harbour, Albany area, Western Australia | **-34.97° +117.9599°** | Recent | - | Roberts & Wells, 1980; Cernohorsky, 1981 |
| **WA003** | Princess Royal Harbour, Albany area, Western Australia | **-35.04917° +117.8897°** | Recent | - | Roberts & Wells, 1980; Cernohorsky, 1981 |
| **WA004** | Minim Cove, Western Australia | **-32.0225°, +115.765°** | Formation unknown | Pleistocene | Reath, 1925; Cernohorsky, 1981 |
| **WA005** | Mosman Park, Western Australia | **-32.01573°, +115.7353°** | Formation unknown | Pleistocene | Reath, 1925; Cernohorsky, 1981 |
| **WA006** | Swan River, Western Australia | **-32.05528°, +115.7353°** | Formation unknown | Pleistocene | Reath, 1925; Cernohorsky, 1981 |

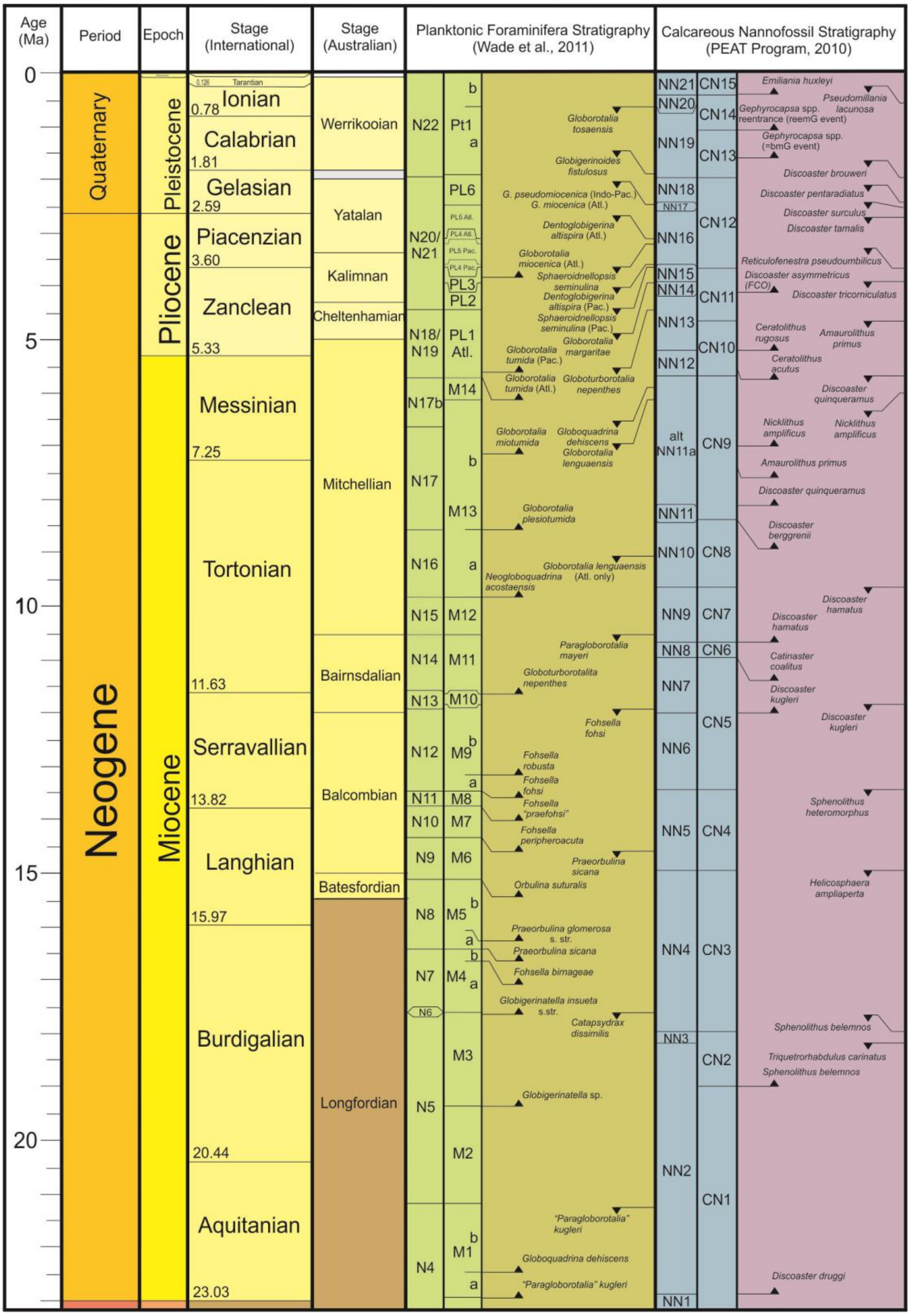
| | | | | | |
|---|---|---|---|---|---|
| **WA007** | Peppermint Grove, Western Australia | **-33.52878°, +115.50537°** | Formation unknown | Pleistocene | Reath, 1925; Cernohorsky, 1981 |
| **WA008** | Perth Water, Western Australia | **-31.96795°, +115.8612°** | Formation unknown | Pleistocene | Reath, 1925; Cernohorsky, 1981 |
| **WA009** | Melville Water, Western Australia | **-32.01156°, +115.8154°** | Formation unknown | Pleistocene | Reath, 1925; Cernohorsky, 1981 |
| **WA010** | Israelite Bay, Western Australia | **-33.561°, +123.885°** | Recent | - | Cernohorsky, 1981 |
| **WA011** | Middleton Beach, King George’s Sound, Western Australia | **-35.013°, +117.922°** | Recent | - | Cernohorsky, 1981 |
| **WA012** | Emu Point, Western Australia | **-34.99434°, +117.9493°.** | Recent | - | Cernohorsky, 1981 |
| **WA013** | Albany, Western Australia | **-35.02°, +117.8838°** | Recent | - | Cernohorsky, 1981 |
| **WA014** | South Point, east of Albany, Western Australia | **-34.967°, +118.189°** | Recent | - | Cernohorsky, 1981 |

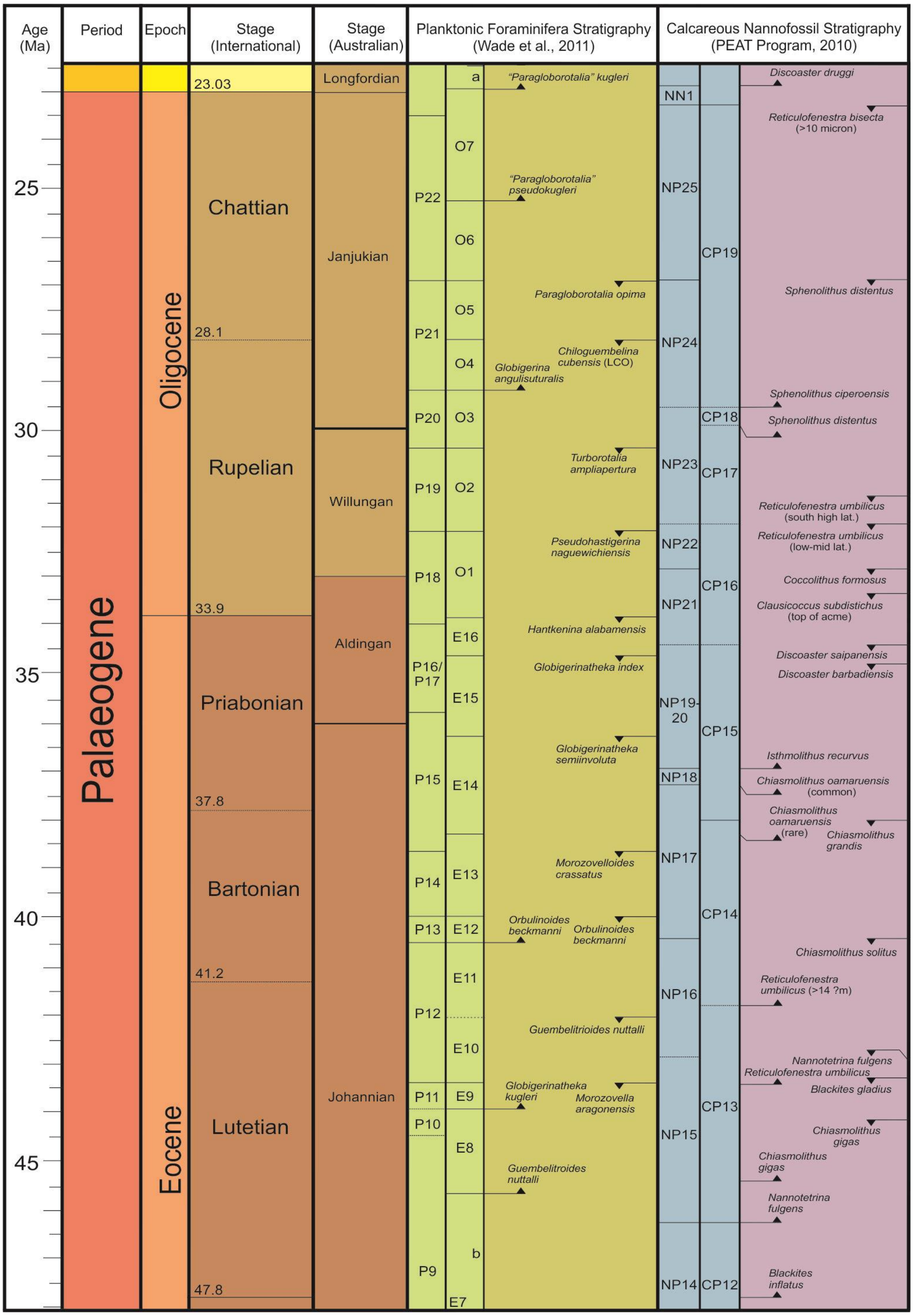
| | | | | | |
|---|---|---|---|---|---|
| **WA015** | Flinders Bay, near Cape Leeuwin, Western Australia | **-34.326°, +115.186°** | Recent | - | Cernohorsky, 1981 |
| **WA016** | Mississippi Bay, 48km east of Esperance, Western Australia | **-33.966°, +122.272°** | Recent | - | Cernohorsky, 1981 |
| **WA017** | Geographe Bay, Western Australia | **-33.625° +115.319°** | Recent | - | Cernohorsky, 1981 |
| **WA018** | Garden Island, Western Australia | **-32.204°, +115.675°** | Recent | - | Cernohorsky, 1981 |
| **WA019** | Fremantle, Western Australia | **-32.056°, +115.746°** | Recent | - | Cernohorsky, 1981 |
| **WA020** | Rottnest Island, Western Australia | **-32.00528°, +115.5125°** | Recent | - | Cernohorsky, 1981 |
| **WA021** | Perth, Western Australia | **-31.952°, +115.859°** | Recent | - | Cernohorsky, 1981 |
| **WA022** | Irwin River, between Thursday Island and Cowaramup Bay, Wester Australia | **-29.259°, +114.920°** | Recent | - | Cernohorsky, 1981 |

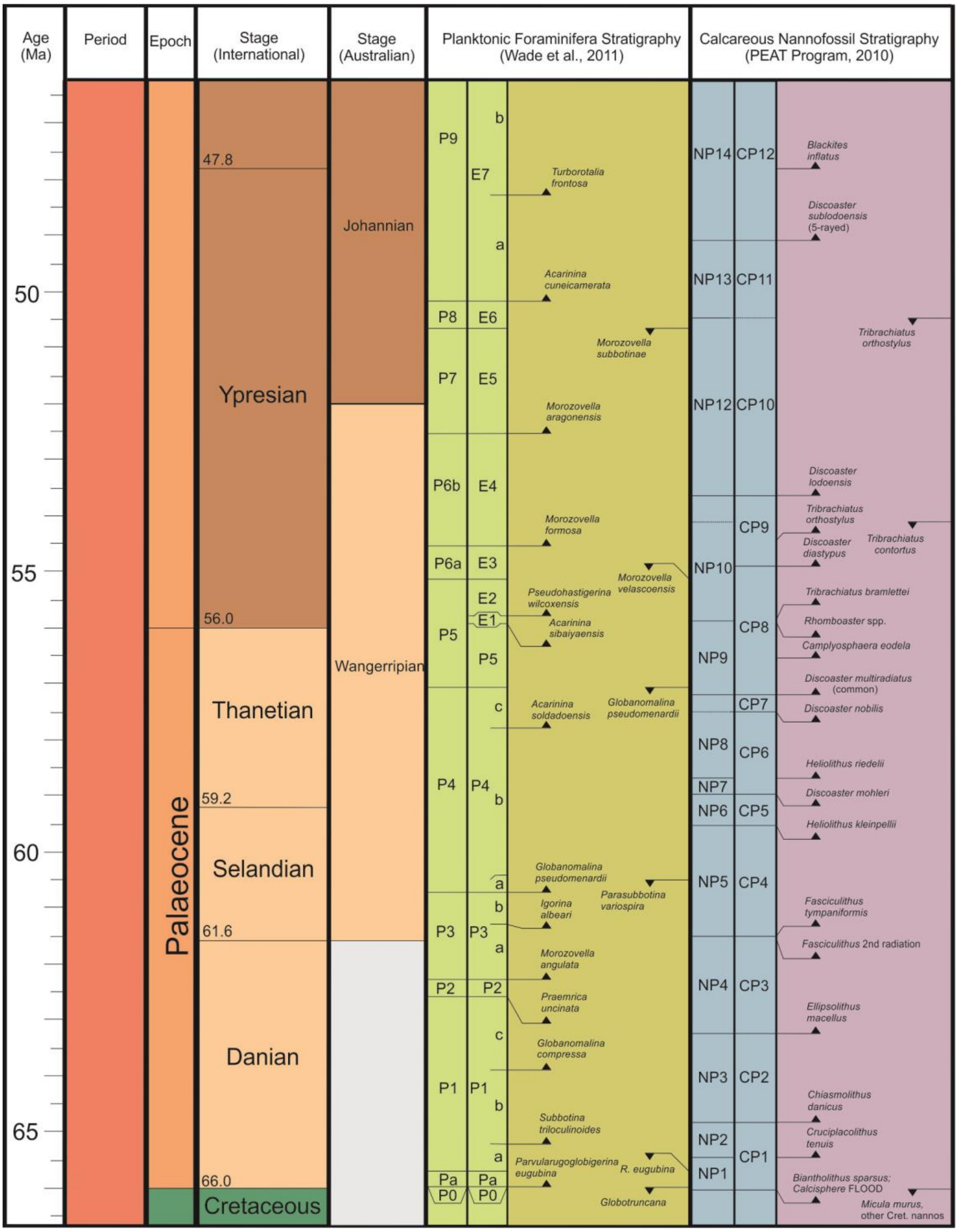
| | | | | | |
|---|---|---|---|---|---|
| **WA023** | Dunsborough, Western Australia | **33.604°, +115.104°** | Recent | - | Cernohorsky, 1981 |
| **WA024** | Eyre Highway, 104km east of Madura, Western Australia | **-31.924193°, +128.078613°** | Formation unknown | | Cernohorsky, 1981 |
| **WA025** | Salt lake, onshore, Rottnest Island, Western Australia | **-32.00528°, +115.5125°** | Formation unknown | Pleistocene | Cernohorsky, 1981 |
| **WA026** | Western Eucla Basin, Western Australia | **-32.069774°, +127.371368°** | Roe Calcarenite | Kalimnan - Yatalan (L. Pliocene) 4.4-2.59Ma | Ludbrook, 1978; Cernohorsky, 1981 |
| **WA027** | Rando's No. 1 Bore, 11 Spring Road, Thornlie, Western Australia | **-28.86145°, +122.9161°** | Ascot Beds | Kalimnan - Yatalan (L. Pliocene E. Pleistocene) .59-1.8Ma | Cernohorsky, 1981 |
| **WA028** | Nullarbor Plain, Western Australian | **-31.149761°, +128.077519°** | Roe Calcarenite | Kalimnan - Yatalan (L. Pliocene) 4.4-2.59Ma | Cernohorsky, 1981 |
| **WA029** | 51km east of Madura, Western Australia | **-31.938178°, +127.556763°** | Roe Calcarenite | Kalimnan - Yatalan (L. Pliocene) 4.4-2.59Ma | Cernohorsky, 1981 |
| **WA030** | 90 miles west of Eucla, Western Australia | **-32.454156°, +126.848145°** | Recent | - | Darragh, 1988 |

| | | | | | |
|---|---|---|---|---|---|
| **WA031** | 78 mile pit, north side of Eyre Highway, 58.5km east of Madura, Western Australia | **-31.798224°, +127.63916°** | Roe Calcarenite | Kalimnan - Yatalan (L. Pliocene) 4.4-2.59Ma | Darragh, 1988 |
| **WA032** | Pit 88km west of Eucla Motel, Eucla, Western Australia | **-31.709476°, +128.012695°** | Roe Calcarenite | Kalimnan - Yatalan (L. Pliocene) 4.4-2.59Ma | Darragh, 1988 |
| **WA033** | Cape Hamelin, Western Australia | **-34.266667°, +115.033333°** | Recent | - | Darragh, 1988 |
| **AUS001** | OLD, NSW, VIC, TAS, SA, WA | | Recent | - | |

# APPENDIX 2 – TIMESCALE (Based on Gradstein et al., 2012)




Age (Ma)
Period
Epoch
Stage (International)
Stage (Australian)
Planktonic Foraminifera Stratigraphy (Wade et al., 2011)
Calcareous Nannofossil Stratigraphy (PEAT Program, 2010)
25
30
35
40
45
Palaeogene
Oligocene
Eocene
23.03
Chattian
28.1
Rupelian
33.9
Priabonian
37.8
Bartonian
41.2
Lutetian
47.8
Longfordian
Janjukian
Willungan
Aldingan
Johannian
P22
P21
P20
P19
P18
P16/ P17
P15
P14
P13
P12
P11
P10
P9
a
O7
O6
O5
O4
O3
O2
O1
E16
E15
E14
E13
E12
E11
E10
E9
E8
b
E7
"Paragloborotalia" kugleri
"Paragloborotalia" pseudokugleri
Paragloborotalia opima
Chiloguembelina cubensis (LCO)
Globigerina angulisuturalis
Turborotalia ampliapertura
Pseudohastigerina naguewichiensis
Hantkenina alabamensis
Globigerinatheka index
Globigerinatheka semiinvoluta
Morozovelloides crassatus
Orbulinoides beckmanni
Orbulinoides beckmanni
Guembelitrioides nuttalli
Globigerinatheka kugleri
Morozovella aragonensis
Guembelitroides nuttalli
NN1
NP25
NP24
NP23
NP22
NP21
NP19-20
NP18
NP17
NP16
NP15
NP14
CP19
CP18
CP17
CP16
CP15
CP14
CP13
CP12
Discoaster druggi
Reticulofenestra bisecta (>10 micron)
Sphenolithus distentus
Sphenolithus ciperoensis
Sphenolithus distentus
Reticulofenestra umbilicus (south high lat.)
Reticulofenestra umbilicus (low-mid lat.)
Coccolithus formosus
Clausicoccus subdistichus (top of acme)
Discoaster saipanensis
Discoaster barbadiensis
Isthmolithus recurvus
Chiasmolithus oamaruensis (common)
Chiasmolithus oamaruensis (rare)
Chiasmolithus grandis
Chiasmolithus solitus
Reticulofenestra umbilicus (>14 ?m)
Nannotetrina fulgens
Reticulofenestra umbilicus
Blackites gladius
Chiasmolithus gigas
Chiasmolithus gigas
Nannotetrina fulgens
Blackites inflatus


Age (Ma)
Period
Epoch
Stage (International)
Stage (Australian)
Planktonic Foraminifera Stratigraphy (Wade et al., 2011)
Calcareous Nannofossil Stratigraphy (PEAT Program, 2010)
50
55
60
65
Palaeocene
Cretaceous
47.8
Ypresian
56.0
Thanetian
59.2
Selandian
61.6
Danian
66.0
Johannian
Wangerripian
P9
E7
b
a
P8
E6
P7
E5
P6b
E4
P6a
E3
E2
E1
P5
P5
P4
P4
c
b
a
P3
P3
b
a
P2
P2
P1
P1
c
b
a
Pa
Pa
P0
P0
Turborotalia frontosa
Acarinina cuneicamerata
Morozovella subbotinae
Morozovella aragonensis
Morozovella formosa
Morozovella velascoensis
Pseudohastigerina wilcoxensis
Acarinina sibaiyaensis
Acarinina soldadoensis
Globanomalina pseudomenardii
Globanomalina pseudomenardii
Parasubbotina variospira
Igorina albeari
Morozovella angulata
Praemrica uncinata
Globanomalina compressa
Subbotina triloculinoides
Parvularugoglobigerina eugubina
R. eugubina
Globotruncana
NP14
CP12
NP13
CP11
NP12
CP10
CP9
NP10
CP8
NP9
CP7
NP8
CP6
NP7
NP6
CP5
NP5
CP4
NP4
CP3
NP3
CP2
NP2
CP1
NP1
Blackites inflatus
Discoaster sublodoensis (5-rayed)
Tribrachiatus orthostylus
Discoaster lodoensis
Tribrachiatus orthostylus
Discoaster diastypus
Tribrachiatus contortus
Tribrachiatus bramlettei
Rhomboaster spp.
Camplyosphaera eodela
Discoaster multiradiatus (common)
Discoaster nobilis
Heliolithus riedelii
Discoaster mohleri
Heliolithus kleinpellii
Fasciculithus tympaniformis
Fasciculithus 2nd radiation
Ellipsolithus macellus
Chiasmolithus danicus
Cruciplacolithus tenuis
Biantholithus sparsus; Calcisphere FLOOD
Micula murus, other Cret. nannos

# APPENDIX 3 – SPECIES DATA

| SPECIES | D | VOL | D/VOL | LARVAL MODE | SPECIES DURATION (MYRS) | NO. OF LOCALITIES | GEOGRAPHIC RANGE (KM) |
|---|---|---|---|---|---|---|---|
| *Athleta (Ternivoluta) antiscalaris antispinosa* | 1.97 | 1.50 | 1.31 | DD | 19 | 7 | 740 |
| *Athleta (Ternivoluta) subcrenulifera* | 1.55 | 1.50 | 1.03 | DD | 6 | 2 | 1 |
| *Athleta (Ternivoluta) antiscalaris antiscalaris* | 1.70 | 1.50 | 1.13 | DD | 17 | 19 | 666 |
| *Athleta (Ternivoluta) wangerrip* | 1.05 | 3.00 | 0.35 | P | 7 | 1 | 1 |
| *Athleta (Ternivoluta) curvicostata* | 1.58 | 1.50 | 1.05 | DD | 3.5 | 2 | 32 |
| *Athleta (Ternivoluta) anticingulata craticula* | 1.68 | 1.50 | 1.12 | DD | 9 | 3 | 284 |
| *Athleta (Ternivoluta) antiscalaris levior* | 2.06 | 1.50 | 1.37 | DD | 17 | 18 | 277 |
| *Athleta (Ternivoluta) anticingulata anticingulata* | 1.68 | 1.50 | 1.12 | DD | 4 | 6 | 331 |
| *Athleta (Ternivoluta) bungae* | 1.90 | 1.50 | 1.27 | DD | 1.5 | 6 | 5 |
| *Lyria semiacuticostata* | 1.07 | 2.50 | 0.43 | P | 17 | 2 | 359 |
| *Lyria acuticostulata* | 1.47 | 1.50 | 0.98 | L | 17 | 12 | 277 |
| *Lyria harpularia* | 2.68 | 1.50 | 1.79 | DD | 17 | 8 | 277 |
| *Lyria gemmata* | 2.11 | 1.50 | 1.41 | DD | 12 | 2 | 52 |
| *Leptoscapha crassilabrum* | 1.05 | 1.50 | 0.70 | L | 25 | 4 | 805 |
| *Scaphella (Aurinia) johannae* | 4.62 | 1.50 | 3.08 | DD | 3 | 1 | 1 |
| *Amoria undulata undulata* | 5.34 | 3.25 | 1.64 | DD | 10 | 19 | 4000 |
| *Amoria costellifera* | 6.39 | 3.25 | 1.97 | DD | 17 | 8 | 666 |
| *Amoria undulata masoni* | 4.64 | 3.25 | 1.43 | DD | 12 | 3 | 52 |
| *Nannamoria ralphi* | 3.64 | 3.25 | 1.12 | DD | 17 | 3 | 256 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Nannamoria fasciculata* | 2.90 | 3.00 | 0.97 | DD | 6 | 3 | 1 |
| *Nannamoria stolida* | 2.78 | 3.00 | 0.93 | DD | 0.9 | 1 | 1 |
| *Nannamoria weldii* | 2.98 | 3.00 | 0.99 | DD | 11 | 4 | 334 |
| *Nannamoria deplexa* | 2.64 | 3.00 | 0.88 | DD | 17 | 9 | 276 |
| *Nannamoria limbata* | 2.93 | 3.00 | 0.98 | DD | 17 | 9 | 282 |
| *Nannamoria cinctuta* | 3.11 | 3.00 | 1.04 | DD | 1 | 1 | 1 |
| *Nannamoria paraboloides* | 2.84 | 3.00 | 0.95 | DD | 13.5 | 8 | 539 |
| *Nannamoria amplexa* | 3.05 | 3.25 | 0.94 | DD | 1.5 | 4 | 65 |
| *Nannamoria trionyma* | 2.96 | 3.00 | 0.99 | DD | 17 | 5 | 666 |
| *Nannamoria strophodon strophodon* | 2.98 | 3.00 | 0.99 | DD | 22.41 | 30 | 682 |
| *Notovoluta saginata* | 6.41 | 3.25 | 1.97 | DD | 2.9 | 2 | 1 |
| *Notovoluta pseudolirata* | 4.92 | 2.25 | 2.19 | DD | 25 | 14 | 2760 |
| *Notovoluta tabulate* | 2.83 | 1.50 | 1.89 | DD | 0.7 | 2 | 120 |
| *Notovoluta differta* | 4.46 | 2.00 | 2.23 | DD | 17 | 4 | 131 |
| *Notovoluta cathedralis* | 3.45 | 2.50 | 1.38 | DD | 17 | 3 | 653 |
| *Notovoluta linigera* | 3.53 | 2.00 | 1.77 | DD | 9 | 3 | 87 |
| *Notovoluta variculifera* | 2.84 | 2.75 | 1.03 | DD | 7 | 2 | 13 |
| *Notovoluta ellipsoidea* | 5.30 | 3.00 | 1.77 | DD | 20.41 | 3 | 587 |
| *Notovoluta capitonica* | 3.43 | 3.00 | 1.14 | DD | 4.5 | 2 | 586 |
| *Notovoluta lintea* | 2.93 | 2.50 | 1.17 | DD | 0.5 | 1 | 1 |
| *Alcithoe (Alcithoe) macrocephala* | 6.02 | 2.50 | 2.41 | DD | 10 | 2 | 467 |
| *Alcithoe (Alcithoe) orphanata* | 5.42 | 1.50 | 3.61 | DD | 1 | 2 | 19 |
| *Alcithoe (Waihaoia) sarissa* | 3.75 | 2.00 | 1.88 | DD | 17 | 17 | 666 |
| *Alcithoe (Waihaoia) cribrosa* | 3.70 | 2.00 | 1.85 | DD | 7 | 3 | 600 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Alcithoe (Waihaoia) pagodoides pagodoides* | 2.44 | 1.50 | 1.63 | DD | 15.5 | 8 | 718 |
| *Alcithoe (Waihaoia) pagodoides sorcula* | 2.58 | 1.50 | 1.72 | DD | 2 | 2 | 47 |
| *Alcithoe (Waihaoia) neglectoides* | 2.54 | 1.50 | 1.69 | DD | 2 | 1 | 1 |
| *Alcithoe (Waihaoia) pueblensis* | 2.49 | 2.50 | 1.00 | DD | 2 | 1 | 1 |
| *Alcithoe (Waihaoia) tateana* | 3.28 | 2.00 | 1.64 | DD | 2.9 | 2 | 1 |
| *Ericusa fulgetroides* | 4.94 | 2.50 | 1.98 | DD | 2 | 2 | 2 |
| *Ericusa sowerbyi sowerbyi* | 3.36 | 1.50 | 2.24 | DD | 6 | 11 | 1525 |
| *Ericusa sowerbyi pellita* | 5.64 | 2.00 | 2.82 | DD | 17 | 9 | 113 |
| *Ericusa macroptera* | 6.08 | 2.00 | 3.04 | DD | 2 | 1 | 1 |
| *Ericusa atkinsoni* | 5.72 | 2.00 | 2.86 | DD | 11 | 7 | 961 |
| *Ericusa ancilloides* | 6.96 | 2.00 | 3.48 | DD | 17 | 15 | 931 |
| *Ericusa hamiltonensis* | 5.04 | 1.75 | 2.88 | DD | 17 | 4 | 277 |
| *Livonia mortoni connudata* | 7.44 | 1.70 | 4.38 | DD | 17 | 2 | 281 |
| *Livonia mortoni mortoni* | 6.54 | 1.50 | 4.36 | DD | 2.9 | 2 | 1 |
| *Livonia voluminosa* | 5.20 | 2.00 | 2.60 | DD | 2.9 | 2 | 1 |
| *Livonia gatliffi* | 9.26 | 1.50 | 6.17 | DD | 4 | 1 | 1 |
| *Livonia stephensi* | 9.08 | 2.00 | 4.54 | DD | 2 | 2 | 314 |
| *Livonia spenceri* | 5.27 | 2.00 | 2.64 | DD | 17 | 6 | 308 |
| *Livonia heptagonalis* | 13.87 | 1.50 | 9.25 | DD | 0.5 | 1 | 1 |
| *Livonia hannafordi* | 9.08 | 2.00 | 4.54 | DD | 17 | 14 | 277 |
| *Notopeplum mccoyi mccoyi* | 2.05 | 1.50 | 1.37 | DD | 2.9 | 2 | 1 |
| *Notopeplum mccoyi translucidum* | 2.70 | 1.50 | 1.80 | DD | 25 | 20 | 1766 |
| *Notopeplum primarugatum* | 3.64 | 2.50 | 1.46 | DD | 3.5 | 1 | 1 |
| *Notopeplum protorhysum* | 3.95 | 2.50 | 1.58 | DD | 4.5 | 4 | 586 |
| *Notopeplum politum* | 4.96 | 2.80 | 1.77 | DD | 4 | 1 | 1 |

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|---|---|---|---|---|---|---|---|
| *Cymbiola macdonaldi* | 1.45 | 3.00 | 0.48 | P | 17 | 5 | 277 |
| *Nassarius (Niotha) sublirellus* | 0.96 | 3.00 | 0.32 | P | 2 | 2 | 2 |
| *Nassarius (Niotha) crassigranosus* | 0.68 | 2.50 | 0.27 | P | 2 | 4 | 255 |
| *Nassarius (Zeuxis) spiraliscabrus* | 1.01 | 3.50 | 0.29 | P | 2.6 | 5 | 2272 |
| *Nassarius (Zeuxis) Pyrrhus* | 0.88 | 3.00 | 0.29 | P | 5.5 | 82 | 2991 |
| *Nassarius (Zeuxis) subcopiosus* | 0.98 | 3.00 | 0.33 | P | 1.81 | 2 | 1085 |
| *Nassarius (Plicarcularia) burchardi* | 0.77 | 3.00 | 0.26 | P | 5.5 | 82 | 3426 |
| *Nassarius (Hima) tatei tatei* | 1.06 | 3.50 | 0.30 | P | 22.6 | 14 | 1735 |
| *Daphnella cuspidatus* | 0.89 | 4.00 | 0.22 | P | 17 | 2 | 42 |
| *Teleochilus gracillima* | 1.88 | 1.20 | 1.57 | DD | 2.9 | 2 | 1 |
| *Tomopleura dilectoides* | 0.57 | 3.00 | 0.19 | P | 1.5 | 3 | 623 |
| *Cryptocordieria variabilis* | 1.42 | 1.80 | 0.79 | L | 3 | 3 | 1 |
| *Borsonia balteata* | 0.66 | 1.50 | 0.44 | L | 17 | 2 | 19 |
| *Borsonia Torquayensis* | 0.81 | 1.50 | 0.54 | L | 2 | 1 | 1 |
| *Borsonia tatei* | 0.95 | 1.60 | 0.59 | L | 22 | 3 | 94 |
| *Borsonia protensa* | 0.68 | 1.50 | 0.45 | L | 3.5 | 1 | 1 |
| *Borsonia otwayensis* | 0.70 | 1.50 | 0.47 | L | 3.5 | 1 | 1 |
| *Borsonia polycesta* | 0.67 | 1.50 | 0.45 | L | 3.5 | 1 | 1 |
| *Zemacies procerior* | 1.20 | 4.00 | 0.30 | P | 5 | 1 | 1 |
| *Microdrillia steiroides* | 0.64 | 4.10 | 0.16 | P | 17 | 4 | 277 |
| *Bathytoma rhomboidalis* | 1.46 | 1.75 | 0.83 | L | 17 | 4 | 666 |
| *Bathytoma fontinalis* | 1.02 | 1.50 | 0.68 | L | 14 | 3 | 219 |
| *Bathytoma decomposita* | 1.48 | 1.50 | 0.99 | L | 17 | 6 | 173 |
| *Bathytoma pritchardi* | 1.17 | 1.50 | 0.78 | L | 1.5 | 1 | 1 |
| *Antiguraleus incises* | 0.87 | 1.75 | 0.50 | L | 1.81 | 1 | 1 |

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|---|---|---|---|---|---|---|---|
| *Guraleus eocenicus* | 0.93 | 3.50 | 0.27 | P | 7 | 4 | 600 |
| *Guraleus adelaidensis* | 0.74 | 3.00 | 0.25 | P | 1.81 | 1 | 1 |
| *Guraleus volutiformis* | 0.72 | 3.00 | 0.24 | P | 4 | 2 | 255 |
| *Guraleus subnitidus* | 0.49 | 2.20 | 0.22 | P | 1.81 | 2 | 9 |
| *Macteola eocenica* | 0.62 | 1.50 | 0.41 | L | 3 | 2 | 1 |
| *Gemmula gellibrandensis* | 0.97 | 2.00 | 0.49 | L | 6.5 | 1 | 1 |
| *Gemmula (Clavogemmula) prima* | 1.25 | 5.00 | 0.25 | P | 3 | 1 | 1 |
| *Lophiotoma murrayana* | 1.26 | 2.30 | 0.55 | L | 0.5 | 1 | 1 |
| *Lophiotoma murndaliana* | 1.42 | 2.00 | 0.71 | L | 17 | 2 | 255 |
| *Turris septemliratus* | 1.09 | 1.50 | 0.73 | L | 17 | 3 | 256 |
| *Optoturris optatus* | 1.12 | 2.00 | 0.56 | L | 17 | 2 | 277 |