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Systematics, phylogeny and biogeography of the larger camaenid land snails of eastern Queensland rainforests (Pulmonata: Stylommatophora: Camaenidae)

Thesis submitted by
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for the degree of Doctor of Philosophy
in the Department of Zoology
at James Cook University of North Queensland

"...pulmonate land snails with their small populations, sedentary habits, and their rapid adaptive response to selective pressures of environment and predators, are unexcelled among metazoa as material for evolutionary investigation."

Gould (1969: 412)

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31. 1. '96

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Long evenings at the computer and drafting table and in mosquito-infested rainforests were enlivened by the fantastic cooking of James True. Thanks for the extra 6kg, pal.

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Most of all, I hope I will never again hear the words - "Have you handed in yet?".

ABSTRACT

Phylogenetic relationships of Camaenidae, a diverse family of pulmonate land snails with a disjunct distribution in Australasia and Central America, were investigated using a cladistic analysis of the superfamily Helicoidea. The analysis was based on anatomical characters from a previous study by Tillier (1989). Monophyly of the family was examined by splitting Camaenidae into two geographical groups (American and Australasian). Successive weighting generated a single most parsimonious cladogram, which suggested that the Camaenidae is a polyphyletic taxon. Evidence from this analysis demonstrated that the American component of the Camaenidae is closely related to the Helicidae (a European family) and Helminthoglyptidae (a North American family), and the Australasian component is sister group to the Bradybaenidae (principally of eastern and south-eastern Asia).

The phylogenetic relationships and worldwide distribution of Helicoidea were used to examine current palaeogeographical hypotheses using cladistic biogeographic methods. The pattern of vicariance for the Helicoidea indicated that families originated with the break up of eastern Gondwana and Laurasia between the late Mesozoic and mid-Tertiary, and possible vicariance events were identified. It was proposed that Asian terranes, located between India and Australia, maintained contact with northern Australia until the late Cretaceous, which is later than is suggested in current palaeogeographical hypotheses.

Over 400 species of Camaenidae have been recorded from Australia, of which approximately 14% have been described from the rainforests of the north-east. The larger camaenids of eastern Queensland and New South Wales rainforests belong to the hadroid camaenids, a monophyletic group within the subfamily Camaeninae defined by the possession of a well-developed eversible headwart. Histological investigations suggested that the eversible headwart of the hadroid camaenids was homologous to the permanently-everted headwart of the Bradybaenidae, sister group to the Australasian Camaenidae. Epithelial cells of the camaenid headwart were columnar and similar in size to those of the

surrounding integument, in contrast to the much thicker epithelium of the bradybaenid headwart. Subepithelial glands in the camaenid headwart were less diverse and less abundant than those in the surrounding integument, suggesting that mucous secretion was not an important function of the headwart. Reduction in amount of pigment under the headwart, together with the siting of the headwart over the cerebral ganglion, may indicate a role in determining photoperiod.

The genera and species of hadroid camaenids from eastern Queensland rainforests were revised in this study, using conchological and reproductive tract characters. Genera recognised within this clade were *Hadra* Albers, *Thersites* Pfeiffer, *Sphaerospira* Mörch, *Varohadra* Iredale, *Zyghelix* Iredale, *Bentosites* Iredale and *Temporena* Iredale and two new genera from mid-east Queensland. Thirty-one species belonging to these nine genera were recognised, including three new species.

Phylogenetic relationships of the hadroid camaenids were determined by cladistic analysis based on anatomical and conchological characters. The New South Wales genus *Meridolum* was identified as the most primitive, while the red-bodied snails (*Bentosites*, *Temporena* and *Gen. nov.* A) were determined to be the most advanced. *Meridolum* and non-hadroid Camaeninae inhabit open woodland, so the evolutionary trend within the hadroids may involve adaptations towards occupation of a more mesic and stable habitat (rainforest).

Reproductive structures which demonstrated the greatest morphological variation within the hadroid camaenids were those of the distal male reproductive tract. These changes were restricted to the epiphallus and penis, both of which are directly involved in copulation. Variation in distal male genitalia was species-specific, but this was not attributable to reproductive character displacement, as there were no differences between the degree of divergence of genitalia in allopatric and sympatric pairs. Female choice might be regarded as the cause of divergence, but evidence in support of this hypothesis is inconclusive.

The biogeography of the hadroid camaenids was examined by cladistic analysis. Distributions of species of hadroid camaenids indicated that eastern Queensland was divided into 41 biogeographical areas, suggesting that continuity in rainforest blocks (e.g.

Wet Tropics) is a secondary phenomenon, the result of re-adjustment of rainforest ranges following vicariance events. Cladistic analysis generated biogeographical hypotheses for Cape York Peninsula and the Wet Tropics, north-east and mid-east Queensland, Bowen and the Whitsunday Group, and south-east Queensland. Results supported the conclusions of Joseph, Moritz and Hugall (1993) about relationships between north-east, mid-east and south-east Queensland. The effect of Tertiary and Quaternary climate changes and the role of aridity, marine transgressions and increased rainfall in fragmenting ancestral rainforests were discussed. Rises in sea level and pluvial inundation were regarded as creating significant barriers for land snails and other taxa.

Principal conclusions of this study are: Camaenidae is a polyphyletic family, which can be separated into American and Australasian components; Bradybaenidae is sister group to the Australasian Camaenidae; Australasian Camaenidae has a Gondwanan origin; South-east Asian terranes rifted from Australia later than current palaeogeographical hypotheses predict; headwart of Australasian Camaenidae is homologous to the bradybaenid headwart; camaenid headwart may not secrete pheromones, but may be important in determining day-length; hadroid camaenids form a coherent group, the phylogeny of which can be represented by cladistic analysis of conchological and anatomical data; eastern Queensland is composed of at least 41 distinct biogeographical areas; the sequence of vicariance events in eastern Queensland may be determined by cladistic analysis of hadroid camaenid genera; major biogeographic barriers may be the result of marine transgressions or pluvial inundation; species-specific genital morphology is not the result of reproductive character displacement; and multiple mating may result in spermatophore displacement.

CONTENTS

FIGURES

Chapter 1

INTRODUCTION

The Camaenidae

The Camaenidae is a widespread and diverse family of pulmonate land snails. Camaenids are mainly tropical, occurring principally in rainforests in South and Central America, eastern Asia and Australia.

Over 400 species of camaenids have been recorded from Australia (Smith, 1992; Solem, 1992, 1993), of which approximately 14% have been described from the rainforests of the north-east (Fig. 1.1). This diversity and the restricted distribution of many species make camaenids useful in phylogenetic and biogeographic studies.

This study discusses the phylogeny and biogeography of the Camaenidae and the superfamily Helicoidea to which it belongs. It investigates the taxonomic composition of the family in Australia and the phylogenetic relationships of a monophyletic group of Australian rainforest camaenids. It examines their evolutionary patterns and presents a biogeographic hypothesis which may be tested subsequently with other invertebrate groups. It presents an alternative hypothesis to that of Solem (1959) about the origin and structure of the family. It also discusses aspects of the taxonomically-important distal reproductive tract and headwart (Taki, 1935; Solem, 1992).

The definitions of the Camaenidae and the five Australian helicoid families erected by Iredale (1937b, 1938) are the source of some confusion (see below). Iredale (1937a, 1937b, 1938) made no reference to the Camaenidae in Australia, but placed all helicoid genera in new families. His classification is largely ignored by modern workers (e.g. Smith, 1992) even though there has been no revision of the group to confirm or refute the validity of his families. A full revision of the Camaenidae or any of the Australian families was beyond the scope of this study, and all references to the Camaenidae in this study imply the family *sensu* Pilsbry, 1939, including the

Australian forms. Other supra-generic groupings are defined in geographical terms, e.g. American Camaenidae. The family names of Iredale (1937b, 1938) are discussed, but not used. The group under study, which includes *Hadra*, the type genus of the family Hadridae Iredale, 1937, is referred to as the hadroid group. It is given no particular family-group ranking.

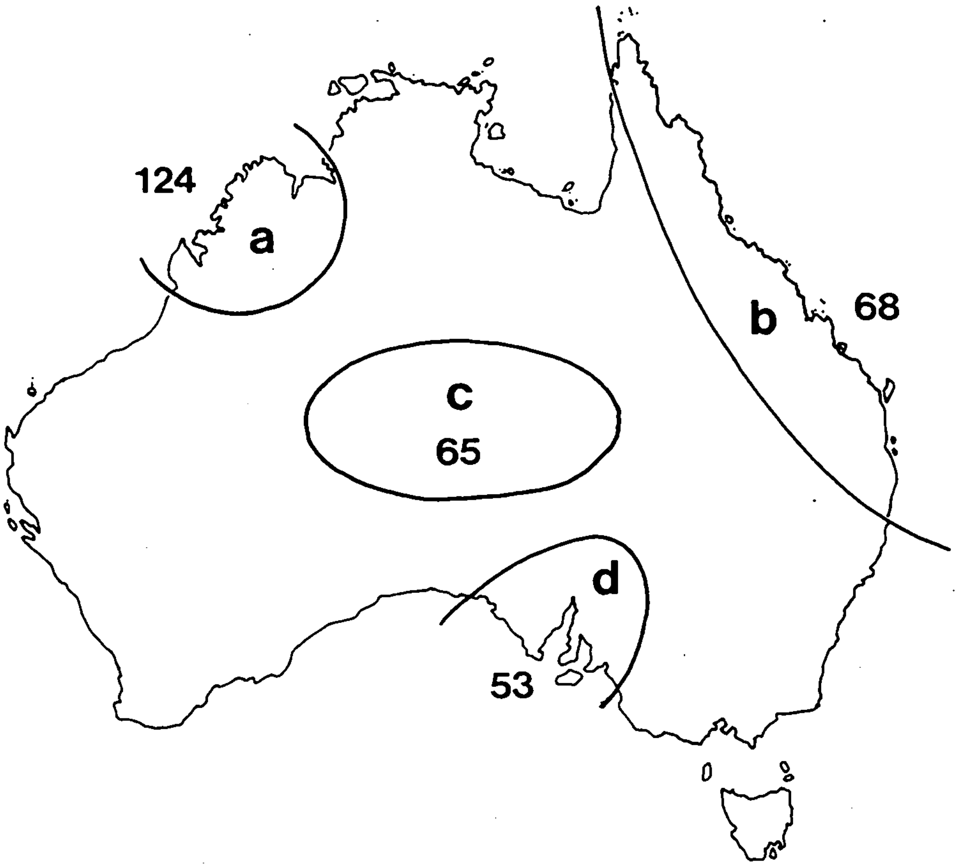


Fig.1.1: Distribution of Camaenidae in Australia, showing areas of greatest diversity: **a** Kimberley and associated ranges (Solem, 1979, 1981a, 1981b, 1984, 1985, 1988, 1989), **b** northern New South Wales to Torres Strait (Smith, 1992; this study), **c** central Australia (Solem, 1993), **d** South Australia, excluding Kangaroo Island (Solem, 1992) (numbers refer to number of described camaenid species in each area)

Systematic position of the Camaenidae

Camaenidae Pilsbry, 1894, is a large family of pulmonate land snails with numerous representatives in central America, eastern Asia, New Guinea and Australia. The family is widespread in tropical areas, and occur in all terrestrial habitats from desert to rainforest.

The family belongs to the superfamily Helicoidea. The arrangement of this superfamily is controversial and confusing as no two classifications agree entirely (Table 1.1). The earliest classification is that of Thiele (1931), who included the Pleurodontidae (= Camaenidae), Fruticolidae (= Bradybaenidae Pilsbry, 1939) and Helicidae Rafinesque, 1815, in the superfamily Helicacea. Zilch (1959-1960) followed this arrangement, adding Helminthoglyptidae Pilsbry, 1939. His definition of the Camaenidae includes the subfamilies Ammonitellinae Pilsbry, 1930, and Oreohelicinae Pilsbry, 1939. The classification of Taylor and Sohl (1962) is essentially the same, but removes the Oreohelicidae from the Camaenidae.

Solem (1978) split the traditional Helicoidea in two and placed the Camaenidae, Oreohelicidae and Ammonitellidae in a separate superfamily, the Camaenacea. His helicoid superfamily contains only the Bradybaenidae, Helminthoglyptidae and Helicidae. Schileyko (1979) included all six families in his superfamily Helicoidea. The classification of Boss (1982) is similar, but the Oreohelicidae is transferred to the Polygyracea, and another family, Helicellidae Wenz, 1923, incorporated. Nordsieck (1985, 1986) divided the superfamily into two: Camaenoidea and Helicoidea. The Camaenoidea contains the Camaenidae and a new family, the Solaropsidae Nordsieck, 1986. The Helicoidea encompasses the Bradybaenidae, Helminthoglyptidae, Helicidae, Hygromiidae Tryon, 1866, Xanthonychidae Crosse and Fischer, 1867, and Sphincterochilidae Zilch, 1959.

The most recent classification, that of Tillier (1989), is also the most radical. Tillier's Helicoidea includes the Camaenidae, Bradybaenidae, Helminthoglyptidae, Helicidae, Vitrinidae Fitzinger, 1833, Helicarionidae Bourguignat, 1888, Polygyridae Pilsbry, 1894, Sagdidae Pilsbry, 1895, and Haplotrematidae Baker, 1925. This arrangement was followed in this study because it is based on new data on the morphology of the nervous, digestive and excretory systems, collected specifically for a revision of the pulmonate land snails. Other classifications, with the exception of that of Nordsieck (1985, 1986), are compiled largely from the literature. Nordsieck's classification (1985, 1986) is based on morphology of the reproductive and excretory organs.

Pilsbry (1939: 411) defined the Camaenidae as `Helices without dart apparatus' in which the `penis [is] continued in an epiphallus and a flagellum (the latter sometimes vestigial or wanting) [and the] spermathecal duct [is] not branched'. This diagnosis includes no characters unique to the family. Delineating a taxon, particularly at suprageneric level, by the absence of characters is not acceptable to current taxonomic practice (Platnick, 1978; Farris, 1979). As a consequence, the Camaenidae, as currently defined, may be polyphyletic, with unrelated taxa lumped together as a result of convergent missing characters, or paraphyletic, where some, but not all, related taxa are grouped together because of the presence of symplesiomorphies (shared ancestral characters or character states) (Hennig, 1966a).

Camaenids are widely thought of as primitive helicoideans because of the absence of a dart apparatus or accessory glands on the terminal genitalia (Solem, 1959, 1992). If this is true, then the absence is plesiomorphic (primitive) and does not provide evidence for camaenid monophyly.

Alternatively this lack means that they may be highly advanced helicoideans, derived from a dart- and gland-bearing ancestor, which have secondarily lost these organs. In this case, the absence is considered to be a synapomorphy (shared derived character or character state), and indicates monophyly. Unfortunately, character absence as a synapomorphy is difficult to prove, unless it is supported by other synapomorphies. Some support was presented by Bishop (1978a) who believed the elongate kidney might be an exclusive feature of the Camaenidae. However, earlier anatomical studies by Wurtz (1955) demonstrate that in the American Camaenidae the ratio of kidney length to width may vary from 2:1 (*Pleurodonte (Eurycratera) jamaicensis* (Gmelin, 1790)) to 12:1 (*Labyrinthus* Beck, 1837, *Caracolus* Montfort, 1810). Further evidence refuting the elongate kidney as unique to the Camaenidae was provided by Tillier (1989), who noted that *Psadara* Miller, 1878 and *Cepolis* Montfort, 1910 (Helminthoglyptidae) both have a kidney longer than that of any other shelled non-orthurethran pulmonate snail.

Two other character states were mentioned by Wurtz (1955) and proposed by Bishop (1978a) as camaenid synapomorphies (derived characters or states unique to a taxon or clade): these were the form of the ovotestis and the disposition of the left parietal and visceral ganglia. Wurtz (1955) was seeking only to distinguish between the Camaenidae and the Oreohelicidae and Ammonitellidae, families which he thought to be closely related. These character states are not unique when the camaenids are compared with all other helicoideans (Tillier, 1989).

The camaenids are thus a loose aggregation of helicoidean species, perhaps the residue left over after species which are easily assignable to other families have been removed. An example of this is provided by *Craterodiscus* McMichael, 1959, a small snail from Hypipamee Crater, north-eastern Queensland. McMichael (1959) described this monotypic genus from a shell, and temporarily assigned it to the Helicarionidae. Solem (1973a) examined the soft parts and removed it to the Camaenidae. His reclassification was a process of elimination - after removing every other possibility, only the Camaenidae remained. However, there are few characters which support the placement, and several which weaken it considerably. The most important of these is the separation of spermiduct and oviduct, a condition found in groups such as the Athoracophoridae (Burton, 1980), Veronicellidae (Oberzeller, 1970), Achatinellidae (Solem, 1972), Endodontidae (Solem, 1976) and Microcystinae (Baker, 1938), but not known in any helicoidean.

It is obvious that a full-scale revision of the family is required. Until that is achieved and at least one family-level synapomorphy is discovered, the classification and definition of the Camaenidae will remain in a state of flux.

Thiele (1931)

- Camaenidae
- (as Pleurodontidae)
- Bradybaenidae
- (as Fruticolidae)
- Helicidae

Zilch (1959-1960)

- Camaenidae
  - Camaeninae
  - Oreohelicinae
- Bradybaenidae
- Helicidae

Taylor & Sohl (1962)

- Camaenidae
- Oreohelicidae
- Bradybaenidae
- Helicidae
- Helminthoglyptidae

Solem (1979)*

- Bradybaenidae
- Helicidae
- Helminthoglyptidae

* Camaenidae placed in superfamily Camaenacea (+ Camaenoidea)

Schileyko (1979)

- Camaenidae
- Ammonitellidae
- Oreohelicidae
- Bradybaenidae
- Helicidae
- Helminthoglyptidae

Boss (1982)

- Camaenidae
- Ammonitellidae
- Bradybaenidae
- Helicidae
- Helminthoglyptidae
- Helicellidae

Nordsieck (1985, 1986)*

- Bradybaenidae
- Helicidae
- Helminthoglyptidae
- Helicellidae
- Hygromiidae
- Xanthonychidae
- Sphincterochilidae

* Camaenidae placed in superfamily Camaenoidea

Tillier (1989)

- Camaenidae
- Bradybaenidae
- Helicidae
- Helminthoglyptidae
- Vitrinidae
- Helicarionidae
- Polygyridae
- Sagdidae
- Haplotrematidae

Table 1.1: Classifications of the superfamily Helicoidea according to Thiele (1931), Zilch (1959-1960), Taylor and Sohl (1962), Solem (1979), Schilyeko (1979), Boss (1982), Nordsieck (1985, 1986), and Tillier (1989).

Recent and fossil distributions

The disjunct distribution of the Camaenidae in central America and Australasia (Fig. 1.2a) is unusual. Explanations have invoked large scale dispersal and extinction (Solem, 1959; Roth, 1988), but these explanations always assume camaenid monophyly.

Fossil records of the Camaenidae are rare. Peake (1978) listed the known fossil occurrences of the family, including two subfamilies, Ammonitellinae and Oreohelicinae, which have now been removed (see above). The oldest record of the Camaenidae *sensu stricto* is in the Palaeocene (56-65 m.y.a.) of North America, while the Oreohelicinae is recorded from the Cretaceous (65-146 m.y.a.). The camaenids became extinct in North America during the Miocene (5-23 m.y.a), while the oldest records of camaenids in South America are Pliocene (2-5 m.y.a), and those of the family in Central America and the Caribbean are Pleistocene (0.01-2 m.y.a.) (Peake, 1978). The Australian fossil record is scanty. *Meracomelon lloydi* McMichael, 1967, is known from late Oligocene - early Miocene deposits at Riversleigh, north-western Queensland (Archer, Hand and Godthelp, 1991). Deep core drilling in Pacific Islands has recovered fossil endodontoids, but no camaenids (Ladd, 1958, 1968; Ladd, Tracey and Gross, 1970; Solem, 1977).

Solem (1959) investigated the disjunct distribution and postulated a North American origin for the family. He proposed dispersal in two directions - southward through the Caribbean and Central America to South America, and eastward through Europe to Asia and Australia - followed by a massive extinction throughout the Holarctic, as an explanation of the present distribution (Fig. 1.2b). The cause of the family's extinction in North America was not suggested, but in Europe it was thought to have been "replaced by advanced helicoids" (Solem, 1959: 322).

Solem (1959: 321) suggested that the Camaenidae arrived in Australia in two invasions from south-east Asia. The first invasion, which included "endemic Australian camaenids" occurred at the start of the Cretaceous. The second, which brought a "Papuan" fauna, including genera such as *Thersites* Pfeiffer, 1855, *Hadra*

Albers, 1860, *Papuina* von Martens, 1860, and *Chloritis* Beck, 1837, was mid-Tertiary.

Modern camaenids are widely distributed in Australia, occurring everywhere except Tasmania (Smith & Kershaw, 1979) and south-west Australia. They are abundant in tropical regions, with a major radiation in the Kimberley region of north-western Australia (Solem, 1979, 1981a, 1981b, 1984, 1985, 1988), and smaller radiations in north-eastern and possibly central Australia. The number of species tends to decrease with increasing latitude, and only one species, *Austrochloritis victoriae*, (Cox, 1868), is recognised from southern Victoria and Bass Strait (Smith & Kershaw, 1979; Smith, 1992). Tropical and subtropical species are abundant in rainforests and deserts, while temperate species may be less common in rainforest, but are widespread in wet and dry sclerophyll (eucalypt) forest. Many tropical and temperate species are strongly saxicoline (Smith, 1992).

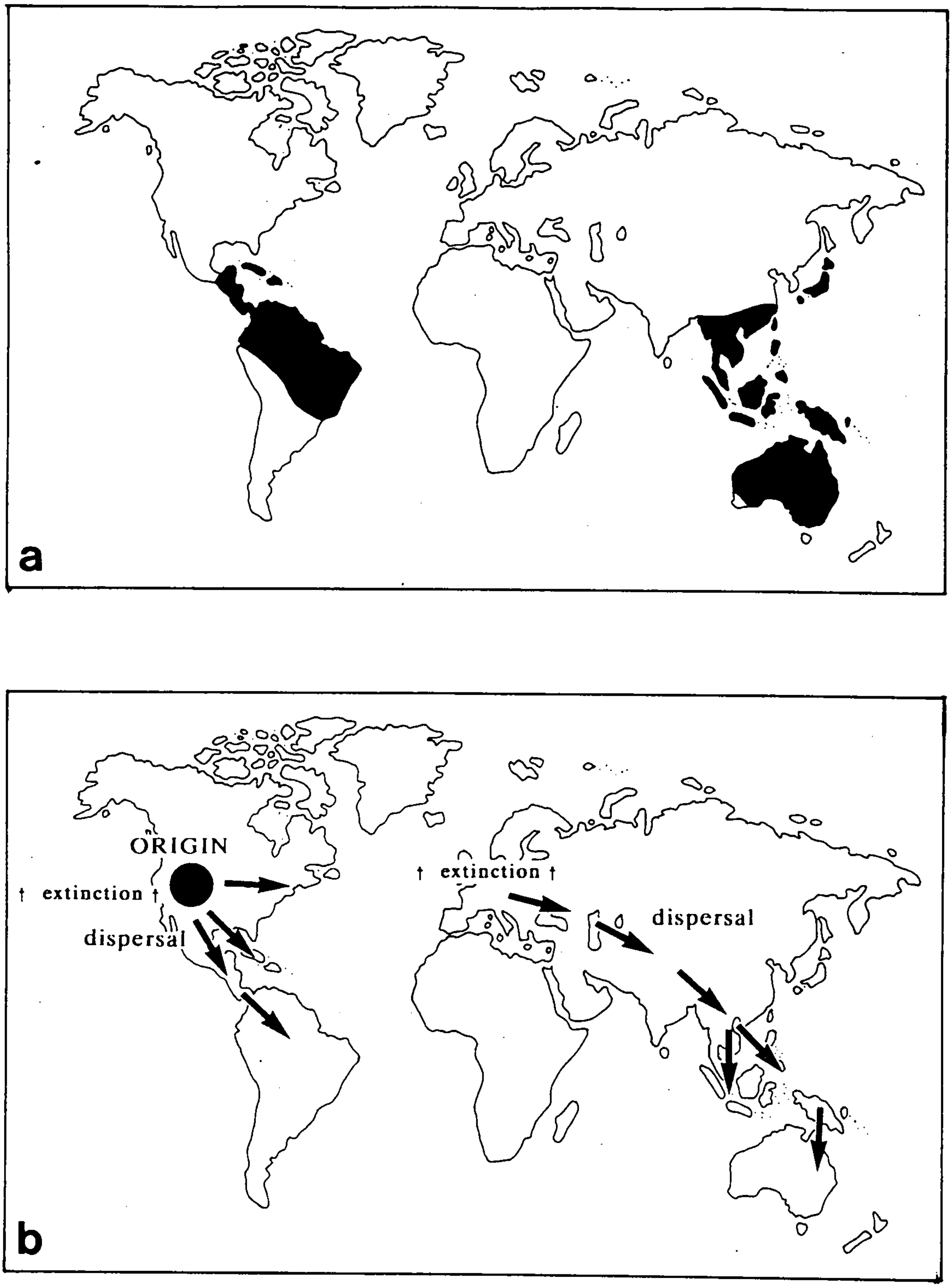


Fig. 1.2: Distribution of Camaenidae: **a**, distribution of Camaenidae *s.l.* (data from Solem, 1992); **b** dispersal hypothesis of Solem (1959).

Classification of the Australian Camaenidae

Cox (1866, 1868) was the earliest author to produce systematic lists of Australian land snails, but the first major taxonomic revision was undertaken by Iredale (1937a, 1937b, 1938), based on decisions made in Iredale's 1933 paper. He recognised that the Helicidae did not occur in Australia and split the large helicoid forms, formerly assigned to *Helix* and its allies, into five families: Hadridae Iredale, 1937, Papuinidae Iredale, 1938, Chloritidae Iredale, 1938, Xanthomelontidae Iredale, 1938, and Rhagadidae Iredale, 1938 (Table 1.2). Shell characters alone were used to construct this classification, with the exception of the Xanthomelontidae, which was also defined by anatomical characters.

Hadridae (type genus *Hadra* Albers, 1860) is by far the largest family, comprising 26 genera and 141 species in eastern and central Australia. It was erected to accommodate the "*Hadra-Sphaerospira-Meridolum* aggregation" (Iredale, 1937b: 19), which was recognised as distinct from *Xanthomelon* and its allies. Twenty-four genera (approximately 92%) were erected by Iredale (1933, 1937b, 1938), but Zilch (1959-1960) listed 23 of these as *incertae cedis*.

The Papuinidae (type genus *Papuina* von Martens, 1860) is a family of arboreal snails confined to tropical and sub-tropical eastern Australia, Solomon Islands, Bismarck Archipelago, Admiralty Islands, Louisiade Archipelago, New Guinea, and the Moluccas (Clench & Turner, 1963). Iredale (1938) listed four genera and 11 species from Australia, and many more from New Guinea (Iredale, 1941). Clench and Turner (1963: 4) agreed that *Papuina* was "a complex assemblage of generic elements and should...be split into as many elements as the data warrant", but were highly critical of Iredale's "poor taxonomy". They rejected the familial status of the Papuinidae, but retained it as a subfamily.

The Chloritidae appear to have been a problematic family for Iredale. The main features of the type genus, *Chloritis* Beck, 1837, are a "hairy shell associated with a pustulate protoconch, flattened spire and wide umbilicus" (Iredale, 1938: 93). *Chloritis* does not occur in Australia, so Iredale included in the Chloritidae not only species which bore a strong resemblance to the type genus, but also a number of those which differed markedly in detail. Thirteen genera and 45 species from northern and eastern Australia are included in this family.

Sixteen genera and 72 species are grouped together in the Xanthomelontidae (type genus *Xanthomelon* von Martens, 1860) on the basis of anatomical characters. Iredale (1938) was cautious about this arrangement, because the family covered disparate shell forms. Xanthomelontid genera are widespread in inland Australia.

Iredale (1938) erected the Rhagadidae (type genus *Rhagada* Albers, 1860) to receive the northern Western Australian genera, which he considered to be more closely related to Indonesian forms than to Australian ones. The Rhagadidae is a small family, containing seven genera and 23 species.

The distributions of Iredale's helicoid families are summarised in Fig. 1.3.

Although Iredale (1937b, 1938) created these families on little or no evidence, the evidence of monophyly of the Camaenidae is equally tenuous. At the start of this study, all Iredale's family-group names were found to be available, as no diagnosis is required to support a family, simply the designation of a type genus (International Commission on Zoological Nomenclature, 1985). However, Smith (1992) revised the Australian non-marine Mollusca, and synonymised Iredale's helicoid families with the Camaenidae.

Solem (1992) investigated the camaenid subfamilies occurring in Australia, and placed *Hadra* in the Camaeninae. Although the Camaenidae may be paraphyletic or even polyphyletic, the Camaeninae appears to be monophyletic. The subfamily is defined by a single anatomical apomorphy: a cephalic organ (Figs. 5.1, 5.2), described by Solem (1992) as an eversible headwart (Taki, 1935). Similar, but permanently-everted, structures occur in members of the Asian family Bradybaenidae (Taki, 1935; Takeda & Tsuruoka, 1979). The Indonesian and Western Australian camaenid *Rhagada* also possesses a non-retractible headwart which resembles that of bradybaenids (Solem, 1985). The presence of this permanently-everted headwart may throw the inclusion of *Rhagada* in the Camaenidae into doubt.

This study investigated a clade of rainforest snails within the Camaeninae. As the clade included *Hadra*, members of the group were referred to collectively as the 'hadroid camaenids'. Much of this project was devoted to a taxonomic revision of members of this clade (Chapter 6), but, before the results of the revision could be published, Smith (1992) published a comprehensive catalogue of the Australian non-marine Mollusca. Taxonomic decisions made by Smith regarding the Camaenidae were based on personal communications from Alan Solem and John Stanisic. Although some decisions coincided with those made in this study, many did not. Data from Smith (1992) and Solem (1992) have been included in this study.

Hadridae

Hadra
Jacksonena
Zyghelix
Spurlingia
Gnarosophia
Temporena
Sphaerospira
Bentosites
Varohadra
Pallidelix
Micardista
Annakelea
Meridolum
Galadistes
Exilibadistes
Chloritobadistes
Ventopelita
Meracomelon
Findomelon
Contramelon
Cupedora
Discomelon
Semotrachia
Dirutrachia
Lacustrelix
Vidumelon

Papuinidae

Rhynchotrochus
Posorites
Rachispeculum
Amimopina

Chloritidae

Austrochloritis
Tolgachloritis
Mussonena
Neveritis
Offachloritis
Obsteugenia
Chloritisanax
Ramogenia
Damochlora
Gloreugenia
Calvigenia
Parglogenia
Kimboraga

Xanthomelontidae

Xanthomelon
Sinumelon
Granulomelon
Basedowena
Pleuroxia
Baccalena
Fatulabia
Glyptorhagada
Divellomelon
Baudinella
Setobaudinia
Cristigibba
Arnemelassa
Torresitrachia
Trozena
Trachiopsis

Rhagadidae

Rhagada
Plectorhagada
Amplirhagada
Parrhagada
Globorhagada
Bellrhagada
Westraltrachia

Table 1.2: Genera of land snails assigned to the families Hadridae, Papuinidae, Chloritidae, Xanthomelontidae and Rhagadidae by Iredale (1937b, 1938).

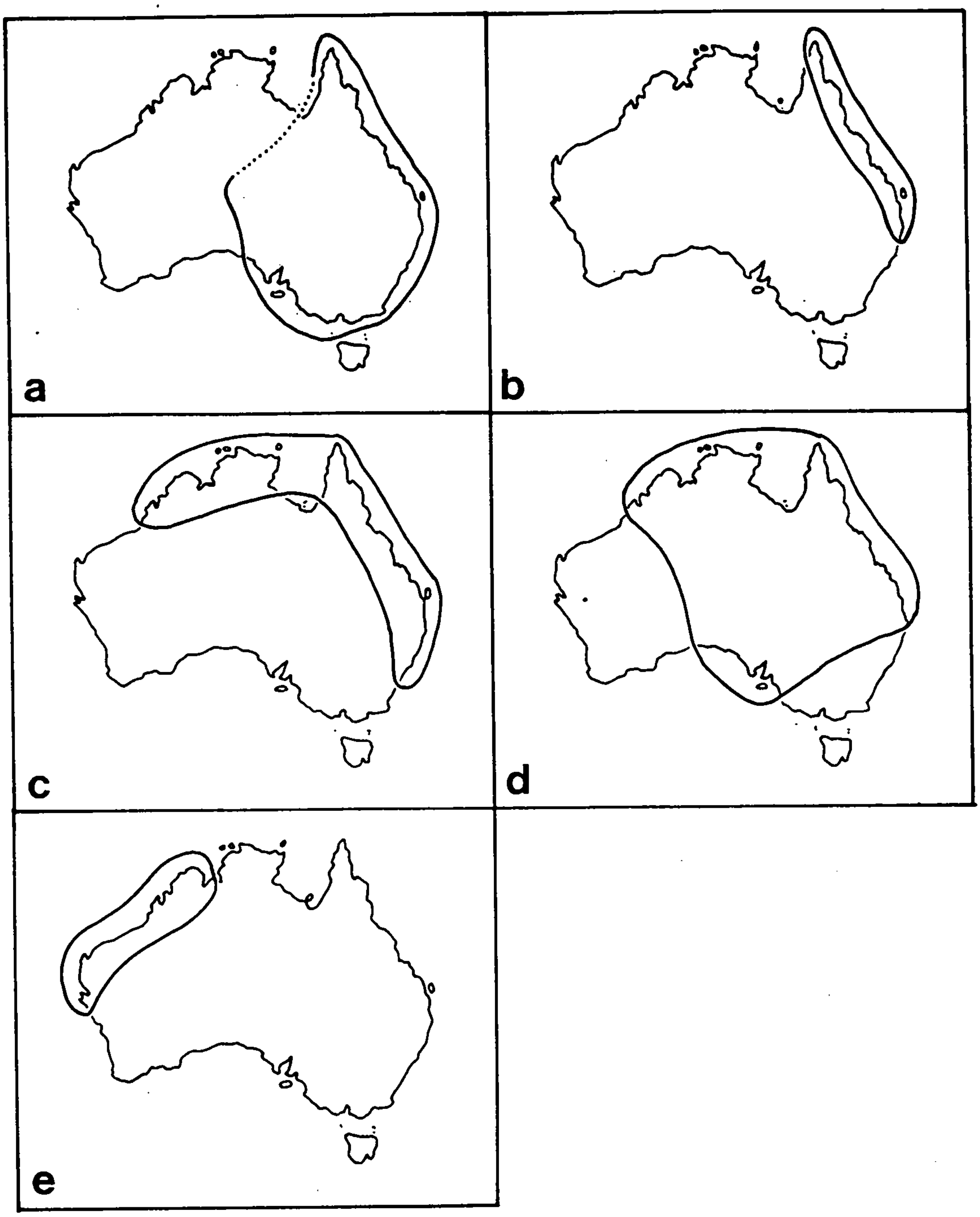


Fig. 1.3: Distribution of helicoid families in Australia (data from Iredale, 1937a, 1938): **a** Hadridae, **b** Papuinidae, **c** Chloritidae, **d** Xanthomelontidae, **e** Rhagadidae.

Aims of this study

The aims of this study were as follows:

1. To investigate the relationships of the helicoidean families by cladistic analysis of the anatomical data of Tillier (1989);

2. To investigate the relationships of the American and Australian Camaenidae, and determine whether the group is monophyletic, paraphyletic or polyphyletic;

3. To hypothesise a sequence of vicariance events leading to the modern distribution of the helicoidean families;

4. To conduct a taxonomic revision of a monophyletic group of Australian rainforest Camaenidae, using new anatomical and conchological data;

5. To investigate the relationships of the genera and species of this group using cladistic analysis of the above data;

6. To hypothesise a sequence of vicariance events leading to the modern distribution of hadroid genera and species (this hypothesis would be available for testing with other groups of terrestrial invertebrates);

7. To examine aspects of taxonomically important anatomical features, namely a) the distal reproductive tract, and b) the headwart.

Chapter 2

LITERATURE REVIEW

Taxonomic, phylogenetic and biogeographic studies of stylommatophoran land snails

Taxa are described, named and classified in the process of taxonomy. Once named, taxa are placed in a hierarchy which ideally reflects lineage (Hennig, 1966; Eldredge & Cracraft, 1980; de Queiroz & Gauthier, 1990, 1992, 1994). Taxonomic revisions which do not consider patterns of descent face the problem of the delineating paraphyletic taxa, obscuring relationships and reducing the information content of the classification system (Nelson, 1971, 1972, 1974; Griffiths, 1974; Donoghue & Cantino, 1988; de Queiroz & Gauthier, 1990, 1992, 1994).

Inextricably bound with the need for a phylogenetic classification is the necessity to define the species taxon adequately. The species taxon is the basic unit of systematic biology, but no single definition of this taxon is universally accepted. Several concepts have been put forward to define the species (e.g. biological species concept, Dobzhansky, 1937; Mayr, 1942, 1963, 1969; recognition species concept, Paterson, 1985; cohesion species concept, Templeton, 1989; phylogenetic species concept, Rosen, 1978, 1979; Nelson & Platnick, 1981; Cracraft, 1983, 1987, 1988; McKitrick & Zink, 1988), but all provoke continuing discussion (e.g. Sokal & Crovello, 1970; Ghiselin, 1974; Scudder, 1974; Cronquist, 1978; van Valen, 1976; Rosen, 1978, 1979; Wiley, 1978, 1981; Eldredge & Cracraft, 1980; Raven, 1980; Nelson & Platnick, 1981; Mishler & Donoghue, 1982; Cracraft, 1983, 1989; Paterson & Macnamara, 1984; Donoghue, 1985; Paterson, 1985; Futuyuma, 1987; de Queiroz & Donoghue, 1988, 1990; Nelson, 1989; Templeton, 1989; Nixon & Wheeler, 1990; Wheeler & Nixon, 1990; Vrana & Wheeler, 1992). Many authors have suggested that there is no single species concept and different ideas are applicable in different situations (e.g. Cain, 1953, 1954; Dobzhansky, 1972; Scudder, 1974; Mishler & Donoghue, 1982), thus taxa labelled as species may not be directly comparable (Davis & Heywood, 1963; Mishler & Donoghue, 1982).

Species concepts

Biological (Isolation) Species Concept

The biological species concept (BSC) (Dobzhansky, 1937; Mayr 1942, 1963, 1969) defines a species by its relationship to other species. Mayr (1942: 120) interpreted biological species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." Later (1982: 273) he added that each species "occupies a specific niche in nature". Biological species are non-dimensional, as time and space are not factors in their existence (Bock, 1979).

Reproductive isolation is achieved through the development of isolating mechanisms which prevent gene flow between species (Dobzhansky, 1937, 1970: Mayr, 1942, 1963, 1970, 1976; Mayr & Provine, 1980). These mechanisms may take the form of pre-mating mechanisms, which prevent mating between individuals of different species, or post-mating mechanisms, which prevent fertilisation or the development of hybrids (Dobzhansky, 1970). Since the BSC of Dobzhansky (1937) and Mayr (1942, 1963, 1969) relies on isolating mechanisms to preserve the integrity of the species, it may also be referred to as the isolation species concept (Paterson, 1985).

Many problems have been identified with the BSC and its dependence on reproductive isolation (e.g. see Sokal & Crovello, 1970; Rosen, 1978, 1979; Mishler & Donoghue, 1982; Cracraft, 1983, 1987, 1988; Donoghue, 1985; Paterson, 1985, 1988; McKitrick & Zink, 1988). For example, although initial differentiation of populations may occur in allopatry, the development of isolating mechanisms depends on closely-related incipient species coming into contact with each other (Fisher, 1930; Dobzhansky, 1940). At the point(s) of contact, pre-mating isolating mechanisms are formed through reproductive character displacement (Butlin, 1987a, 1987b, 1989) and reinforcement (Dobzhansky, 1951). Selection processes thus act against the formation of hybrids through the promotion of assortative mating.

However, closely-related species which remain in allopatry cannot be regarded as species under the BSC as there are no tests of reproductive isolation. Geographical separation does not allow pre-mating isolating mechanisms to form, unless they are the product of `ethological drift', in which aberrant reproductive behaviour becomes established in small populations (Mayr, 1963). A group of allopatric species, each of which may be considered distinct under other species concepts, may be assigned to the category `superspecies' under the BSC (Mayr, 1963).

Parthenogenetic species are also difficult to fit into the BSC (Sonneborn, 1957; Oliver, 1971; Slobodchikoff & Daly, 1971). Each obligate parthenogenetic individual is reproductively isolated from every other individual in the population to which it belongs as well as from individuals in other populations. It can interbreed neither with individuals of its own lineage nor with those of others. An extreme solution would be to refer every parthenogenetic individual to a new species (Endler, 1989). Proponents of the BSC avoid this obstacle by distinguishing between the concept of a species as a basic evolutionary phenomenon (to which parthenogenetic individuals do not belong) and the taxonomic category (which provides a species name for parthenogenetic groups).

Recognition Species Concept

The recognition species concept (RSC) defines species as an inclusive population of biparental organisms sharing a common fertilisation system (Paterson, 1985). It offers an alternative interpretation of the role of isolating mechanisms as governors on gene flow. Instead of these isolating mechanisms ensuring that reproduction (i.e. gene flow) does not occur between species (as they do in the BSC), their role in the RSC is to facilitate reproduction within species. Fertilisation systems involve the basic reproductive sequence of meiosis, gamete formation and fertilisation, but the definition does not extend to zygote development.

The specific-mate recognition system (SMRS) is a fundamental part of the common fertilisation system of any species (Paterson 1978, 1980). A SMRS is made up of one or more signal-response units. Each develops in a series of small steps with modification under natural selection moderated by stabilising selection (Paterson, 1978). Specific-mate recognition systems send, receive and process specific signals between reproductive adults of the same species or their gametes (Paterson, 1982, 1989). Adults may recognise each other through visual, auditory, tactile or olfactory cues and responses (gametes `recognise' each other through chemical signals) (Paterson 1989). Under the RSC mate recognition systems allow individuals to recognise conspecific mates (Paterson, 1980). This differs from Templeton's (1979) interpretation in which these systems *prevent* individuals from recognising non-specific mates.

Speciation under the RSC occurs in allopatry. A new species is formed when the SMRS of a daughter population has diverged far enough from that of the parent population to prevent gene flow between the two populations should individuals of both populations make contact (Paterson, 1980). Speciation may be an incidental result, the product, via pleiotropy, of adaptations of the daughter population to a new niche.

As with the BSC, the RSC is seriously constrained by its inapplicability to parthenogenetic organisms (Scoble, 1985; Vrba, 1985; Templeton, 1987). Paterson (1989) points out that most parthenogenetic eukaryotes have been derived recently from biparental antecedents, often as interspecific hybrids. Parthenogenesis may provide a hybrid with a mode of reproduction which continues its lineage and avoids the problems with gene flow associated with hybridisation (Darlington, 1958). Selection thus acts on hybrids to maintain viability (Paterson, 1978).

Cohesion Species Concept

The Cohesion Species Concept (CSC) is an eclectic concept, combining elements of the BSC and RSC. Cohesion species are defined as "the most inclusive group of organisms having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (Templeton, 1989: 12). Phenotypic variation is thus limited by genetic and environmental mechanisms which control gene flow and niche utilisation (Endler, 1989; Templeton, 1989). Intrinsic cohesion mechanisms are those which promote genetic and demographic exchangeability within a species, maintaining the group as an evolutionary lineage.

Genetic exchangeability involves the propagation of novel genetic variants within a species. If these variants arise within a population, they may be spread through that and other populations via the medium of a common fertilisation system and subsequent developmental system. The idea of common fertilisation systems is derived from the RSC, but has been extended to include those systems by which zygotes develop into reproductive adults. The spread is limited to a species because there is no genetic exchange between species. The CSC thus takes from the BSC the assumption that genetic identity is preserved through reproductive isolation.

Environmental factors regulate demographic exchangeability. Individuals in a species exploit, with varying success, the same niche (Hutchinson, 1965; Templeton, 1989). The fundamental niche of a species is delimited by the range of environmental tolerances imposed upon individuals by their genotypes. The realised niche is usually only part of the fundamental niche because ecological, physiological or geographical factors prevent individuals of a species occupying the whole niche at any point in time. Individuals in a fundamental niche are demographically interchangeable (Templeton, 1989).

Natural selection will fix favourable or neutral mutations in a demographically exchangeable population, as every individual in a population can be regarded as a potential ancestor to future populations. This includes parthenogenetic species, as there are clear patterns of ancestor-descendant relationships (Templeton, 1989).

Phylogenetic Species Concept

The phylogenetic species concept (PSC) does not rely on reproductive or genetic characters to define a species. Phylogenetic species are diagnosed by Eldredge and Cracraft (1980: 92) as groups of individuals "within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind". The PSC thus introduces the dimension of time to the definition of species. A species must have a common ancestor, and all descendants of the ancestor are included within that species. Similarly, all species in a monophyletic clade, such as a genus, demonstrate similar ancestor-descendant lineages. The limits of a phylogenetic species are defined by successive speciation events (Hennig, 1966). A phylogenetic species originates when an ancestral species is split into two by a vicariance event, and persists until it in turn is split and gives rise to two daughter species.

The PSC uses development and differentiation of characters and character states to distinguish species. Cracraft (1989) argues against it being treated as a rejuvenated morphological species concept, as characters used may be any inherent traits, including those of the genome. Reproductive isolation is not of primary importantance in the recognition of phylogenetic species. Although reproductive isolation contributes to the inception of novel characters, the reverse is not always true: the formation of new characters may not affect reproductive behaviour or physiology (Cracraft, 1989). Therefore differentiation is not correlated with reproductive isolation.

Species are recognised by the presence of unique combinations of characters (Nelson & Platnick, 1981), which may not include autapomorphies (Nixon & Wheeler, 1990; Wheeler & Nixon, 1990). There is argument over whether a species should be defined by at least one autapomorphy (Hill & Crane, 1982; de Queiroz & Donoghue, 1988, 1990), but non-convergent character state transformations such as reversals and parallelisms may be treated as autapomorphies or synapomorphies (Brundin, 1976; Platnick, 1979; Saether, 1979; Nixon & Wheeler, 1990). However, these states can only be identified after cladistic analysis as there can be no *a priori* determination of either the direction of evolution (character state polarity) or the primary or secondary origin of an apparently homologous state (Nixon & Wheeler, 1990).

Characters used to diagnose a phylogenetic species may include any or all parts of the phenotype and genotype. Ideally, the diagnostic character(s) should be found in all members of the species, although in practice it may only be detected in a subset (e.g. all adults or all males) (Cracraft, 1989). Reproductive compatibility cannot be used as a diagnostic character, as it can be with the three biological species concepts, as the ability of individuals to interbreed is regarded as a primitive character under the PSC (Rosen, 1979; Vrana & Wheeler, 1992). Parthenogenetic species can be included in the PSC as long as they display a diagnostic combination of characters

The PSC allows allopatric populations to be distinguished as separate species if they show divergence, although they can be treated as a single species if there is no variation between populations (Nixon & Wheeler, 1990).

Applications of species concepts to stylommatophoran snails

No tests of species concepts have been applied to land snails. Large-scale breeding trials, which would establish the validity or otherwise of any of the reproduction-based species concepts (BSC, RSC, CSC) have never been conducted.

Usefulness of distal genitalia in genus and species level taxonomy is held to imply that these characters are important in species recognition (e.g. Solem, 1978b: 65). That is, snails use their distal genitalia to distinguish between conspecific and non-conspecific individuals through a `lock and key' mechanism (e.g. Webb, 1948, 1952, 1959, 1961; Solem, 1978b).

Hybridisation is known in terrestrial pulmonates (e.g. polygyrids, Grimm, 1975, Webb, 1980; *Cerion*, Gould & Woodruff, 1986, 1990, Woodruff, 1989; *Mandarina*, Chiba, 1993; *Partula*, Johnson, Murray & Clarke, 1993), indicating that differing genital morphologies do not necessarily prevent non-conspecific matings. Although this does not affect the use of genitalic characters in taxonomy (*contra* Johnson, Murray & Clarke, 1993), it does cast doubt on the validity of the application of the lock and key hypothesis to land snails.

The phylogenetic species concept regards species as units which may be analysed using cladistic method (Nixon & Wheeler, 1990). Placing species into historical context, as the PSP does, allows the lineages of both taxa and characters to be traced (e.g. Emberton, 1988, 1991; Mordan, 1992).

Characters used in systematic and phylogenetic studies of stylommatophoran land snails

No distinction can be made between characters which are useful in taxonomy and those which are useful in phylogenetic reconstruction. This is obvious if taxonomy reflects phylogeny. The levels at which characters are applicable vary. For example, characters of the excretory system may be useful in distinguishing between lineages, but provide little information at genus level or below.

Taxonomic and phylogenetic studies of land snails have developed since Linnaeus (1758) first classified gastropods according to the shape, colour and sculpture of the shell, placing all land snails into two genera, *Helix* and *Bulla*. Shell characters such as these were used by subsequent workers in the field of conchology for almost a century, until Leidy (1851), Moquin-Tandon (1855), Schmidt (1855) and others started to investigate the anatomy of land snails.

Pilsbry (1893) recognised that physical, physiological and ecological constraints on the production of shells in a terrestrial environment leads to convergence in shell characters in a wide range of taxa. He proposed that systematic studies of land snails should be based on as many characters as possible, to avoid the misleading conclusions which might result from examination of shells alone. Many modern malacologists use several characters (e.g. shell form, radula, male genitalia) to define taxa (e.g. Clench & Turner, 1959, 1962, 1964, 1966, 1968; Solem, 1979, 1981a, 1981b, 1984a, 1985, 1988, 1989a, 1992, 1993; Hill, Johnson & Merrifield, 1983; Mordan & Tillier, 1986; Emberton, 1991).

The following review of taxonomic and phylogenetic characters is not exhaustive, as it is impossible to synthesise the results of over two centuries of scientific investigation in a few pages. It is a commentary on the scope and use of characters in land snail research.

Shells

At least one shell character (number of parts to the shell: 0, 1, 2, 8) is among those characters which are used to divide the phylum Mollusca into classes. The utility of shell characters varies in lower taxonomic levels: members of the subclasses Prosobranchia and Pulmonata may be distinguished by the presence and absence of the operculum respectively, but there have been multiple losses of this structure in the former (Ponder, 1973) and independent development of a pseudo-operculum in the latter (Hubendick, 1945; Solem, Tillier & Mordan, 1984), reducing the universal applicability of this character. The structure of the epiphragm, which is secreted across the aperture of the shell in response to falling humidity, may be diagnostic at the family level but there have been no investigations of its use at lower levels (Solem, 1974, 1985).

New genera and species of snails were once commonly described from single shells or from a few specimens from one population. This led to a proliferation of names based on colour patterns, degree of keeling, size, aperture shape and spire elevation. The problems which may result from this approach are demonstrated by the Caribbean land snail genus *Cerion* Roding, 1798, and the Florida tree snail *Liguus fasciatus* (Müller, 1774). Two hundred `species' of *Cerion* from the northern Bahamas were reduced to two distinct morphotypes when material of all forms was compared directly (Gould & Woodruff, 1978; Woodruff, 1978).

Fifty-eight species, subspecies and races of *Liguus fasciatus* were described from Florida, with further forms recorded from Cuba (Clench, 1946, 1954, 1965; Jones, 1979; Roth & Bogan, 1984). All taxa were based on small samples of shells, and most importance was placed on qualitative characters such as ground colour and overlying pattern. The only quantitative character was size, measured as height and diameter. Pilsbry (1912) and Simpson (1929) recognised three species of *Liguus* in Florida, with many subspecies, while Clench and Fairchild (1939) recognised only *Liguus fasciatus* and three subspecies. Pilsbry (1946) agreed that the only species represented in Florida was *L. fasciatus* but divided it into eight subspecies in three subspecies groups. Investigations using allozyme electrophoresis indicates that genetic divergence within and between populations of *Liguus fasciatus* is very low, suggesting that only one species occurs in Florida (Hillis, Rosenfield & Sanchez, 1987; Hillis, 1989; Hillis, Dixon & Jones, 1991). The variation in pattern of *L. fasciatus* is thought to be the result of partial self-fertilisation within isolated populations (Hillis, Rosenfield & Sanchez, 1987; Hillis, 1989; Hillis, Dixon & Jones, 1991).

Quantitative characters used in species descriptions include standard measurements (e.g. height, diameter) and ratios derived from these (e.g. height/diameter). Gould (1969) used 45 measurements and derived ratios in a factor analysis of fossil and recent *Poecilozonites s.str.* Boettger, 1884 (Gastrodontidae). Emberton (1988) used eight characters in his analysis of the eastern North American Triodopsinae (Polygyridae), including relative spire height, density of surface striae, glossiness of shell and shade of colour.

Many shell characters are qualitative. The sculpture and microsculpture of the protoconch and later whorls can be useful in diagnosis (e.g. Solem, 1979, 1981a, 1992, 1993; Nordsieck, 1976; Coppois & de Vos, 1986; Emberton, 1988; Stanisic, 1990). Shell sculpture and microsculpture are frequently the only clues to identification for archaeologists who use land snails common in Quaternary deposits as indicators of environmental history and human impact. The identification problems are enormous as fossil shells are often nothing more than fragments, lack periostracal sculpture, and may be juvenile or subadult. Preece (1981) illustrated the microsculpture of some Recent European species from several families, showing that the same type is found in congeners, and in some cases is specific. The sculpture of Western Australian *Xanthomelon* (Camaenidae) is diagnostic, even in juvenile shells (Solem, 1979). In *Torresitrachia* Iredale, 1939 (Camaenidae) of northern Australia, which has a strong sculpture of radial ribs, the nature of the microsculpture is important, and varies between species (Solem, 1979).

Shells of some taxa lack detectable sculpture and microsculpture, their surfaces being smooth, except for growth ridges. In others, sculpture is present, but may be of use neither in taxonomy nor in phylogenetic reconstruction. Solem (1981a) found that there are three elements to the sculpture of *Amplirhagada*, but the differences between species are qualitative rather than quantitative, and intraspecific variation is sometimes confusing. Abrasion and acid etching may also distort sculpture, further hindering identification.

Other characters, such as lamellae and plicae (folds of the lip and columella) are also used in identification. They are widespread in many families, and their number and positions are usually consistent within species (e.g. van Benthem Jutting, 1949, 1961; Breure, 1974; Heller, 1976; Gittenberger, 1978; Mordan, 1986; Solem, 1986; Stanisic, 1990). While Nordsieck (1986) thought that most external shell characters have little phylogenetic significance, he believed some internal ones, such as lamellae and plicae, are important. The shell of his hypothetical pulmonate ancestor has a high spire, both basal and parietal lamellae, palatal plicae, and a weak siphonal canal. It resembles the shells of some pulmonate taxa which are widely considered to be primitive, such as Ellobiidae (Basommatophora) and Achatinellidae (Stylommatophora) (Morton, 1955; Solem, 1982). He believed that multiple convergence for these structures was "very improbable" (Nordsieck, 1986: 94). However, Solem (1973b) examined the microsculpture of lamellae and plicae in Pacific Endodontidae and Charopidae, and concluded that not only did these structures evolve independently in the two families, but that they arose several times within the Charopidae. Lamellae and plicae are considered to be adaptations against water loss and predation, which are hazards faced by all pulmonate land snails.

Character state convergences (homoplasy) is so widespread among pulmonates that family level synapomorphies (shared derived character states) are rare (Goodfriend, 1986a; Nordsieck, 1986). Siphonal canals and lamellae may be solutions to problems rather than primitive characters (symplesiomorphies) which have been retained by descendants of a common ancestor.

Convergence in shape and colour also confuse taxonomic and phylogenetic studies. Cain (1982) noted the similarity between *Amphidromus* Albers, 1850 (arboreal camaenids from tropical Asia) and some American Bulimulidae. He found that in Central and South America, where camaenids and bulimulids occur sympatrically, the shells of camaenids are subglobular to depressed. In Asia, however, where bulimulids are absent, some camaenids possess tall rounded shells. He concluded that "convergence...in land snail shells is a highly pervasive and highly organised phenomenon which can be due to nothing else but natural selection, and indicates how closely members of a fauna are limited in respect to one another" (Cain, 1982: 14).

Radula and jaw

Radular characters are often used in land snail taxonomy, but injudicious application may result in the same problems which are associated with shell characters. Radular formulae are often given as part of a species diagnosis, but the number of lateral and marginal teeth may vary between individuals at different locations (Aiken, 1981). Not only is there intraspecific variation in tooth number, but there may also be variation within individuals over time. Adult snails have larger radulae than juveniles, with an associated increase in the number of teeth as well as the number of rows (Verdcourt, 1950).

Cusp position and structure are strongly correlated with diet, leading to convergences in species which exploit similar food sources (Solem, 1973c; Breure & Gittenberger, 1982). The presence or absence of specific cusps, such as the ectocone on the central tooth of some genera of cerastines, may be useful (Mordan, 1992). It is unlikely that loss of cusps in herbivorous species is diet-related, as there is a tendency toward the development of multiple cusps on the teeth of grazers (Solem, 1974). Breure (1978) recorded the position and number of cusps of central, lateral and marginal teeth in South American bulimulids. Many combinations were not unique, but were shared by several species. Variations such as these probably do have a phylogenetic basis, with secondary adaptations imposed by diet.

Radular teeth in many snails have a complicated system of interrow support, in which teeth in adjacent rows are locked together during the feeding stroke of the odontophore (Solem, 1972a). In many species, each tooth possesses a basal plate which is attached to the radular membrane. The tooth points backward at an acute angle to the basal plate, and the interaction between the basal plate of one tooth and the lower edge of the tooth behind it increases the efficiency of the radula in slicing, cutting or rasping food. The configuration of the transverse rows may have some effect on the efficiency of the support mechanism. The angle of each half-row of teeth has been used to distinguish between genera (Watson, 1920; Mordan, 1986, 1992). Solem (1972a) thought that although the pattern of interrow support varies between taxa, it would not be useful in determining phylogenetic affinities.

Mörch (1860) investigated jaw structure, basing a classification on its variation between taxa. Many carnivorous species lack a jaw, and its loss has occurred repeatedly in different lineages. Solem (1978b) felt that as variation in jaw structure is so great, it cannot be used effectively in systematics.

Reproductive tract

Most pulmonates are simultaneous or protandrous hermaphrodites (Tompa, 1984). Fertilisation is internal, and sperm may be exchanged simultaneously during copulation or be transferred from male-acting individuals to female-acting ones. The structure of the reproductive tract is complex as it must not only produce, maintain and convey both ova and autosperm, but also receive and carry allosperm from a mate. This complexity has produced a wide variety of characters which may be used in taxonomic and phylogenetic studies. Accidental contact between gametes is prevented by separation of genital ducts, and the arrangement of these ducts is often used as a taxonomic and phylogenetic character (e.g. Visser, 1977, 1981; Burton, 1980). Problems exist in extending this use to phylogenetic analyses as the arrangement may be influenced by body shape (Burton, 1980).

Ova and sperm are both produced by the single ovotestis, which is composed of numerous alveoli bundled into lobes. The number and shape of lobes are variable between species, but Tompa (1984) considered the form of the gonad not generally useful in taxonomic study. There are some exceptions, and genera of American Camaenidae, for example, can be distinguished by the shape of their alveoli (Wurtz, 1955).

Gametes produced by the ovotestis travel a common route until they reach the uterus (= oviduct of some authors) and prostate. At this point the paths of ova and autosperm diverge and do not reunite. Autosperm pass down the prostate, which, in many taxa, is adjacent or attached to the uterus. The degree of attachment between prostate and uterus may vary within families (Burton, 1980). This variation may be the product either of common descent (Nordsieck, 1985) or of differing reproductive strategies (Tompa, 1984).

Autosperm is packaged into chitinous spermatophores for transfer to the mating partner during copulation (Mann, 1984; Tompa, 1984). Spermatophore walls usually harden within the epiphallus prior to exchange, but in some Polygyridae the sperm mass acquires its final configuration after transfer (Webb, 1974). The form of the spermatophore is determined by the shape and sculpture of the epiphallus and associated caeca and flagella. Spermatophores are strongly divergent, and vary between species (e.g. van Goethem, 1977; Davies, 1979; Henriquez, Ibáñez & Alonso, 1993). However, because of their mode of formation, they can be of no greater taxonomic use than the epiphallus itself. Phylogenetic content of spermatophores may not be great as they are an adaptation to the terrestrial environment and have probably evolved independently many times (Clarke, 1981; Mann, 1984).

Sperm or spermatophores are tranferred via an intromittent organ or penis. In some taxa, such as limacid slugs, exchange of sperm is mutual, simultaneous, and occurs externally (Fischer, 1917; Chace, 1953; Quick, 1960). The sculpture of the penis and the presence or absence of a verge, papilla or other appendages are taxonomically-important (e.g. Laidlaw & Solem, 1961; Breure, 1978, 1979; Gittenberger, 1978; Solem, 1979, 1981a, 1981b, 1984a, 1987, 1988, 1992, 1993; Breure & Eskens, 1981; Cookson, 1982; Emberton, 1988, 1991; Mordan, 1992). Species of *Sonorella* Pilsbry, 1900 (Helminthoglyptidae) are diagnosed by the relative lengths of the verge and penis (e.g. Naranjo-Garcia, 1988), and the proportions of genitalic elements may be significant in other taxa (e.g. Breure, 1979; Burton, 1980; Solem, 1981a, 1981b; Emberton, 1988).

Reproductive character displacement may obscure phylogenetic relationships, but evidence of its existence in land snails is equivocal. Solem (1976, 1979, 1981a, 1981b) recorded changes in the structure of the spermatophore and male and female terminal genitalia in sympatric populations of some endodontoids and camaenids, and regarded this as proof of character displacement. However, Emberton (1988, 1991) examined over 80 species of Polygyridae, and found no support for displacement in genitalic characters.

Allosperm is received by the spermatheca (= bursa copulatrix), vagina or free oviduct (Lind, 1973; Mann, 1984). The spermatheca commonly lies on the female side, connected to the vagina or genital atrium by a duct, but in some species the duct connects to the male side (Solem, 1976; Wiktor, 1979). Length of the spermathecal shaft and shape of the head vary between taxa (e.g. Breure, 1978, 1979; Solem, 1979, 1981a, 1981b, 1984a, 1987, 1988, 1992, 1993; Emberton, 1988, 1991; Mordan, 1992).

Eggs, which have been fertilised by allosperm in the receptaculum seminis or fertilisation pouch, pass down the uterus, where they receive nutritive and protective secretions. Accessory glands may be associated with the uterus, and as these vary in form, they may have taxonomic value (Burton, 1980; Tompa, 1984).

Stimulatory structures are associated with the reproductive tracts of some land snails and slugs. These include the sarcobelum or stimulator in the penis in *Deroceras* Rafinesque, 1820, the hook-shaped atrial stimulator associated with glands in *Milax* Gray, 1855, the penial appendage in some genera of Vitrinidae (e.g. *Vitrinobrachium* Kunkel, 1929, *Semilimax* Agassiz, 1845), and the atrial ligula in *Arion* Férussac, 1819 (Quick, 1960; Kerney & Cameron, 1979; Castillejo, Rodriguez & Outeiro, 1989). The presence of these structures is diagnostic at the genus-level, and the form of the structure is diagnostic at species-level.

Mineralised darts occur in several families (Tompa, 1980). Darts may be used in taxonomy: two closely-related species of European Helicidae, the white-lipped snail *Cepaea hortensis* (Müller, 1774) and the brown-lipped snail *C. nemoralis* (Linné, 1758), can be told apart more readily by the shape of the dart in cross-section than by the colour of the shell lip (Kerney & Cameron, 1979). Darts intermediate in form occur in hybrids between these two species (Lang, 1908). Secondary reduction or loss may occur in some taxa (Watson, 1923; Prieto *et al*, 1993).

Characters of the reproductive tract are readly discernible and static within taxa, and are thus useful and popular in taxonomic and phylogenetic studies.

Sperm ultrastructure

Sperm morphology is useful in phylogenetic reconstructions at family level or above, as sperm characters generally do not vary at lower taxonomic levels (Thompson, 1973; Afzelius, 1983; Selmi, Giusti & Manganelli, 1988; Healy, 1989). Giusti, Manganelli and Selmi (1991) examined monophyly of the superfamily Helicoidea by comparing the sperm morphology of four non-helicoid and eleven helicoid genera. They found variation at family level in the form of the acrosome, paracrosomal body and nucleus, in the relative lengths of the axoneme and glycogen helices, in the sculpture of the glycogen helices, and in the structure of the end of the flagellum. Consistency of characters in helicoid genera suggested that the group was monophyletic.

Excretory system

Gross structures of the excretory system (shape and size of the kidney and the nature of the ureteric tube) have been used in higher-level taxonomic studies. Pilsbry (1900a, 1919, 1948) constructed a ordinal classification of the Stylommatophora based on work by Semper and Simroth (1894), which was extended by Baker (1955, 1965a, 1965b). Stylommatophorans were divided into five groups (Heterurethra, Mesurethra, Orthurethra, Sigmurethra, Tracheopulmonata), according to the disposition of the ureter. This arrangement was criticised by Wächtler (1934) and Thiele (1931), who noted that intermediate states were recognisable. Solem (1974) recognised that this variation may be due to limacisation, and included both the Heterurethra and Tracheopulmonata in the Sigmurethra. Differences between the Mesurethra and Sigmurethra are also not consistent (Tillier, 1989).

Finer scale variation in the descending ureter and the ureteric interramus may be of taxonomic rather than phylogenetic use, as convergences are widespread (Goodfriend, 1986b; Tillier, 1989; Emberton, 1991).

Nervous system

Concentration and subsequent fusion of ganglia in the visceral chain of the pulmonate nervous system are regarded as advanced characters (Bishop, 1978c). Bargmann (1930) identified eight patterns of fusion, ranging from Type I, in which the left and right pleural, left and right parietal, and visceral ganglia are separated by primitively long connectives, to Type VIII, in which the connectives are lost and all five ganglia are fused. This may provides information on character state polarity, as fusion of ganglia is commonly regarded as permanent (Bishop, 1978c; Tillier, 1989). However, there is evidence to suggest that it is reversible (Emberton, 1991) and, furthermore, it is impossible to determine whether fusion has occurred once or several times (Bishop, 1978c).

Morphology of the procerebrum has been used as a phylogenetic character (van Mol, 1967). The procerebrum is linked to the cerebral ganglion by the procerebral connectives. It has been suggested that characters such as the degree of inclusion of the cerebral gland in the procerebrum, the size of procerebral cells, and the arrangement of connectives and nerves are useful in determing patterns of evolution within the Pulmonata (van Mol, 1967).

Chromosomal characters

Pulmonate chromosomes range in number from five pairs in primitive succineids (Butot & Kiauta, 1964) to 44 pairs in athoracophorids (Patterson & Burch, 1978). Patterson and Burch (1978: 186) believed that the highest chromosomal complements are generally found in the `more advanced taxa'. Nordsieck (1987), however, regarded n = 29 as the plesiomorphic state for Helicoidea and related subfamilies, with a decrease in the chromosome number as the apomorphic state.

Differences in chromosome numbers have been used to revise family-level taxa (Butot & Kiata, 1969); however, there is variation within families and even within genera (Burch, 1965; Burch, Patterson & Natarajan, 1966; Butot & Kiata, 1967; Rainer, 1967; Laws, 1971, 1973a, 1973b; Fatterson & Burch, 1978).

Molecular characters

Mitochondrial DNA (mtDNA) and large-ribosomal-RNA (LrRNA) have been used to construct family- and genus-level phylogenies (Emberton *et al*, 1990; Murray, Stine & Johnson, 1991). Highly conserved regions, which exhibit little variability, can be used in higher level taxonomic studies. These regions change slowly, so reflect evolutionary patterns over greater periods of time. Between these conserved regions are sequences which show high variability and thus rapid divergence, and so may be used in lower level taxonomy.

Emberton *et al* (1990) investigated the utility of LrRNA data in resolving stylommatophoran phylogeny. The Stylommatophora were supported by seven nucleotide synapomorphies, families (Polygyridae, Haplotrematidae, Zonitidae) were distinguished by 0-2 transformations, while no differences at all were detected between four species of Polygyridae.

Mitochondrial DNA has been used to determine relationships among species of *Partula* on Moorea and Tahiti (Murray, Stine & Johnson, 1991; Johnson, Murray & Clarke, 1993). Common shell types were shown to be the result of convergence. However, three hypotheses were presented to explain common genotypes, which were widespread: shared genotypes were plesiomorphic, they were the product of selection (Murray, Stine & Johnson, 1991), or the result of hybridisation (Johnson, Murray & Clarke, 1993).

Allozyme electrophoresis

Allozyme electrophoresis is a useful tool in taxonomic and phylogenetic studies (e.g. Avise, 1974). Studies have examined the relationships between populations (e.g. Brussard & McCracken, 1974; Gould *et al*, 1974; Woodruff, 1975; Gould & Woodruff, 1978; Crook, 1981; Hill, Johnson & Merrifield, 1983; Madec, 1991; Kemperman & Degenaars, 1992; Guiller, Madec & Daguzan, 1994) or between taxa (e.g. Woodruff & Solem, 1990).

Hill, Johnson & Merrifield (1983) used allozyme electrophoresis to investigate two forms of the Western Australian bulimulid *Bothriembryon bulla* (Menke, 1843), and demonstrated them to be distinct species. The same technique was applied to sympatric philomycid slugs in North America (Fairbanks, 1986), which were also shown to be distinct.

Phylogenies may be constructed or tested with allozyme data. Woodruff and Solem (1990) examined allozyme variation in a sample of species from the Ningbing Ranges, and found that although variations within genera were small, they were detectable, and so appropriate for phylogenetic studies. Allozyme data have also been used to test phylogenetic hypotheses based on morphological characters (Emberton, 1988, 1991).

Character weighting: are some characters more important than others?

Some characters may reflect phylogeny more accurately than others. In the absence of information about the significance of each character during the course of evolution of a lineage, all characters may be subjected to assumptions of significance (subjective weighting) (Cain, 1959; Cain & Harrison, 1960; Jardine & Sibson, 1971) or treated equally.

Haszprunar (1990) argued that differential weighting is necessary because of the *a priori* assumption of high levels of homoplasy within the Gastropoda. This may be true at class level, but may also become increasingly untrue and less relevant at lower levels, where taxa are composed of smaller numbers of less variable units (the product of nested classifications).

Nordsieck (1990) attempted to introduce objectivity to the process of character weighting. He listed four criteria which should be applied to characters in order to determine whether they should be weighted or not: constancy, complexity, non-adaptivity, and non-tendency to parallel evolution. Employing these criteria, the character states which should be most heavily weighted are those which occur frequently, form part of a complex structure, are not obviously adaptive, and which do not occur frequently in different groups. Conversely, little or no weighting should be applied to plesiomorphic character states.

Emphasis on a single character can be misleading. However, single character may produce an accurate phylogeny if that character has undergone a series of linear transformations. That is, it has become increasingly elaborate in each taxon under investigation, with no reversals (secondary simplifications). Multi-character analyses reduce the potential confusion of single-character studies.

Phylogeny

Cladistic method

The cladistic method is a technique of phylogenetic analysis in which taxa are arranged in a relational tree or cladogram. Recency of common ancestry is the criterion for grouping taxa (Hennig, 1966). Closely-related taxa are grouped into clades on the basis of shared derived characters (synapomorphies) and each clade is monophyletic, that is, contains all descendants of a single ancestor. The cladistic method conflicts with the phenetic method (Colless, 1969; Sneath & Sokal, 1973; Sokal, 1975), in which organisms are arranged in a relational tree according to their overall similarity. This includes character states resulting not only from common ancestry, but also from parallelisms and convergences (homoplasies). Unlike phenetics, cladistics seeks to combine classification with hypotheses about phylogeny (Farris, 1979).

Hennig's methods for inferring phylogenies require that each character is defined by two character states (present/absent) and that the ancestral (plesiomorphous) state is known (Hennig, 1966). Each derived character state provides evidence for monophyly. This is based on two assumptions: that each derived character arises only once, and that no derived character reverts to the ancestral state (reversal). This does not allow for internal inconsistencies in the data, but Hennig (1966) believed that any conflict was the product of missing or misinterpreted data, and that detailed investigation of these characters would resolve that conflict.

Alternative approaches to resolving incompatibility within the data were developed by subsequent workers. As these methods usually produce trees longer than those of Hennig's, all are based on the law of parsimony: the simplest hypothesis is preferred, even though others are possible. Camin and Sokal (1965) introduced parsimony methods to phylogenetic systematics. Camin-Sokal parsimony allows multiple origins for individual derived character states (0 to 1), but no reversals, and also permits more than two states for each character. It is assumed that the ancestral character states are known.

Kluge and Farris (1969) presented a similar method (Wagner method) in which assumptions about ancestral character states are not required. Multiple solutions are found as changes may occur in both directions (0 to 1, 1 to 0). As long as no information about ancestral states is known the tree remains unrooted, but the introduction of such information in the form of an outgroup places the root on the branch leading to the outgroup taxon. Although Kluge and Farris (1969) restricted Wagner parsimony to binary characters, Mickevich (1982) extended its application to characters with more than two discrete states by means of transformation series analysis.

Farris (1977) also developed the method of Dollo parsimony (Le Quesne, 1974). This is based on Dollo's Law: evolution is irreversible, and characters once lost are unlikely to be regained (Crowson, 1970). This method allows only a single origin for a derived character state (usually assumed to be the most complex), but permits multiple losses of that state. Dollo parsimony uses binary data, but can be extended to multistate characters (Felsenstein, 1983).

Polymorphism parsimony was proposed by Throckmorton (1965). He reasoned that homoplasies result from genetic polymorphisms which remain for one or more speciation events. The polymorphism parsimony method (Farris, 1978) allows ancestral and derived character states to exist as polymorphisms for some time, before reverting to either state (01 to 0, 01 to 1). The polymorphic state arises only once for any character (0 to 01), and is always a forward change. Polymorphic reversals (1 to 01) are not permitted.

Camin and Sokal (1965) justified the use of parsimony methods by assuming that evolution proceeds parsimoniously. That is, "*given the goal of reaching the observed species*, evolution has taken the shortest path" (Felsenstein, 1983: 321). This, as Felsenstein (1983) points out, suggests that evolution has a target - the production of a species - which cannot be the case. Parsimony is simply a criterion used in choosing between phylogenetic hypotheses.

Confusion may arise from incorrect assessment of the ancestral state for any character. Where fossil material is lacking, two methods are used to determine character state polarities: ontogenetic analysis (Nelson, 1978) and outgroup analysis (Watrous & Wheeler, 1981).

Ontogenetic analysis requires estimation of the ancestral character states based on the biogenetic law (Haeckelian recapitulation) (Nelson, 1978). Following this law, characters transform from a more general (primitive) to less general (advanced) state. A character state transformation series proceeds from the most general state to the least general or most specialised state (von Baer's second law) (Gould, 1977). Assumptions about character state polarities are based on knowledge of or inferences about development. Ontogenetic method may only be applied where the transformation sequence follows this pattern, and problems arise if the progression runs from least to most general (de Queiroz, 1985).

Outgroup analysis requires knowledge of taxa (outgroup) closely related to those under investigation (ingroup). For any character the state which occurs in an outgroup is generally considered to be plesiomorphic. Inclusion of one or more outgroups in the analysis establishes character state polarities. Apparent contradictions of ancestral character states which may be caused by the application of multiple outgroups can usually be resolved (Maddison *et al*, 1984).

Maddison *et al* (1984) suggested that it is not always necessary to use the sister group as an outgroup, and that the use of more distantly related outgroups will not severely affect the arrangement of the ingroup. Under these circumstances, assessments of ancestral character states may change from certain to equivocal, but can never be shifted completely.

Outgroup analysis was employed in this study, because it is a largely objective method. Ontogenetic method requires a number of assumptions which are currently unsupported.

Phylogenetic analyses of terrestrial pulmonates

Cain (1982: 17) stated that "it is doubtful whether any class of characters is especially valuable in tracing out phylogenies, but secondary sexual characters may be". Unfortunately, "secondary sexual characters" are difficult to define in hermaphroditic land snails, but probably include structures involved with courtship (e.g. bradybaenid headwart, Taki, 1935, Takeda and Tsuruoka, 1979; urocyclid frontal organ, Binder, 1969, 1976) or those that are part of the reproductive tract but are not directly involved in the production of gametes or the transfer or reception of sperm (e.g. dart sac, Ashford, 1883; Tompa, 1980). Reproductive tract morphology has traditionally been used in the construction of land snail phylogenies at the familial and lower levels, while characters of the pallial cavity have been used at the superfamilial and higher levels (Pilsbry, 1900; Baker, 1955; Solem, 1959; Zilch, 1960).

Characters appropriate for use in phylogenetic reconstructions vary with the taxon investigated (see above). Morphology of the proximal reproductive tract (shape of the ovotestis and degree of fusion of the spermoviduct, for example) may be used at family or subfamily level. Gross morphology of the genitalia and presence or absence of accessory structures, such as dart sacs, epiphallic flagella or penial caeca, may be suitable for distinguishing between genera, while the configuration of these elements (length of flagellum, penial sculpture) can be used at species level (Pilsbry, 1893; Solem, 1978b). Emberton (1988) used a transformation series analysis (Mickevich, 1981) based on penial characters to develop a phylogeny for the Triodopsinae, which was then tested with allozyme data.

More diverse characters may be used at higher taxonomic levels. Mordan (1992) analysed ten genera of the Cerastinae, using characters of ureter, reproductive tract, shell, foot and radula.

No cladistic analyses of Australian land snails have been undertaken, apart from that of Stanisic (1990) on subtropical eastern Charopidae and this study on tropical eastern Camaenidae. Stanisic (1990) investigated 50 species of charopids in 17 genera, occurring in the rainforests of southern Queensland and northern New South Wales. The subtropical Charopidae are probably polyphyletic (Stanisic, 1990). This would explain inconsistencies in the cladogram, which shows several species appearing within non-congeneric clades. Stanisic (1990) presented a phenetic hypothesis, showing a triple origin for the subtropical Charopidae. The cladistic and phenetic hypotheses show a number of similarities, but until the techniques of cladistic analysis are applied to a monophyletic group, any cladograms produced will be of limited utility.

Woodruff and Solem (1990: 138) believed that a cladistic analysis of endemic camaenid taxa from the Ningbing Ranges, northern Western Australia, might be impossible, due to the "numerous apparent cases of parallel evolution, convergent evolution, and reversal".

Biogeography

Biogeography is the study of distributions of organisms. It is commonly divided into two fields: ecological biogeography, in which distributions of taxa are related to their habitats, and historical biogeography, in which the phylogenetic histories of taxa are related to the palaeogeographical evolution of the areas in which those taxa occur (Rosen, 1978; Parenti, 1989).

Biogeographic models

The study of historical biogeography is dominated by models of dispersal and vicariance. The dispersal model is the traditional explanation for species distributions (Darwin, 1859; Darlington, 1957, 1959; Briggs, 1970a, 1970b, 1973; Baker, 1978; Morain, 1984; Stehli & Webb, 1985). According to this theory, species arise in, then move out (disperse) from, a centre of origin. The centre of origin for a genus may be identified variously as the area with the largest number of congeneric species, with the most advanced species, or with the most primitive species (Humphries, 1981). In the first case, the number of species attenuates as the observer moves further from the centre of origin. In the second, more advanced species arise in the centre, displacing the primitive species to the edge of the range (Darlington, 1959; Briggs, 1973). Finally, the third definition invokes the progression rule (Hennig, 1966), in which primitive species remain at the centre, while more advanced species migrate to the edges of the range (Hennig, 1966).

Dispersalist models dominated until Croizat (1958) developed a model of vicariance, which he named panbiogeography. Panbiogeography searches for congruent patterns (tracks) in taxon distributions: tracks which coincide for a large number of organisms are known as generalised tracks and estimate the ranges of ancestral taxa. The most important aspect of Croizat's panbiogeographic model was the elucidation of the fundamental role played by geological processes in the development of new taxa.

Cladistic biogeography

Cladistic methods may be applied to historical biogeography. Cladistic biogeography assumes a direct correlation between the evolutionary relationships of taxa and the historical relationships of the areas which they occupy (Crisci *et al*, 1991): a taxon occupies its present range because it evolved *in situ* following interruption of its ancestral range by a vicariance event.

Hennig (1966) introduced the application of cladistic analysis in biogeographical studies when he investigated centres of origin using phylogenetic hypotheses to identify primitive and advanced species. Rosen (1976) first combined panbiogeography with cladistics in an investigation of the biogeography of the Caribbean region, and found that the hypothesis generated was supported by geological evidence. This provided a foundation for Platnick and Nelson (1978) to develop models of cladistic biogeography using the presence or absence of taxa in discrete areas to generate biogeographic hypotheses.

Hypotheses in cladistic biogeography are inferred from cladograms demonstrating recency of common ancestral biotas (Humphries and Parenti, 1989). Area cladograms are constructed from phylogenetic cladograms by replacing taxa with the areas in which each occurs. If each taxon is confined to its own area of endemism, then the resulting area cladogram provides a biogeographic hypothesis of the relationships and patterns of vicariance of the areas under investigation. Problems arise if some or all taxa are widespread (occur in more than one area) (Platnick & Nelson, 1978). Widespread taxa obscure relationships between areas, as areas may appear more than once on each branch of the cladogram (are redundant). Widespread areas may be dealt with in three ways according to assumptions about the phylogenetic hypotheses on which they are based (Nelson & Platnick, 1981; Zandee & Roos, 1987).

Assumption 0 regards widespread taxa as monophyletic and not subject to further resolution (Zandee & Roos, 1987). Distributions which take in several areas of endemism are accurate, and the phylogenetic cladogram is the best representation.

Assumption 1 states that what is true of a taxon in one part of its range is also true of that taxon in other parts of its range. Assumption 1 treats widespread taxa as monophyletic, but allows the possibility of resolution of a widespread taxon into two or more endemic taxa with no disruption to the area relationships (Nelson & Platnick, 1981). That is, if a taxon occurs in two areas, those areas will remain as sister areas even if that taxon is subsequently resolved into two taxa.

Assumption 2 states that what is true of a taxon in one part of its range is not true of that taxon in other parts of its range (Nelson & Platnick, 1981). This allows both dispersal and extinction, and may regard areas as polyphyletic (Humphries, 1992).

If cladograms of several monophyletic groups demonstrate an identical pattern of distribution between the same areas, then it is likely that they share a common biogeographical history, rather than being the product of repeated dispersal events. In reality, area cladograms of unrelated taxa are rarely identical, and problems of incongruence are solved by component analysis and consensus trees (Nelson & Platnick, 1981) or by parsimony method (e.g. Mickevich, 1981; Zandee & Roos, 1987).

Biogeographic studies on pulmonate land snails

Ecological biogeography remains the principal focus of research among land snail biogeographers (e.g. Branson & Batch, 1970; Cameron, Down & Pannett, 1980; Boag & Wishart, 1982; Solem, 1984b; Solem & Climo, 1985; Cameron, 1986), while dispersal models dominate studies of historical biogeography (e.g. Solem, 1959, 1981c; Peake, 1978; van Bruggen, 1980; Thake, 1985).

Adherence to dispersal paradigms has resulted in unparsimonious and untestable solutions for biogeographic problems. The disjunct distributions of both Bulimulidae and Camaenidae (South and Central America - Australasia) have been explained as the result of dispersal from and subsequent extinction in North America and Europe (Solem, 1959, 1981c). However, cladistic analysis of the Bulimulidae (Breure, 1979) and Camaenidae (this study, chapter 4) indicate that vicariance is a simpler explanation. Dispersal from the Northern Hemisphere has also been invoked to account for the presence of Rhytididae in South Africa, Australia, New Zealand, Seychelles and Indonesia (Solem, 1981c).

Nordsieck (1986) applied ideas of centres of origin to modern land snail families, but conceded that range adjustment had probably either not occurred or been moderate. Families thus occupy areas approximating their centre of origin, with no large-scale dispersal.

Vicariance biogeographers may regard snails as `vicariant conformists' (Springer, 1981: 230), differentiating rapidly within disrupted populations and having little ability to cross barriers. Low vagility means they are useful both in developing vicariance hypotheses which may be tested with other taxa, and in testing existing hypotheses.

Chapter 3

MATERIALS AND METHODS

The taxonomic revision which forms the basis of this study was based on existing shell and anatomical material in Australian museums, supplemented by material specially collected for this study and subsequently deposited in the Museum of Tropical Queensland, Townsville. As much material as possible was examined to record inter- and intraspecific variation and geographical distribution.

Extralimital camaenid material for comparison with Australian forms came from Cuba and Jamaica. No camaenid material was available from New Guinea, Indonesia or mainland Asia. Bradybaenids from Indonesia and the Philippines were also examined.

Specimens used in this study were held in the following collections:

AM	Australian Museum, Sydney, NSW.
ANSP	Academy of Natural Sciences, Philadelphia, USA
JW	Private collection of Jack Worsfold, Charters Towers, Qld.
MTQ	Museum of Tropical Queensland, Townsville, Qld.
MV	Museum of Victoria, Melbourne, Vic.
QM	Queensland Museum, Brisbane, Qld.
SAM	South Australian Museum, Adelaide, SA.
WAM	Western Australian Museum, Perth, WA.

Type and topotypic material

Until relatively recently collectors concentrated on shells, which were light, dry and easy to transport. As shells were thought of as the most important part of the molluscs, the soft parts were discarded. This has caused problems for subsequent revisers, particularly among groups, such as the Camaenidae, where shell characters can be unreliable. In this study, type material held in Australian collections was examined, and for all species I referred to original descriptions and illustrations of types. As no anatomical material existed among the types, this revision was based on topotypic wet material (i.e. specimens collected from the type locality) compared directly with types, and with type descriptions and illustrations.

The accuracy of type localities varied. Some were accurate (e.g. Stone Island), while others were vague (e.g. Port Denison). In no cases were map co-ordinates given. Reference to the reports of early expeditions assisted in assessing the veracity of some localities.

Shells

The hadroid Camaenidae have generalised shells, with few diagnostic characters useful in either taxonomic studies or cladistic analyses. The variation in shell shape, size and colour in the hadroid camaenids made it impossible to use most of the characters listed by Emberton (1988), such as quantitative records of sculpture and colour. The shell characters in this study were restricted to three direct measurements (height, diameter, number of whorls), a ratio derived from those measurements (height/diameter), the degree of occlusion of the umbilicus, and the postapical shell sculpture (Solem, 1979).

Sculpture

In all adult specimens, the embryonic sculpture of the protoconch or apex was eroded. Only juvenile shells retained protoconch sculpture, but as these shells could not, in many cases, be reliably identified, no embryonic sculpture was recorded.

Postapical shell sculpture was examined under low magnification with a dissecting microscope. The surfaces of adult shells were frequently worn and pitted, making sculpture patterns difficult to distinguish. In these cases the terminal part of the body whorl was examined: here sculpture was protected from abrasion by the curve of the lip, remaining clear even though the rest of the shell was damaged. Sometimes sculpture was visible in the umbilicus of openly-umbilicate specimens.

Measurements

Only adult shells, that is, shells with a fully formed lip, were measured. Two measurements, height and diameter, were taken for each shell (Fig. 3.1a). Vernier callipers were used, with measurements recorded to the nearest 0.1mm. Emberton (1989) investigated measurement error using this method and demonstrated it to be low: no greater than 4% for height and 1% for diameter.

Height was the vertical height of the shell from the lowest part (usually the lip) to the tip of the apex, parallel to the coiling axis. This differed from the measurements made by workers at the turn of the century, who often measured the height of a shell as it rested on a flat surface. Discrepancies between certain heights reported here and those of the type descriptions can thus be ignored.

Diameter was measured at the widest part of the shell, usually from the outer lip to the periphery of the body whorl, perpendicular to the coiling axis.

The ratio of *height to diameter* was used to determine the elevation of the shell. Tall shells had a ratio > 1, discoidal shells had a ratio < 1.

Number of whorls was measured by placing the shell over a circle marked out in 45^0 sectors, numbered 1 - 8 (Fig. 3.1b). The starting point was the apical notch (Solem, 1976), which was aligned with radius 1. Each complete revolution was counted as a single whorl, and partial whorls were recorded to the nearest 0.125 (45^0).

Plates

Shells are usually very variable and reproductive morphology provides more reliable diagnostic characters. The type specimens (shells) of many species included in this revision have been figured in original or later descriptions, so there was no need to reproduce them here. Photographs of the shells of most species discussed in this study are available in works by Iredale (1937b) and Marshall (1927) so only the shells of new species are illustrated here.

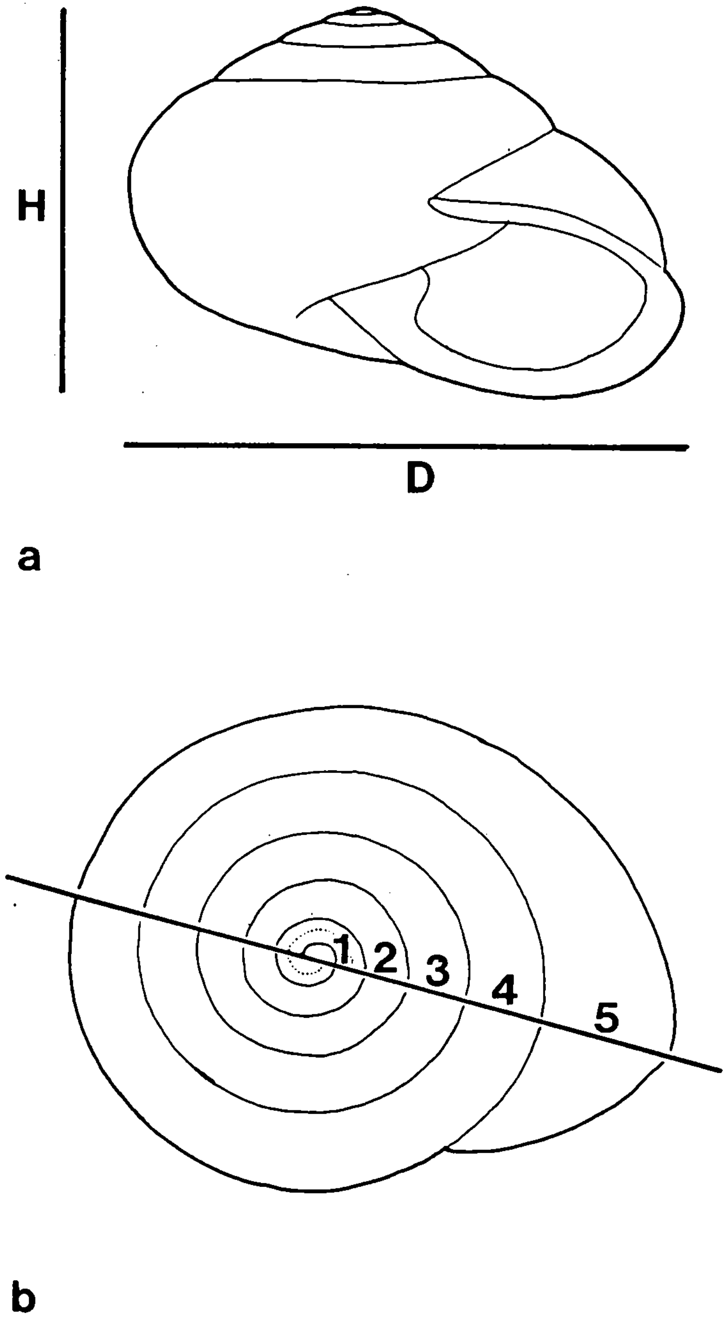


Fig. 3.1: Shell measurements used in this study: **a** shell height and diameter, **b** number of whorls.

Anatomy

The processes of killing, fixing and preserving soft-bodied animals often results in contraction or distention of the internal organs. Although dimensions of the terminal genitalia are given in some taxonomic descriptions, body retraction results in distortion of most parts, making the measurements difficult to interpret. The length of the penis and sheath may vary by 20% between extension and retraction, by 53% between individuals, and by 27% between repeated measurements (Emberton, 1989).

Emberton (1989) noted that retraction had little effect on penial sculpture, so structures on the functional surface of the penis could be measured and compared with minimal error. There were no characters which could be regarded as quantitative among the hadroid camaenids. All characters used in this study were qualitative.

Dissection was chosen as the simplest and most effective way of displaying the terminal genitalia. Other methods, such as snap-freezing mating snails to examine everted penes or clearing and sectioning material, were impractical given the scope of the study.

Preparation of anatomical material

The snails were killed by placing them in plastic bags half-filled with water, which were sealed after the air had been squeezed out. The bags were frozen in a domestic freezer at about -4^{0}C. Once frozen solid, the bags were removed and the specimens thawed by running cold water over them. Snails which had been only partly frozen withdrew into the shell when thawed. They would not extend again and died retracted.

Freezing proved to be a faster and more reliable method than the traditional ones of drowning overnight in deoxygenated water or narcotising with magnesium sulphate before killing in alcohol or formalin. Almost every snail died in a fully-extended position, which was convenient for dissection of both the terminal and apical genitalia. Freezing had other advantages over the methods outlined above: there was none of the danger of material decaying as there was with drowning, specimens could be kept without deterioration for extended periods, and complete relaxation of the columellar muscle allowed the whole animal to be withdrawn from the shell quickly and without damage (Scott, 1991). The main disadvantage to this method was that prolonged freezing rendered tissue unusable for histological examination. Material used for that purpose was prepared separately.

Once wholly thawed, specimens were extracted by holding the foot with a pair of forceps and pulling gently and steadily, while the shell was rotated anti-clockwise. In almost all cases the entire animal was removed with no damage to the apical viscera. Specimens were either dissected immediately after extraction or were made more robust by fixing for at least an hour in 70% ethanol. Immersion in ethanol turned semi-translucent tissue opaque, which made it much easier to see sculptural detail. Material was stored in 70% ethanol.

Gross morphology

Snails were cut open along the mid-dorsal surface (fully extended specimens) or along the right side (partly-retracted specimens). The cut continued through the mantle collar and as far up the skin of the visceral mass as possible, the length of the cut depending on the degree of extraction from the shell (Fig. 3.2). The apical genitalia (ovotestis, talon, hermaphrodite duct, albumen gland, uterus, prostate, head of spermatheca) and terminal genitalia (base of spermatheca, free oviduct, vagina, vas deferens, epiphallus, penis) were examined in specimens which had been removed from their shells (Fig. 3.3). In snails which could not be fully extracted only the terminal genitalia were dissected. In these cases the retractor muscle anchoring the epiphallus/penis to the body wall was cut and the male terminal genitalia freed of surrounding tissue, allowing these structures to be examined in isolation.

Several drawings were made of the genitalia, recording each phase of the dissection. In most species illustrations covered the spermathecal/free oviduct/vas deferens complex, the epiphallus/penis, and the penis lining. Penis lining was omitted for the two species in Gen. nov. B where the penis was so thin it was impossible to dissect. Where present, epiphallic caeca were opened and the lining illustrated. Illustrations were drawn free-hand.

Abbreviations used in illustrations

Abbreviations used in the anatomical illustrations (Chapter 6) are as follows:

A	genital atrium
AG	albumen gland
E	epiphallus
EC	epiphallic caecum
F	flagellum
G	gut
O	free oviduct
P	penis
PR	prostate gland
PS	penial sheath
RM	penial retractor muscle
SH	head of spermatheca
SS	shaft of spermatheca
TR	tentacular retractor muscle
U	uterus
V	vagina
D	vas deferens

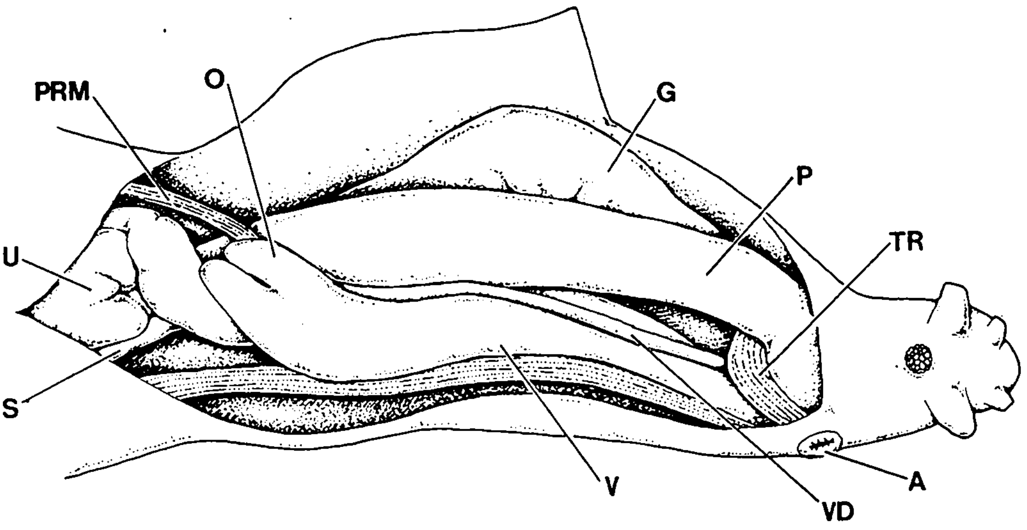


Fig. 3.2: Initial phase of snail dissection, with internal organs *in situ*

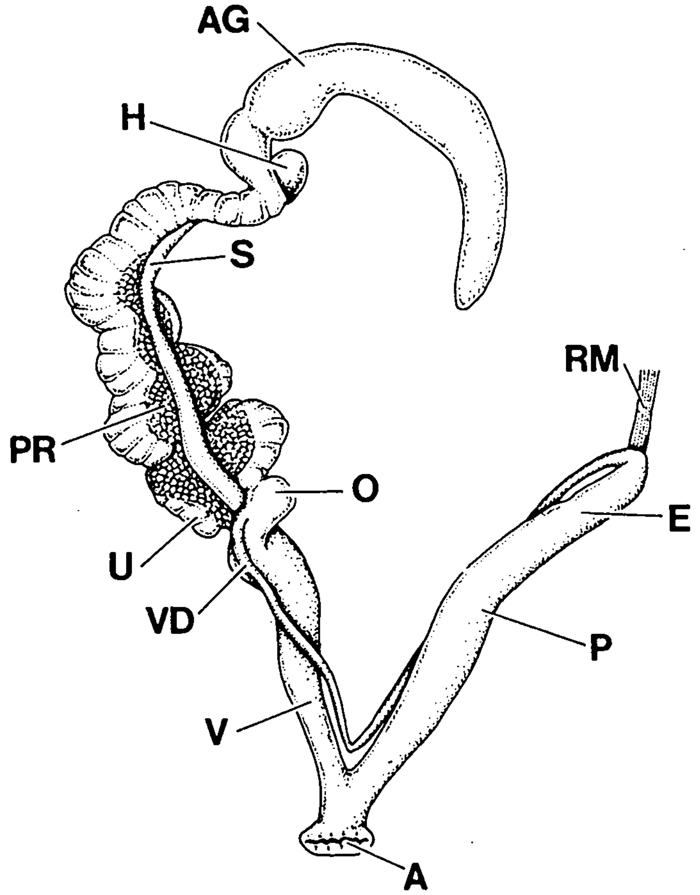


Fig. 3.3: Dissection of reproductive system of *Bentosites zebina* Brazier (Calcium)

Structure of the headwart

Gross structure of the headwart was investigated using a dissecting microscope and a scanning electron microscope (SEM). Living and preserved specimens of all genera were examined with the dissecting microscope, but only *Bentosites rawnesleyi* was studied with the SEM. Material fixed and stored in 70% ethanol was prepared for the SEM by dehydration in 90% and 100% alcohol, followed by immersion in *Peldri*, a proprietary fluorocarbon compound. Use of *Peldri* as a sublimation dehydrant avoids placing delicate tissues in a critical point dryer, where they may collapse or become distorted. *Peldri* is solid below 23.8^0C and becomes a volatile liquid at temperatures above this. Dehydrated material was placed in a solution of 50% ethanol-50% *Peldri* for 4 hours, after which it was placed in 100% *Peldri* for a further 4 hours. It was cooled, allowed to solidify, then left to sublimate. The protusible cephalic organ and surrounding tissue were mounted and coated with a fine layer of gold using a gold sputter coater, and examined with James Cook University's JEOL 840 scanning electron microscope, set at 10kV with a secondary detector.

Material was prepared for histological examimation by live decapitation. The head and anterior foot from each specimen was fixed immediately in formol calcium acetate. Decapitation and subsequent fixation resulted in severe muscle contractions. Freezing specimens would have avoided this reaction, but might have resulted in histological artefacts.

The heads were embedded in paraffin wax. Longitudinal sections were 6 mm thick. Five stains were used: alcian blue - periodic acid Schiff (AB-PAS), paraldehyde fuchsin (PAF), chrome alum haematoxylin - phloxine (CAHP), Martius yellow - brilliant crystal scarlet - soluble blue (MSB), azocarmine - aniline blue (Heidenhan's AZAN), and mercury bromophenol blue (BPB).

Phylogenetic analyses

Hennig86

Analyses were conducted on a personal computer, using the cladistic program *Hennig86* (Farris, 1988). No assumptions were made about character polarity, so all data, with the exception of the Helicoidea data (Tillier, 1989), were regarded as unordered (non-additive) and unweighted. Data matrices were constructed using the MS-DOS line editor *edlin* in the *Hennig86* subdirectory, and all output was directed back to specific log files in *edlin*.

Wherever possible the implicit enumeration command, *ie**, was used. This is guaranteed to find the most parsimonious tree(s). If the first pass through the data did not yield a single most parsimonious tree, the iterative weighting command, *xs w*, was applied. This successively weights characters according to their fit to the trees (the better the fit, the higher the weight), and can be used in conjunction with *ie** (Farris, 1969, 1988). Iterative or successive approximations weighting emphasises the importance of synapomorphic and thus non-homoplasious characters and reduces the effect of homoplasious ones (Farris, 1969, 1988). Problems may arise if character conditions are mis-identified and non-homoplasious characters are mistaken for homoplasious ones, but this is not confined to successive weighting. Indeed, *a priori* character weighting may result in serious and irretrievable error, as may other weighting techniques which rely on external theory for justification (e.g. LeQuesne, 1969; Felsenstein, 1981; Gauld & Underwood, 1986; Sharkey, 1989; Goloboff, 1991).

When several trees were found to be equally parsimonious, they were combined to form a Nelson consensus tree (Nelson, 1979), using the *nelsen* command.

Details of character state transformation series were obtained with the *xs h* command, which lists the state of each character at each node. The numbers of steps, consistency index and retention index for each character were provided by the *xs m* command which also, in the case of Nelson trees, gave information about best and worst fits.

Data

Data were recorded in taxon-by-character matrices. Character state data were either binary (0,1) or multistate (0,1,2,...n), and missing data were represented in the data matrices by `?'. The type species of each genus was used to determine the state of each character in the genus-level analyses.

Uninformative characters (where the character state is the same for all members of the clade) and autapomorphies (character states unique to a single taxon) were not included in the data matrices as they might have produced misleading values in consistency indices (Farris, 1989).

Characters

Characters useful in cladistic analysis are those homologous characters which show some progressive change (Hennig, 1966). Hadroid camaenids demonstrated conservatism in characters of the proximal reproductive tract, alimentary, nervous and excretory systems. Only characters of the distal reproductive tract and shell were suitable for analysis.

Outgroup selection

Outgroup method (Watrous & Wheeler, 1981; Maddison *et al*, 1984) was used to root all cladograms. The outgroup for the Helicoidea was the Zonitoidea, typified by *Zonites* Montfort, 1810 (Tillier, 1989; Giusti *et al*, 1991). The outgroup for the hadroid cladogram was *Bradybaena*, which is the type genus of the Bradybaenidae, shown in this study to be sister group to the Australian Camaenidae. This genus was used rather than one from within the Australasian Camaenidae as the internal taxonomy and phylogeny of the camaenids are not well-known. A family-level revision would be necessary before an appropriate outgroup could be selected from within the Australasian Camaenidae.

Presentation of results

Data matrices used in cladistic analyses are presented in different forms in Chapter 6 and Appendix 2. Those in the chapter on analysis display information on each character in the following order: character state, case, consistency index. Case indicates whether the states were found to be autapomorphic (A), synapomorphic (S), homoplasic (H), or to have undergone a reversal (R). There are no autapomorphic character states for binary characters (see above), but autapomorphic states do occur in multistate characters.

Biogeographic analyses

Distribution maps

Distribution maps were constructed from locality data of material examined in this study. They covered all genera and species included in the systematic review. Precision in plotting the ranges depended on the accuracy of the locality data, so not all records were used. Gaps in the ranges of some species (e.g. *Hadra bipartita*) have been marked by '?'. For these species it is impossible to know whether records do not exist because fieldwork has failed to collect specimens or because fieldwork has never been undertaken in that part of the range (apparent gap). A single non-rainforest species of *Hadra* was omitted from the analysis. This species occurs at Chillagoe, north-eastern Queensland. As it is not sympatric with any other species of hadroid camaenid, its omission does not affect the area relationships of the rainforest patches.

Maps of *Zyghelix, Meridolum,* and *Thersites* were compiled from literature records (Bishop, 1978a, 1978b; Iredale, 1937, 1938; Smith, 1992; Solem, 1985, 1992).

Definition of areas for use in the construction of area cladograms

Areas were based on distributional data from Te (1976) (Helicoidea) and from this study (hadroid camaenids). Areas varied in size between different taxonomic levels: northern Australia, for example, was an appropriate area for family-level analysis, but it was divided into smaller areas to accommodate genus- and species-level analyses.

Although broad distributions could be identified (e.g. SE Asia in the case of helicoid families, Australian Wet Tropics in hadroid camaenids), rarely did the geographical limits of taxa coincide. As a consequence, distributions at each appropriate taxonomic level (e.g. family for Helicoidea, genus for hadroid camaenids) were broken down into successively smaller components until they were reduced to fundamental units from which the distribution of any taxon could be constructed (Axelius, 1991; Liebherr, 1991; Wallace *et al*, 1991). At species level, the Whitsunday Islands, for example, can be interpreted as a single biogeographical area if the island endemic *Bentosites macleayi* is used in an analysis. However, if distributional data from *Temporena coxi* and *T. macneilli*, which are restricted to certain islands within the Whitsunday Group, are introduced, that single area may be split into two smaller areas of endemism (e.g. northern islands, southern islands). In this case, *B. macleayi* is occurs in both areas, whereas the species of *Temporena* occur in one area each as well as the adjacent mainland.

Construction and analysis of area cladograms

Area cladograms were produced by replacing each terminal taxon of a phylogenetic cladogram with the areas in which it occurred. Data were presented as cladon-by-area matrices, in which each cladon was recorded as present (1) or absent (0) in each area (Zandee & Roos, 1987). Data were ordered. The cladogram was rooted using an `outarea' (equivalent to an outgroup), a hypothetical area in which none of the ingroup occurred. Absence of a taxon from an area was regarded as plesiomorphic.

Area cladograms were constructed under Assumption 0 (Zandee & Roos, 1987) using the cladistic program *Hennig86*. Assumption 0 assumes that the phylogeny used is accurate and there will be no subsequent changes (Zandee & Roos, 1987).

Nelson consensus trees (Nelson, 1979) were constructed when multiple trees were generated under Assumption 0.

Evolution of characters of the distal reproductive tract

Patterns of sympatry and allopatry were recorded for each congeneric species pair. Differences in characters of the penis, epiphallus, spermatheca and vagina were recorded for each pair, and quantitative and qualitative comparisons were made between species pairs exhibiting sympatric or allopatric distributions. Phylogenetic distance was measured and plotted against the number of differences.

Chapter 4

PHYLOGENETIC RELATIONSHIPS OF THE HELICOIDEA

Phylogenetic analysis of the Helicoidea

Data

Data for this analysis were modified from the stylommatophoran data matrix of Tillier (1989), who examined characters of the nervous system, digestive tract and kidney in 47 families of land snails. Type genera were used as exemplars of families, except in the Vitrinidae (*Phenacolimax* was used following Tillier, 1989) and Camaenidae. For this analysis the Camaenidae was split into the Australasian Camaenidae ('Austcam'), represented by *Amplirhagada*, and the American Camaenidae ('Amcam'), represented by *Pleurodonte*, to investigate whether the family was monophyletic or not. If the family was monophyletic, they would appear as sister groups.

Seventeen characters were used in the stylommatophoran matrix (Tillier, 1989), but five of these were removed for this study as they became uninformative (symplesiomorphic, autapomorphic) within the helicoid matrix. Of the twelve remaining characters (Table 4.1), one character (fusion of visceral ganglion) was further modified after Emberton (1991). Two characters (presence/absence of dart sac and degree of shell calcification) were added. Both binary and multistate characters were used, with characters states recoded from Tillier (1989) in sequence (Table 4.2). Data were unordered and initially unweighted.

The outgroup was *Zonites* (Zonitidae, Zonitoidea), shown by Tillier (1989) and Giusti *et al* (1991) to be phylogenetically close to the Helicoidea.

Results

One hundred and ten most parsimonious trees were found on the first pass through the data (see Appendix 2). These were each 33 steps in length, with consistency indices of 0.57 and retention indices of 0.53. Successive weighting generated a single most parsimonious cladogram (Fig. 4.1).

Seven nodes (12 - 18) were supported by single character transformations, while only one node (11) was supported by three transformations. The patterns of change of characters 0 (oesophageal crop) and 9 (fusion of visceral ganglion) were difficult to determine, due to missing data and equivocal states at several nodes.

The ratio of lengths of left and right cerebro-pedal connectives transformed at node 18. The connectives were primitively equal in length, and this state occurred in the Sagdidae and as a reversal in the Bradybaenidae. The difference in the lengths increased at node 18, so the left connective might be up to 2.5 times the length of the right. This persisted at all nodes and terminal taxa, until a subsequent transformation at node 11 (see below).

The kidney, primitively with proximal lamellae, transformed at node 17. The advanced state, with lamellae reaching the distal region and the level of the kidney pore, was found at all nodes and terminal taxa, until a reversal at node 12 (American Camaenidae, Helicidae and Helminthoglyptidae).

The distribution of the character states for shell structure (character 10) was conservative. The transformation from the primitive decalcified shell to the advanced state of full calcification occurred at node 16. The Sagdidae, which was presented as the family with the largest number of most plesiomorphic characters, also possessed calcified shells.

The gastric crop changed in shape from cyclindrical to funnel-shaped (widening from oesophagus to stomach) at node 15.

The other kidney character was transformed at node 14. The plesiomorphically short- to medium-length kidney became shortened, this condition persisting in the Haplotrematidae, American Camaenidae and Helminthoglyptidae. There was a second transformation in the Helicidae, where the kidney enlarged to become medium-length.

The synapomorphy which supported the Australian Camaenidae and Bradybaenidae as sister families (node 13) was the advanced state of the intestine, in which the intestinal loops reached a level between the distal limit of gastric pouch and the middle of the gastric crop. An identical state also occurred as a homoplasy in the Helicarionidae.

Two of the three synapomorphies which supported the Helicidae and Helminthoglyptidae as sister families (node 11) were characters of the nervous system. Both were changes in lengths of neural connectives: the right cerebral connective became shortened and the discrepancies in lengths of the cerebro-pedal connectives decreased until the left was only slightly shorter than the right. The third character state was the presence of the calcified dart (see below).

Reversals were not widespread. Two occurrences were recorded: character 4 (kidney morphology) at node 12, and character 6 (ratio of lengths of cerebro-pedal connectives) in the Bradybaenidae.

Homoplasy occurred in more than 63% of characters. It was most marked in the presence of the calcified dart (c.i. = 0.33). Other homoplasious characters (c.i. = 0.50) had a restricted distribution, arising at no more than two points. These characters were advanced conditions of intestinal length, kidney morphology, right cerebral connective, position of visceral ganglion, position of left parietal ganglion, fusion of visceral ganglion, and shell structure.

Two characters (0 and 9) were equivocal at several nodes, so they could not be interpreted.

Digestive tract

0 Oesophageal crop (OC): separated from the gastric crop by a distinct portion of the oesophagus (0); absent (1); separated from the gastric crop by a simple constriction (2); as in 2, but extending forward to the nerve ring (3)

1 Gastric crop (SC): cylindrical (0); funnel-shaped, widening from oesophagus to stomach (1)

2 Intestinal length (IL): intestinal loops long, reaching proximally at least the level of the distal limit of gastric pouch (0); intestinal loops reaching a level between the distal limit of gastric pouch and the middle of the gastric crop (1)

Excretory system

3 Kidney length (LR): kidney short to medium (0); kidney very short (1); kidney medium (2); kidney long (3)

4 Kidney morphology (RR): kidney with two distinct regions, the distal one lacking lamellae (0); kidney undifferentiated internally, with lamellae reaching the distal region and the level of the kidney pore (1)

Nervous system

5 Right cerebral connective (CPD): between one and two times width of right cerebral ganglion (0); shorter than width of right cerebral ganglion (1); more than twice as long than width of right cerebral ganglion (2)

6 Ratio of lengths of the cerebro-pedal connectives (left/right) (CPR): between 0.9 and 1.2 (0); from 1.2 to 2.5 (1); less than 0.9 (2)

7 Position of visceral ganglion (VG): median (0); median plane of the visceral ganglion on the right side of the median plane of the pedal ganglion (1)

8 Position of the left parietal ganglion (PAG): in contact with both the left pleural and visceral ganglion (0); in contact with the visceral ganglion only (1)

9 Fusion of visceral ganglion (FG): fused with right parietal ganglion (0); not fused with parietal ganglia (1); fused with left parietal ganglion (2)

Shell

10 Structure of shell: non-calcified (0); calcified (1).

Reproductive tract

11 Presence of calcified dart: calcified dart present (0); calcified dart absent (1).

Table 4.1 Characters used for the cladistic analysis of the superfamily Helicoidea. Letters in parentheses indicate abbreviations used by Tillier (1989).

character	Zonitidae	Sagdidae	Vitrinidae	Helicarionidae	Polygyridae	'Austcam'	Bradybaenidae	Haplotrematidae	'Amcam'	Helicidae	Helminthoglyptidae	character state	consistency index
				DIGESTIVE TRACT									
0. Oesophageal crop	0	0	0	2	0	3	3	0	1	2	3	?	0.60
1. Gastric crop	0	0	0	0	0	1	1	1	1	1	1	S	1.00
2. Intestinal length	0	0	0	1	0	1	1	0	0	0	0	SH	0.50
				KIDNEY									
3. Kidney length	?	3	?	?	0	0	0	1	1	2	1	AS?	1.00
4. Kidney morphology	0	0	0	1	1	1	1	1	0	0	0	SR	0.50
				NERVOUS SYSTEM									
5. Right cerebral connective	1	0	2	0	2	0	0	0	0	1	1	SH	0.50
6. Ratio of lengths of cp connectives	0	0	1	1	1	1	0	1	1	2	2	SR	0.66
7. Position of visceral ganglion	0	0	0	1	0	0	0	0	0	1	0	H	0.50
8.. Position of left parietal ganglion	0	0	0	0	0	0	0	1	0	1	0	H	0.50
9. Fusion of visceral ganglion	1	0	0	0	1	1	2	0	0	0	0	?	0.50
					SHELL								
10. Shell structure	0	1	0	0	1	1	1	1	1	1	1	SH	0.50
					DART								
11. Calcified dart	0	0	0	1	0	0	1	0	0	1	1	SH	0.33

Table 4.2 Superfamily Helicoidea data matrix (modified from Tillier, 1989). 0, plesiomorphy; 1,2,3 apomorphy; ? not known; A, autapomorphic for a single family; S, synapomorphic; H, homoplasy; R, reversal.

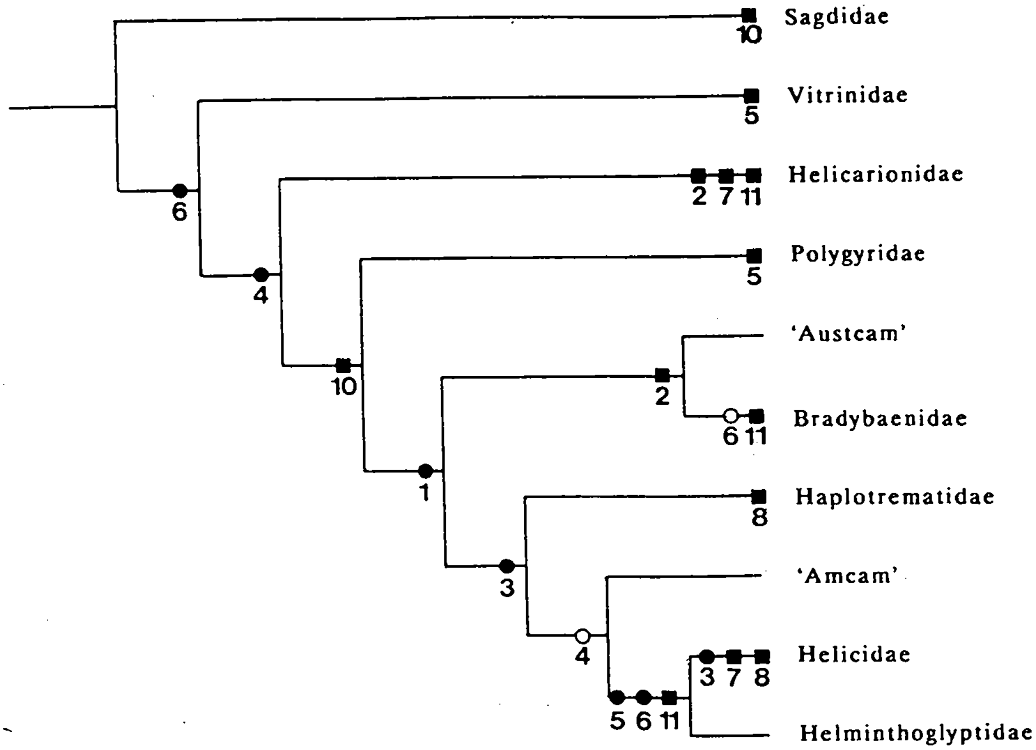


Fig. 4.1: Character transformations of superfamily Helicoidea: cladogram, ● apomorphy, ○ reversal, ■ homoplasy, □ reversal (length = 198; c.i. = 0.61; r.i. = 0.64)

Biogeography of the Helicoidea

Areas

Taxa were replaced by the areas in which they occurred. Areas used were modified from Te (1976), and many followed political boundaries which also coincided with major geographical features such as rivers or mountain ranges (Table 4.3). Africa, South America and Australia were treated as composite areas (Platnick and Nelson, 1978) (Fig. 4.2). Many taxa were widespread, with only the Sagdidae and Polygyridae occupying single areas (Fig. 4.3).

Results

Twenty-four most parsimonious area cladograms were generated by *Hennig86*. Each was 24 steps in length, with a consistency index of 0.79 and a retention index of 0.87 (Fig. 4.4). The principal differences between cladograms were in the clustering of the Gondwanan areas, and the identity of the basal area in the Laurasian clade. Combining the multiple cladograms in a Nelson consensus tree produced two unresolved polytomies which encompassed parts of Gondwana and Laurasia (Fig. 4.4).

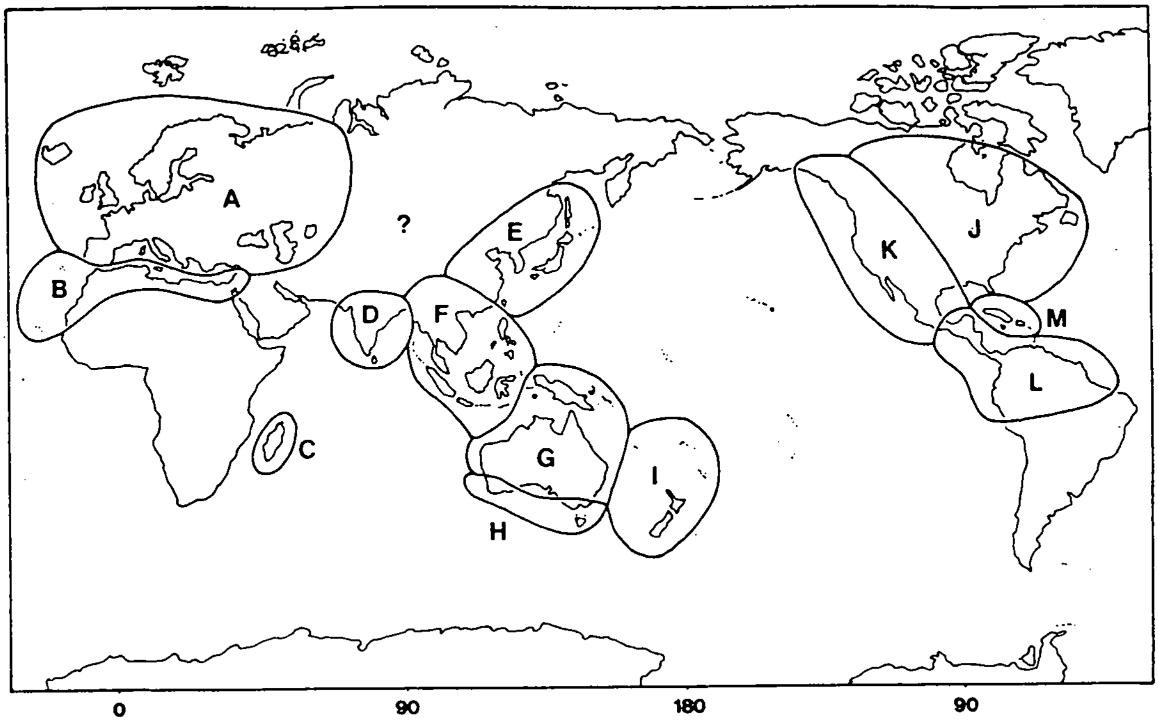


Fig. 4.2: Biogeographic areas used in this study

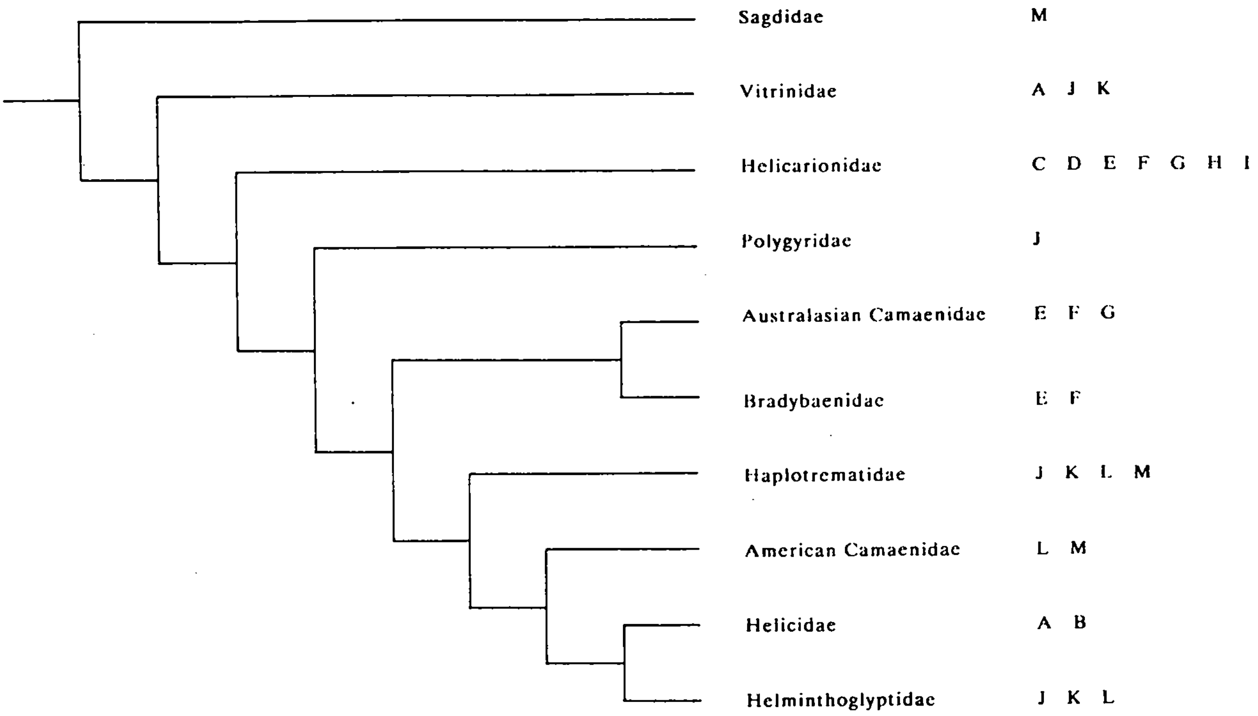


Fig. 4.3: Area cladogram of superfamily Helicoidea based on phylogenetic cladogram (letters refer to geographic areas in Table 2).

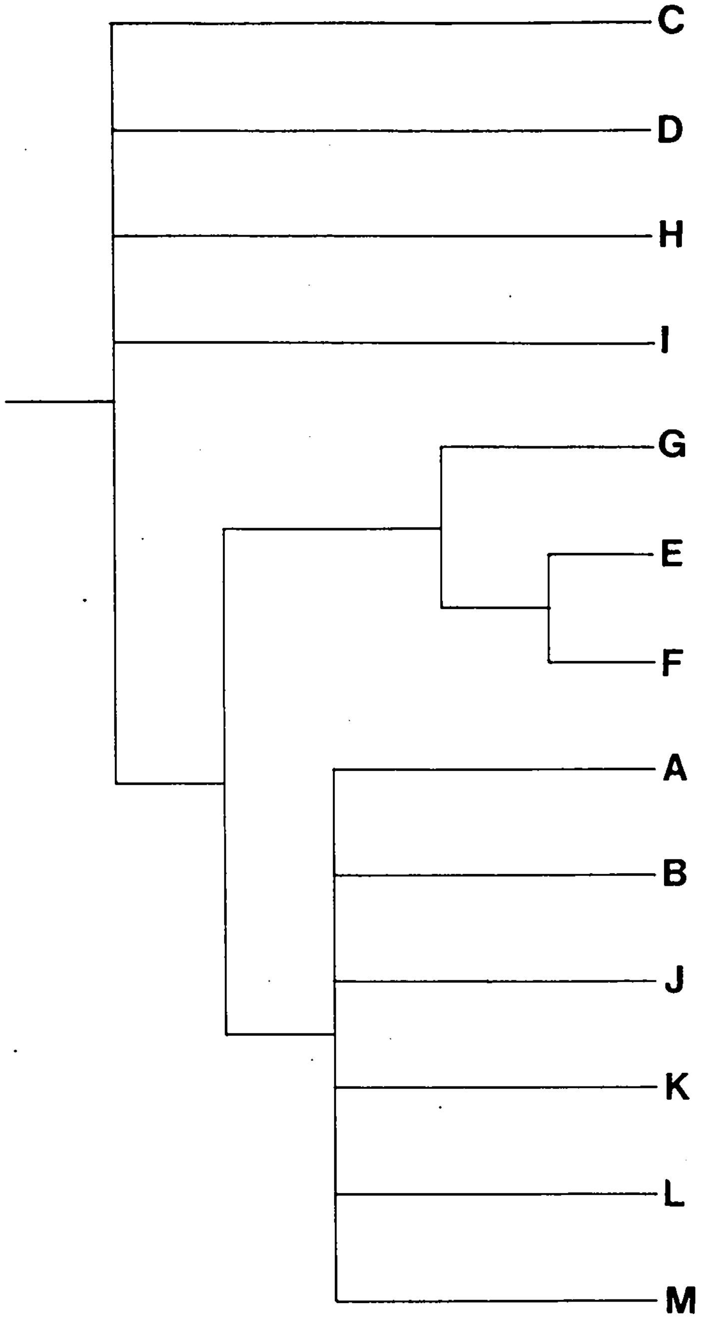


Fig. 4.4: Nelson consensus cladogram generated under Assumption 0 (length = 24, c.i. = 0.79, r.i. = 0.87).

code	area	area code of Te (1976)
A	western Palaearctic	1-3, 5
B	North Africa	4
C	Madagascar	14
D	India	16, 17
E	eastern Asia	6-8, 10, 11
F	south east Asia	18-20
G	northern Australia	21, 22 (in part)
H	southern Australia	22 (in part), 23
I	western Pacific	24, 25, 26 (in part)
J	eastern North America	27 (in part), 33, 34
K	western North America	27 (in part), 29-32
L	Central America	35, 37 (in part)
M	Caribbean	36

Table 4.3: Areas used in constructing area cladograms for the superfamily Helicoidea compared with the areas used by Te (1976).

Chapter 5

STRUCTURE OF THE HADROID CAMAENID HEADWART

A headwart (Taki, 1935) was found on the head of all hadroid camaenids, between and slightly posterior to the optical tentacles. This structure is normally retracted in a transverse groove, but can be protruded. Solem (1992) regarded the headwart as an apomorphy for the Camaeninae.

The headwart is also found in members of the predominantly Asian family Bradybaenidae (Taki, 1935; Takeda & Tsuruoka, 1979; Takeda, 1980, 1981). Evidence from cladistic analyses suggested the Australasian species were more closely related to the Bradybaenidae than they were to the American species. A preliminary investigation of the structure and function of camaenid headwart was undertaken to provide data for subsequent research into the relationships of these complex groups.

Cephalic structures occur in several families of land snails. The headwart was first described from camaenids and bradybaenids by Taki (1935). In all bradybaenid and most camaenid genera which possess a headwart, the structure is permanently everted (Solem, 1992). Only in the Camaeninae is the headwart retractible. A more elaborate frontal organ is found in the African urocyclid genus *Gymnarion* (Binder, 1969, 1976). This structure is everted from the front of the head, between the two pairs of tentacles, and in some species is armed with calcareous hooks (Binder, 1965). The African genus *Achatina* (Achatinidae) does not possess an everted or eversible structure, but instead bears a cephalic dimple, a depression on the head between the upper tentacles (Chase & Piotte, 1980).

The function of the organs is poorly understood. The frontal organ of *Gymnarion* is used in courtship, and species possessing a frontal organ have a longer and more complicated courtship than those which do not (Binder, 1976). Takeda and Tsuruoka (1979) suggest that the headwart of the bradybaenid *Euhadra peliomphala* secretes pheromones, which are also involved in courtship and mating. Evidence for this comes from observed changes in snail behaviour following injection of headwart extract (Takeda & Tsuruoka, 1979).

The role of the headwart in camaenids is unknown. A preliminary investigation of the tissue structure and glandular secretions of the headwart and adjacent head area demonstrated that although there were differences between the headwarts of camaenids and bradybaenids, the differences were relatively minor. However, despite the similarity in structure to the bradybaenid headwart, the camaenid headwart may not have a reproductive role. It is not involved in an obvious way in courtship and copulation in the Queensland species *Sphaerospira fraseri* (Griffith & Pidgeon) (King, 1975), nor in that of *Hadra bipartita* Férussac (Scott, unpubl.). It may be important in determining changes in photoperiod. Material for study of the headwart was obtained from specimens of *Bentosites rawnesleyi*. It was assumed that the structure of the organ is constant between species.

Structure of the headwart

Gross structure

The headwart was a small warty structure, with an anterior boundary at the intratentacular ridge of the optical tentacles. During foraging, the headwart was everted (Fig. 5.1a), but when the snail was at rest, with the tentacles partly withdrawn, the entire headwart could be retracted into a transverse slit which lay at the front edge of the headwart. When retracted the headwart was visible only as a small indentation which might be overlooked in cursory examination. When protruded, the organ was distinguished from the skin which surrounded it by its contours and the colour of its surface.

The tubercles of the integument were small and polygonal in front of the intratentacular ridge and large and square behind it. The tubercles of the headwart were indistinguishable in size and shape from those of the surrounding integument.

Under the SEM the surface of the headwart appeared sponge-like, with minute indentations. This contrasted with the remainder of the head integument, which was irregular and covered in flakes of mucus. No mucus was observed on the organ, despite the proximity of the mucus-secreting epidermal tissue of the head region (Fig.5.1b).

The headwart lay directly over the circum-oesophageal nerve-ring, which was overlain by a thick layer of adipose tissue. A small muscle ran from the tissue above the nerve-ring to the underside of the headwart (Fig. 5.1c). Subdermal longitudinal muscle fibres ran either side of the headwart, but appeared not to cross it.

Fine structure

The fine structure of the headwart differed from that reported for the bradybaenid *Euhadra peliomphala* by Takeda & Tsuruoka (1979) in both the shape of the epithelial cells and in the presence of unicellular glands. Epithelial cells in the camaenid headwart were approximately 3-5mm x 10-15mm, compared with 3-5mm x 60-75mm in the bradybaenid headwart (Takeda & Tsuruoka, 1979). No mucus was found on the surface of the camaenid headwart, although secretory cells were present. The bradybaenid headwart lacks secretory cells (Takeda & Tsuruoka, 1979). Findings are summarised in Tables 1 - 4.

Refractive layer

The epithelium of the headwart of *Bentosites rawnesleyi* was overlain by a thin refractive layer, which may be microvilli. This layer continued on the surrounding integument, but did not occur in the epipodial groove, where there was a distinct ciliated border, or on the sole of the foot, which was also ciliated. This refractive layer was weakly PAS positive, suggesting the presence of neutral mucopolysaccharides.

Epithelium

The headwart was covered by a columnar epithelium with a well defined basement membrane (Fig. 5.2a). Epithelial cells possessed large, centrally-placed nuclei. Material at the ectal margin of the cells was both PAS- and BPB-positive indicating the presence of both mucopolysaccharide and protein. Exposure to Heidenhan's azan suggested that a combination of acid and basic mucopolysaccharides was present, with acid mucopolysaccharides displaced towards the ectal margin (Table 1). Regular channels between cells contained globules of material which failed to take any stain, except BPB. The path of the channels was difficult to determine because of the resistance of ental cell material to most stains, but they appeared to run to the surface of the epithelium.

The epithelium of the surrounding head integument was composed of columnar cells, with scattered nuclei. Material was distributed evenly within the cells.

Epithelial glandular secretions

Material within vacuoles in the headwart epithelium did not adopt any stains, except for a moderate reaction to BPB (protein) and MSB (mottled pink-grey) (Table 1).

A wider range of secretions occurred in the epithelium on the head surrounding the headwart. These materials reacted positively with both AB and PAS (indicating neutral and acid mucopolysaccharides), azan (sparse acid mucopolysaccharides), BPB (proteins), MSB (mottled pink-grey), and PAF (Table 2).

Sub-epithelial glandular secretions

The tissue of the headwart contained numerous large lacunae, which may be blood lacunae or ducts for the distribution of secretions (Fig. 5.2a, b). Five sub-epithelial gland cell types were recorded from the headwart and adjacent head region (Fig. 5.2a, b):

cell type I	elongate cells with granular material
cell type II	large flat-staining cells immediately below the epithelium
cell type III	cells with largely non-staining contents and strongly-staining localised material
cell type IV	cells with strongly-staining contents
cell type V	cells with vacuole containing granular material

Cell types I and II occurred in the headwart, while cell types II - V were found in the surrounding integument (Table 3). Type I cells were elongate, and the granular material within them was PAS positive, suggesting neutral mucopolysaccharides. Type II cells stained pale pink with azan and MSB (acid mucopolysaccharides), and deep purple-blue with BPB (proteins), indicating that the material within these cells was probably a glycoprotein.

Cell types present in the head integument all stained more strongly than those of the headwart (Table 4). The concentrated materials in type III cells were acid and basic mucopolysaccharides, staining red and orange with azan. Type IV cells were filled with acidic mucopolysaccharides. Type V cells contained basic mucopolysaccharides as granular material in cell vacuoles (blue-grey in MSB). There was no evidence of neurosecretion in any cell types.

Pigment

Pigment occurred between the cells in both the headwart and surrounding integument. It occurred in greater concentration in the head area than in the headwart.

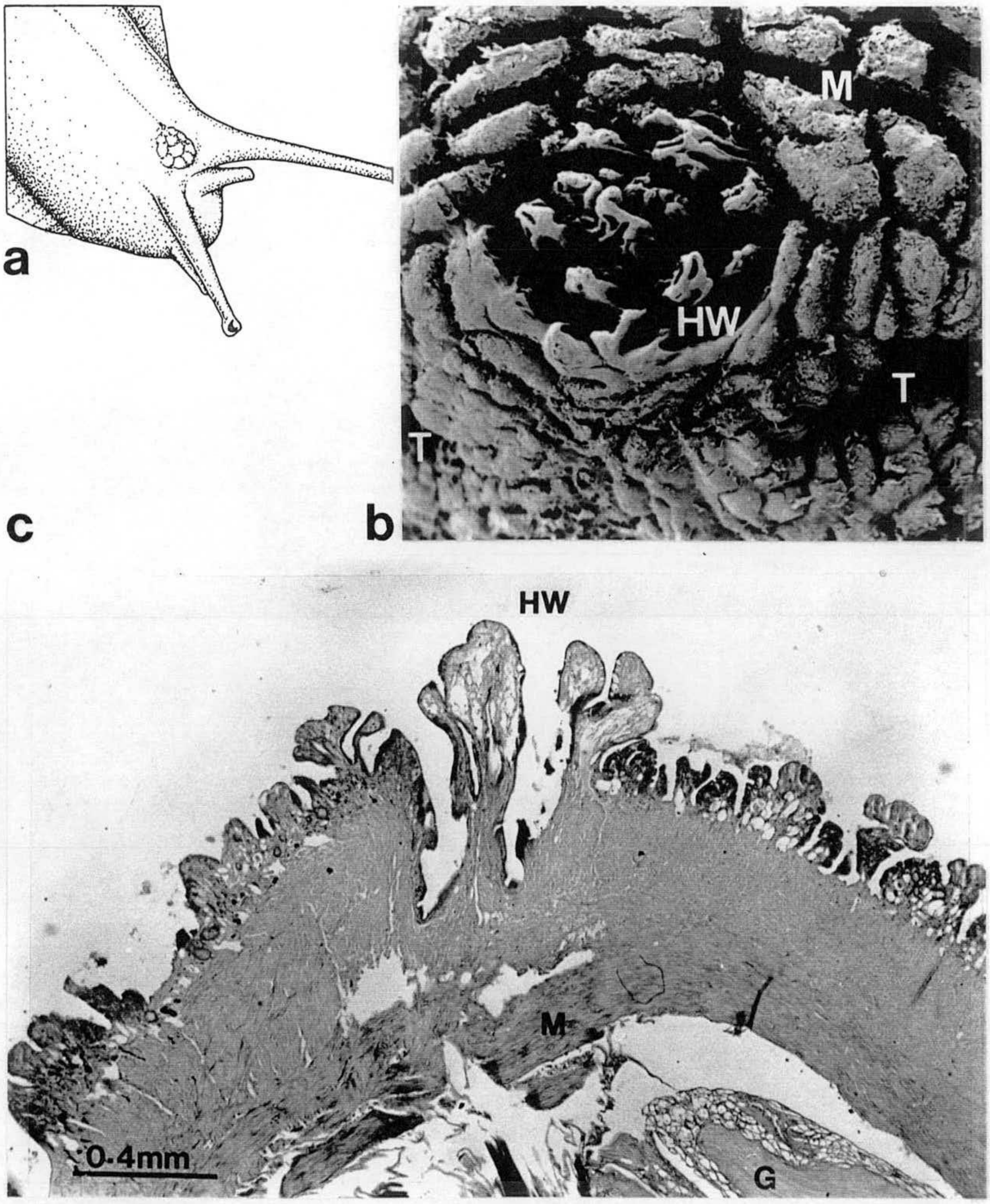


Fig. 5.1: Headwart of *Bentosites rawnesleyi* (Cox) (Magnetic Island): **a** everted during foraging; **b** HW, headwart; M, mucus flakes; T, inverted cephalic tentacle (SEM, x20); **c** HW, headwart; G, cerebral ganglion; M, muscle extending from underside of headwart (azan)

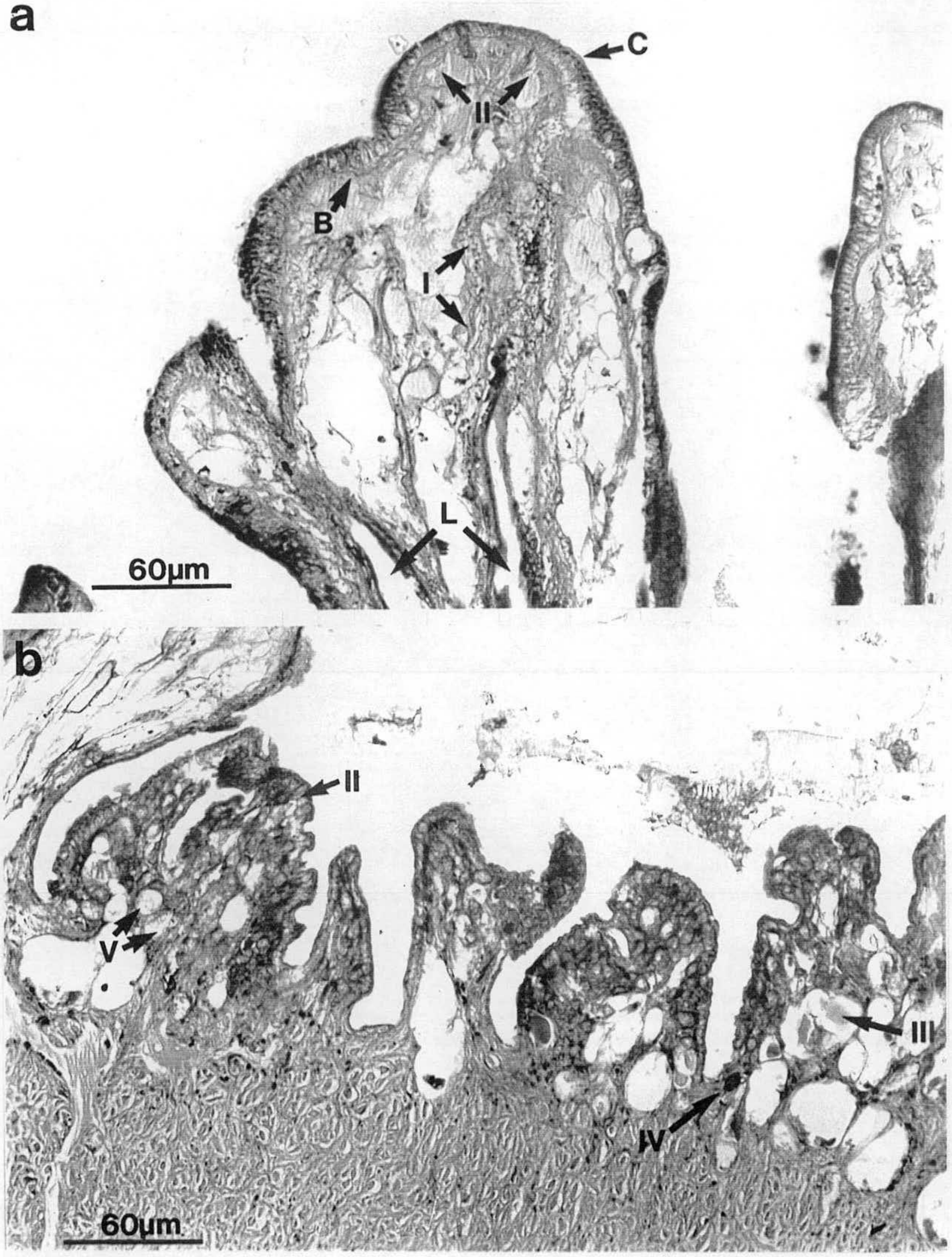


Fig. 5.2: Distribution of cell types of headwart and surrounding head integument of *Bentosites rawnesleyi* (Cox) (Magnetic Island): **a** headwart with refractive layer (R), basement membrane (B), lacunae (L), and cell types I and II; **b** adjacent integument showing cell types II - V (azan).

STAIN	DIFFERENTIATED CELL CONTENTS	
	ectal	**ental**
AB-PAS	magenta	pale pink
AZAN	red	pale orange
MSB	red	non-staining
PAF	non-staining	non-staining
BPB	dark purple	mid-blue
CAHP	pale pink	pale pink
RESULTS	acid mucopoly-saccharide protein	neutral mucopoly-saccharide protein

Table 5.1: Staining reactions of headwart epithelium

STAIN	UNDIFFERENTIATED CELL CONTENTS
AB-PAS	pale magenta blue
AZAN	red to orange
MSB	red
PAF	non-staining to dark purple
BPB	mid-blue to dark purple
CAHP	non-staining to magenta
RESULTS	acid and basic mucopolysaccharides protein

Table 5.2: Staining reactions of head epithelium

STAIN	CELL TYPE				
	I	II	III	IV	V
AB-PAS	magenta	pink	not seen	not seen	not seen
AZAN	non-staining	pink	not seen	not seen	not seen
MSB	non-staining	pink	not not	not seen	not seen
PAF	non-staining	non-staining	not seen	not seen	not seen
BPB	non-staining	dark purple	not seen	not seen	not seen
CAHP	non-staining	pink	not seen	not seen	not seen
RESULTS	neutral mucopolysaccharide	undetermined mucopolysaccharide protein			

Table 5.3: staining reactions of subepithelial cells of headwart

STAIN	CELL TYPE				
	I	II	III	IV	V
AB-PAS	not seen	pink	magenta blue	magenta	non-staining
AZAN	not seen	red	red	red	blue
MSB	not seen	red	red	red	blue
PAF	not seen	non-staining	pink	pink	non-staining
BPB	not seen	dark purple	dark purple	dark purple	blue
CAHP	not seen	magenta	magenta	grey	grey
RESULTS		acid & neutral mucopolysaccharide protein	acid & neutral mucopolysaccharide protein	acid mucopolysaccharide protein	basic mucopolysaccharide

Table 5.4: staining reaction of subepithelial cells in head epithelium

Chapter 6

SYSTEMATIC REVIEW OF THE HADROID CAMAENIDS

Shell , radula and reproductive anatomy

All hadroid camaenids had medium to large shells, usually with a wrinkled sculpture (Fig. 6.1a-c), which was occasionally coarse and pustulose (Fig. 6.1d). The sculptures of *Spurlingia* and *Bentosites zebina* were entirely pustulose (Fig. 6.1e), and Gen. nov. A lacked all sculpture other than growth ridges (Fig. 6.1f).

The radulae of the hadroid camaenids are typically camaenid, with no unusual features (Solem, 1985). The basal support system comprises a single support ridge on the outer (ectoconal) side of the base plate, and two support ridges on the central tooth, one on either side (Fig. 6.2a). The mid- to late lateral teeth possesses a diminutive endocone, separated from the mesocone by a small notch (Fig. 6.2b). The transition from lateral to marginal teeth involves gradual reduction of the basal support, sharpening of the mesocone, and enlargement of the ectocone.

The eastern hadroids also shared similarities in genitalia. In all species, the ovotestis was composed of numerous lobes, the hermaphroditic duct entered on a small talon, the shaft of the spermatheca was long and the spermathecal head reached the base of the albumen gland, an epiphallus was present, and a penis sheath enclosed the distal epiphallus and penis (Fig. 6.3).

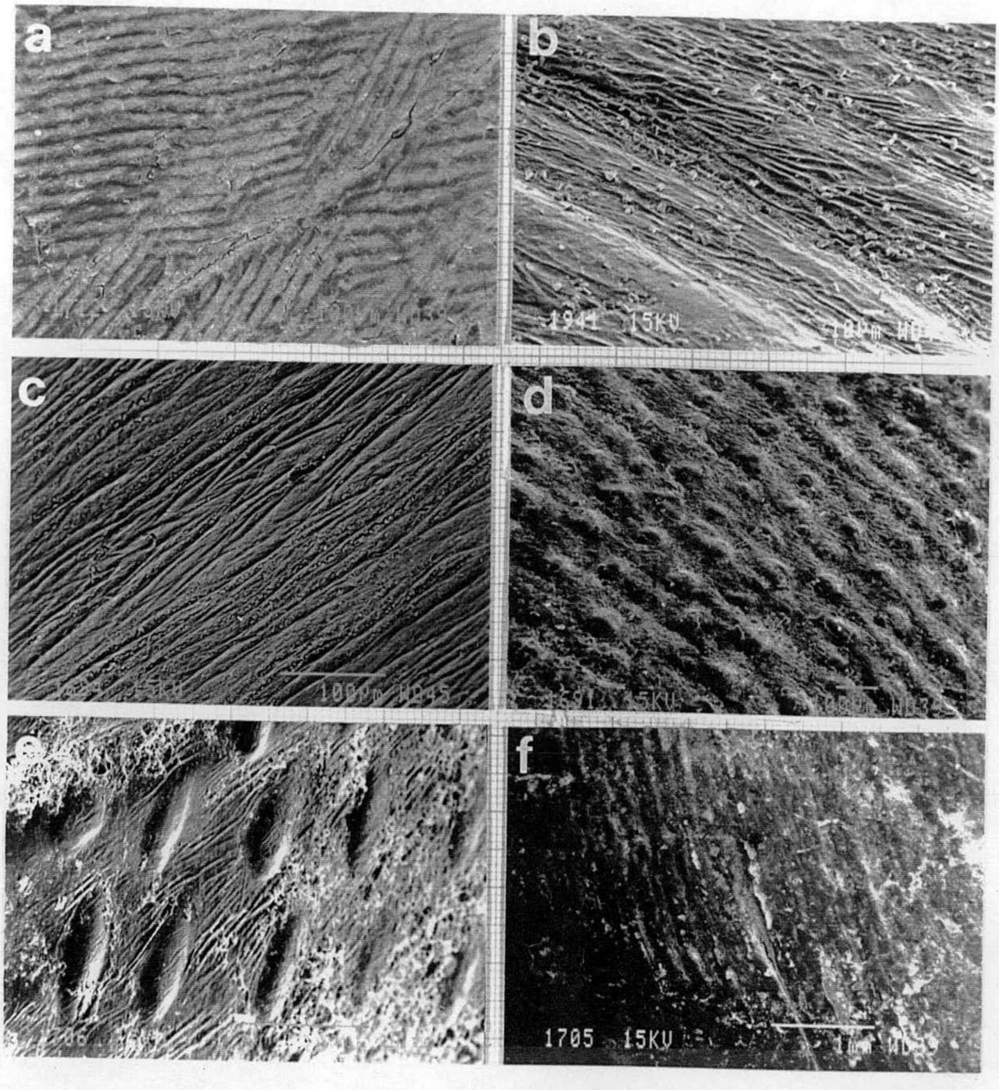


Fig. 6.1: Postapical sculpture on shells of hadroid camaenids: **a** *Hadra bellendenkerensis* (x 50), **b** *Bentosites macleayi* (x 2500), **c** *Sphaerospira fraseri* (x 150), **d** *Hadra barneyi* (x 50), **e** *Bentosites zebina* (x 150), **f** Gen. nov. A *incei* (x 15).

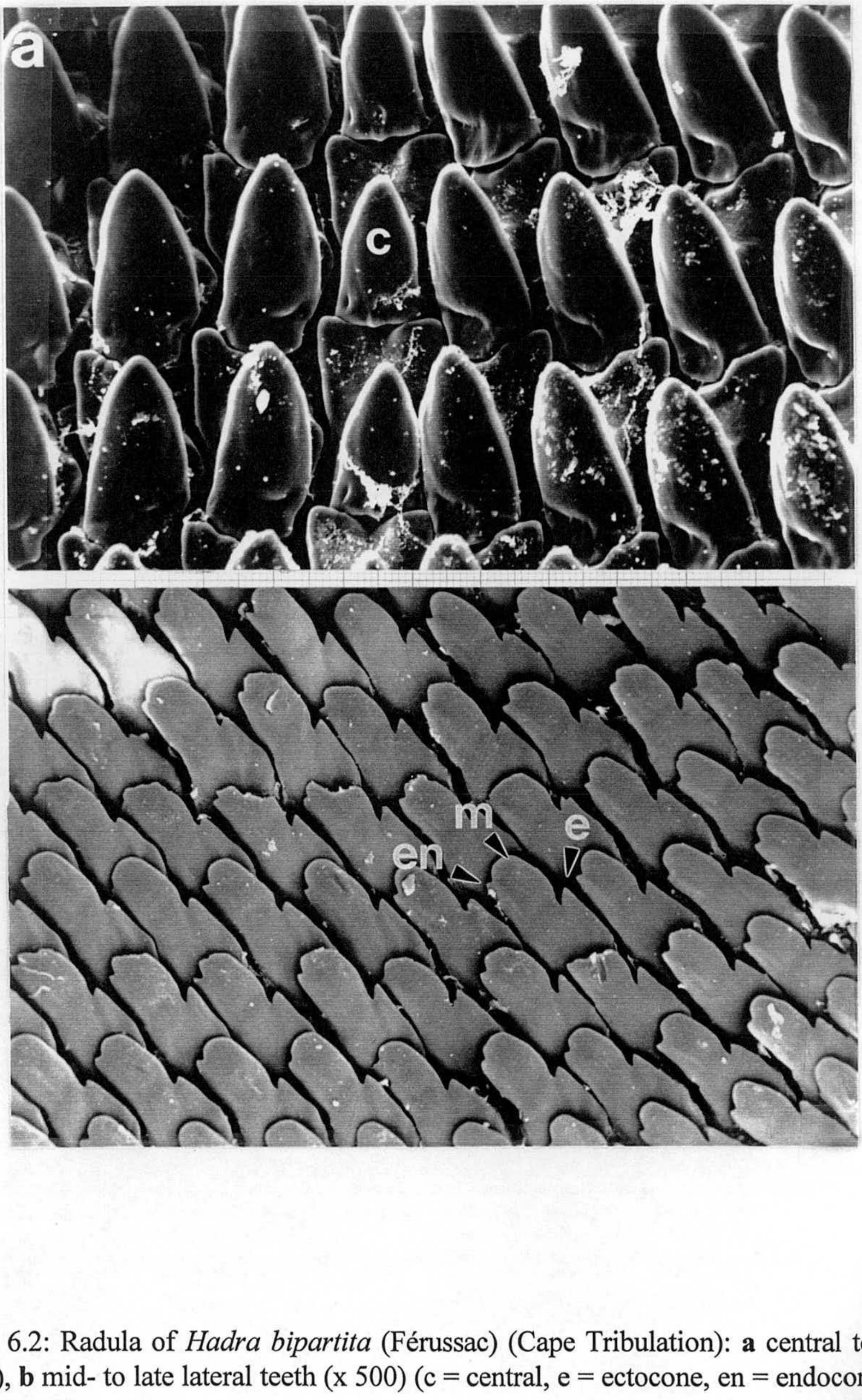


Fig. 6.2: Radula of *Hadra bipartita* (Férussac) (Cape Tribulation): **a** central tooth (x 500), **b** mid- to late lateral teeth (x 500) (c = central, e = ectocone, en = endocone, m = mesocone)

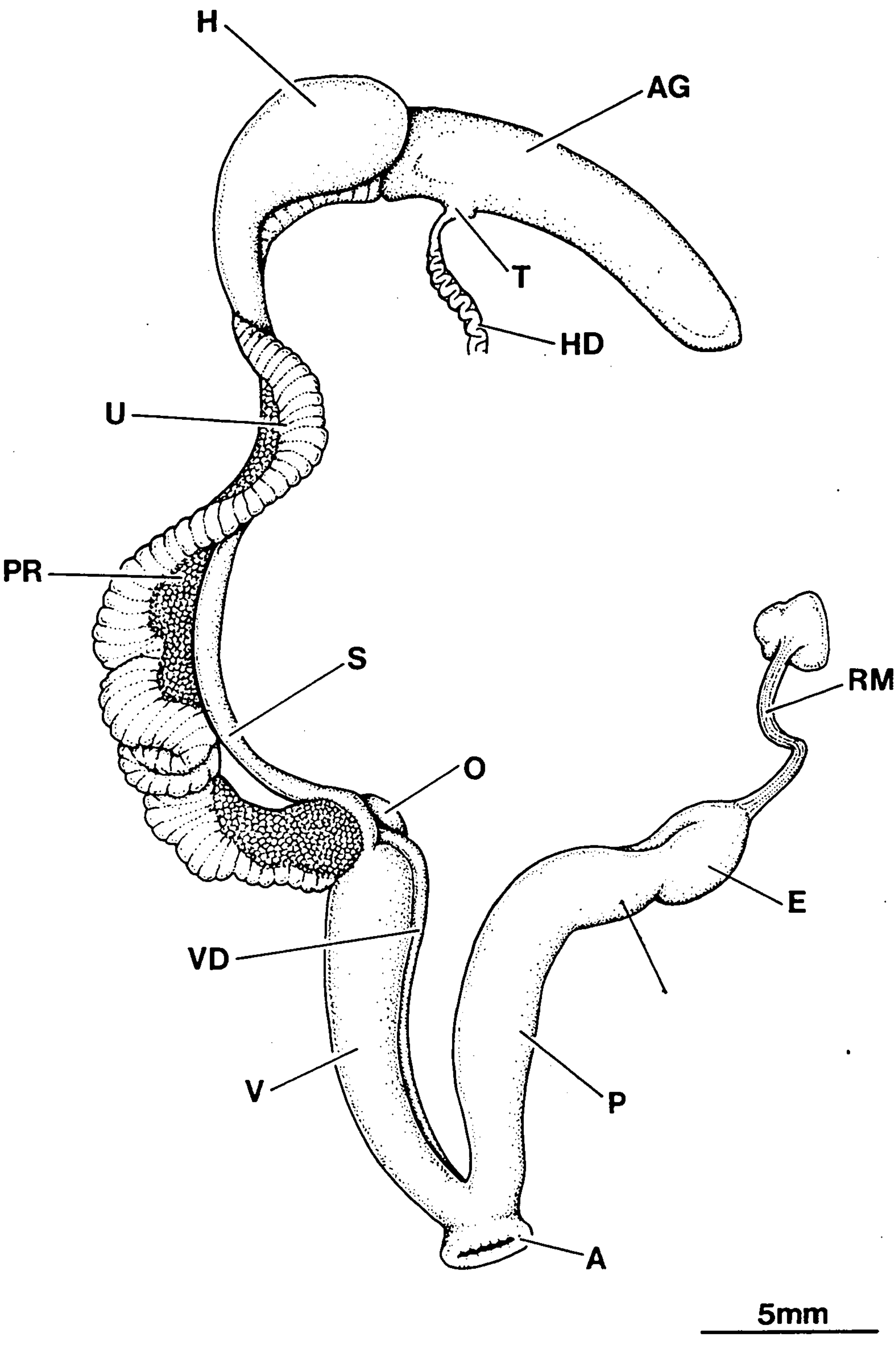


Fig. 6.3: Genitalia of *Bentosites macleayi* (Cox) (Whitsunday Island) (for key to abbreviations, see p. 50)

Key to the genera of larger camaenids in eastern Queensland rainforests

Anatomy

1.	Foot grey	2
	Foot orange	8
2.	Epiphallus with two caeca (may be contained within penis sheath)	3
	Epiphallus with single caecum or flagellum or both absent	4
3.	Epiphallus with two caeca proximal to penis sheath	*Hadra*
	Epiphallus with two caeca, one within penis sheath	*Zyghelix*
6.	Penis degenerate, in highly muscular penis sheath	Gen. nov. B
	Penis not degenerate, sheath thin (where present)	5
5.	Penis sheath runs from penial retractor muscle to genital atrium	6
	Penis sheath absent or much reduced	7
6.	Penis with penial papilla	*Sphaerospira*
	Penis without penial papilla	*Varohadra*
7.	Penis with large conical penial papilla	*Thersites*
	Penis with tubular penial papilla (terminal opening)	`*Meridolum*'
8.	Muscle fibres present in penial-epiphallic bend	Gen. nov. A
	Muscle fibres absent.	9
9.	Penis sheath of uniform thickness	*Bentosites*
	Penis sheath thin proximally, thicker distally	*Temporena*

Genus *Thersites* Pfeiffer, 1855

Thersites Pfeiffer, 1855: pl. 70, sp. 365; Iredale, 1933: 43; Iredale, 1937b: 37; Bishop, 1978b: 10; Richardson, 1985: 292; Smith, 1992: 161. Type species, *Helix richmondiana* Reeve, 1852, by subsequent designation (Martens, 1860).

Annakelea Iredale, 1933: 43; Iredale, 1937b: 37; Bishop, 1978b: 10; Richardson, 1985: 292; Smith, 1992: 161. Type species, *Helix richmondiana* Reeve, 1852, by original designation

Diagnosis

Thersites can be distinguished from related genera by the combination of large, frequently keeled shell, dark foot with light dorsal stripe, long epiphallic caecum, and large pointed penial papilla (Bishop, 1978b).

Description

Bishop (1978b) revised the genus, and described the shells and anatomy of the three species. I examined *Thersites richmondiana*, which is the type species, and found the anatomical description adequate. However, in the specimens I examined there was no evidence of the periostracal granules recorded by Bishop (1978b), only the wrinkled shell sculpture which is shared by most hadroid camaenids.

Species of *Thersites*

Three species of *Thersites* are known from southern Queensland and northern New South Wales:

- *Thersites richmondiana* (Reeve, 1852) - type species
- *Thersites novaehollandiae* (Gray, 1834)
- *Thersites mitchellae* (Cox, 1864)

Discussion

Bishop (1978b) presented the three species of *Thersites* as linearly parapatric. According to him, the most northerly distributed is *Thersites richmondiana*, which is found from the Conondale Ranges in Queensland to about Mullumbimby, in northern New South Wales. At the southern end of the *Thersites* range is *T. novaehollandiae*, occurring between Glen Innes and Port Stephens, New South Wales. Between these two fairly widespread species is *T. mitchellae*.

Thersites mitchellae is known largely from shell material and a single wet specimen in the Academy of Natural Sciences, Philadelphia. The anatomy was examined and figured by Pilsbry (1890), whose illustration was redrawn by Bishop (1978b). Although Bishop (1978b) believed the species to be extinct, small populations may exist in northern New South Wales (J. Stanisic and D. Potter, pers. comm.).

The principal differences between the three species of *Thersites* are in the size and shape of the shell and the epiphallic flagellum. *Thersites richmondiana* has an acutely keeled trochiform shell, *T. novaehollandiae* has a depressed to subglobose shell with a rounded periphery, while *T. mitchellae* has an almost trochiform shell with a rounded periphery. The sizes and shapes of epiphallic flagellum are similarly distributed within the three species, with *T. richmondiana* and *T. novaehollandiae* representing the extremes and *T. mitchellae* approximately midway.

Genus *Hadra* Albers

Hadra Albers, 1860: 165; Pilsbry, 1894: 131-132; Iredale, 1937b: 19-22; Solem, 1979: 133-141; Richardson, 1985: 150; Smith, 1992: 128-131. Type species *Helix bipartita* Férussac, 1823, by original designation.

Gnarosophia Iredale, 1933: 46; Iredale, 1937b: 25; Richardson, 1985: 148; Smith, 1992: 129. Type species *Helix bellendenkerensis* Brazier, 1875, by original designation.

Micardista Iredale, 1933: 47; Iredale, 1937b: 37; Solem, 1979: 133; Richardson, 1985: 288; Smith, 1992: 129. Type species *Helix (Camaena) barneyi* Cox, 1873, by original designation.

Spurlingia Iredale, 1933: 47; Iredale, 1937b: 24; Richardson, 1985: 290; Smith, 1992: 160. Type species *Helix nicomede* Brazier, 1878, by original designation.

Jacksonena Iredale, 1937b: 22; Richardson, 1985: 163; Smith, 1992: 131. Type species *Planispira rudis* Hedley, 1912, by original designation.

Diagnosis

Hadra can be distinguished from related genera by the combination of large to very large shell with sculpture of irregular wrinkles, proximal epiphallus with two caeca, and the presence of one or more sphincters in the penis.

Description

Shell medium to very large. Apical sculpture of weak to strong pustules and interrupted ridges, postapical sculpture of short ridges to shallow wrinkles. Shell periphery rounded to strongly keeled, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, partly occluding it. Umbilicus deep. Lip white or dark, solid. Foot colour grey.

Free oviduct short, less than 25% length of vagina, which is usually much shorter than penis. Epiphallus complicated with two well-developed caeca, which may be either quite distinct or compacted. The distal caecum may be long or short. Epiphallus is separated from penis by single sphincter, a single sphincter and distal flap of tissue, or two sphincters.

Species of *Hadra*

Five species of *Hadra* occur in Queensland rainforests:

- *Hadra bipartita* (Férussac, 1823) - type species
- *Hadra dunkiensis* (Forbes, 1851)
- *Hadra barneyi* (Cox, 1873)
- *Hadra bellendenkerensis* (Brazier, 1875)
- *Hadra rudis* (Hedley, 1912)
- \+ one other not in rainforest ('*Spurlingia*' *praehadra* from Chillagoe caves)

Discussion

Albers introduced the generic name *Hadra* in 1860 to cover the large and distinctive snail *Helix bipartita* Férussac 1823. The most recent investigation into the genus was that of Solem (1979), who published a description of the reproductive anatomy of *Hadra bipartita*, but did not present a formal diagnosis. He did not wish to revise *Hadra*, but needed to discuss the type species as Iredale's family Hadridae was based upon it.

Gnarosophia Iredale 1933 was proposed to cover a series of very similar large shells from North Queensland. *Helix bellendenkerensis* Brazier 1875, from the Bellenden Ker mountains, was designated as type, and its resemblance to both *Hadra* and *Sphaerospira* noted. Iredale thought its "strongly wrinkled sculpture" (1933: 46) indicated a close relationship to the latter. Dissection of the type species in this study demonstrated that it should be included in *Hadra*, so *Gnarosophia* is here considered a junior synonym.

The monotypic genus *Micardista* Iredale 1933 was thought by Iredale (1937b) to be far removed from either *Hadra* or *Gnarosophia*. Iredale (1933) mentioned it at the end of a lengthy exposition on *Hadra*, noting a possible affinity with *Spurlingia* Iredale 1933, which he placed under a section on *Badistes*. In his list of Australian land shells (Iredale, 1937b), he positioned *Micardista* between *Pallidelix* Iredale 1933, and *Annakelea* Iredale 1933, reinforcing his impression that it was not a *Hadra*, *Gnarosophia* or *Sphaerospira*. The type species, *Helix barneyi* Cox 1873, was examined by Solem (1979), who described the shell. It was indicated to him that *Hadra* and *Micardista* were synonymous, a decision made on the basis of reproductive tract morphology.

Spurlingia was introduced by Iredale in 1933 for the series of shells which included *Helix dunkiensis* Forbes, 1851, and *Helix nicomede* Brazier, 1878. Iredale (1933) remarked on the similarities between *H. barneyi* and the *dunkiensis* group, but erected the new genus, prinicipally on the basis of shell sculpture. Similarities between the genital morphology of *Spurlingia dunkiensis* and *Hadra bipartita* indicate that *Spurlingia* and *Hadra* are synonymous. Smith (1992) synonymised *Zyghelix* with *Spurlingia*, but an examination of the anatomy in this study indicated that there was not enough evidence to support this decision.

Jacksonena was erected by Iredale in 1937, to accommodate two species of *Planispira* with acutely keeled, subdiscoidal shells. Iredale (1937b) considered them to be allied to *Hadra*, but gave no reasons for this opinion.

Keys to the species of *Hadra* in eastern Queensland rainforests

Shell features

1.	Shell with white lip	2
	Shell with dark lip	4
2.	Shell bipartite	*bipartita*
	Shell unicolour	3
3.	Shell flattened and sharply keeled	*rudis*
	Shell rounded or weakly keeled	*dunkiensis*
4.	Shell yellow with paler peripheral band	*barneyi*
	Shell with several dark bands	*bellendenkerensis*

Genitalia

1.	Epiphallus/penis with one sphincter	2
	Epiphallus/penis with two sphincters	*bipartita*
2.	Penis lined with papillae only	*bellendenkerensis*
	Penis lined with ridges	3
3.	Free oviduct diverges at right angle	4
	Free oviduct does not diverge at right angle	*barneyi*
4.	Penis sheath thin near retractor muscle and much thicker near atrium	*dunkiensis*
	Penis sheath of even thickness	*rudis*

***Hadra bipartita* (Férussac)**

Helix bipartita Férussac, 1823: 17, pl. 75A, fig. 1 - Australia; Gray, 1825: 410; Wood, 1828: 23, pl. 7, fig. 59; Beck, 1837: 41; Deshayes, 1838: 108; Pfeiffer, 1847: 319; Albers, 1850: 85; Hombron & Jacquinot, 1851: pl. 3, figs 7-9; Reeve, 1852: sp. 359; Hombron & Jacquinot, 1854: 3-4; Dohrn, 1862: 209-210; Cox, 1864: 11; Cox, 1868: 54, pl. 5, fig. 7 - Cape York, Albany Island, Cape Direction, north eastern Australia; Semper, 1877: 159-161; Hedley, 1888: 57; Iredale, 1937b: 20 - restricted type locality to Cooktown, north eastern Queensland.

Helix semicastanea Pfeiffer, 1849: 77 - Nova Hollandia?; Pfeiffer, 1853: 222; Reeve, 1854: sp. 1348; Martens, 1860: 165; Cox, 1864: 11; Cox, 1868: 56, pl. 5, fig. 10; Hedley, 1888: 61; Iredale, 1937b: 20-21 - restricted type locality to Lizard Island, north eastern Queensland.

Helix funiculata Reeve, 1854, sp. 1363, pl. 194 - islands in Torres Strait, northern Queensland; Pfeiffer, 1854: 147; Cox, 1864: 15; Cox, 1868: 46, pl. 11, fig. 15; Tryon, 1887: 215, pl. 50, figs. 22-24; Hedley, 1888: 54; Iredale, 1937b: 22 - restricted type locality to Stephen's Island, Torres Strait, northern Australia.

Euhadra (Hadra) bipartita minor Pilsbry, 1890: 126, pl. 21, fig. 44 - no type locality; Pilsbry, 1894: 132; Iredale, 1937b: 20.

Chloritis (Hadra) bipartita unicolor Pilsbry, 1893: 276; Pilsbry, 1894: 132; Iredale, 1937b: 20.

Thersites webbi Pilsbry, 1900c: 473 - northern Queensland; Iredale, 1937b: 20 - restricted type locality to Cairns district, north eastern Queensland.

Thersites (Hadra) bipartita (Férussac) Marshall, 1927: 3-4, pl. 1, fig. 3.

Thersites (Hadra) lizardensis lizardensis Marshall, 1927: 4, pl. 2, fig. 7 - Lizard Island, north eastern Queensland; Iredale, 1937b: 21; Smith, 1992: 130.

Thersites (Hadra) lizardensis rada Marshall, 1927: 5, pl. 2, fig. 4 - Lizard Island, north eastern Queensland; Iredale, 1937b: 21; Smith, 1992: 130.

Thersites (Hadra) semicastanea alma Marshall, 1927: 7, pl. 3, fig. 8 - Cape York, northern Queensland; Iredale, 1937b: 21.

Thersites (Hadra) bartschi bartschi Marshall, 1927: 8, pl. 2, fig. 1 - Darnley Island, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 130.

Thersites (Hadra) bartschi mobiagensis Marshall, 1927: 8, pl. 1, fig. 1 - Mobiag Island, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi yamensis Marshall, 1927: 8, pl. 1, fig. 4 - Yam Island, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi oma Marshall, 1927: 9, pl. 3, fig. 2 - Yam Island, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi nura Marshall, 1927: 9, pl. 3, fig. 7 - Yam Island, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi nesia Marshall, 1927: 10, pl. 3, fig. 5 - Yam Island, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi paulensis Marshall, 1927: 10, pl. 3, fig. 10 - St Paul's Island, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi murrayensis Marshall, 1927: 10, pl. 1, fig. 5 - Murray Islands, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi fama Marshall, 1927: 10, pl. 3, fig. 9 - Murray Islands, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi elfa Marshall, 1927: 10, pl. 3, fig. 3 - Murray Islands, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi diva Marshall, 1927: 12, pl. 2, fig. 2 - Murray Islands, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) bartschi cepa Marshall, 1927: 12, pl. 3, fig. 1 - Murray Islands, Torres Strait, northern Queensland; Smith, 1992: 129.

Thersites (Hadra) waltoni Marshall, 1927: 12, pl. 2, fig. 3 - Murray Islands, Torres Strait, northern Queensland; Iredale, 1937b: 21; Smith, 1992: 129.

Thersites (Hadra) dalli Marshall, 1927: 13, pl. 2, fig. 8 - Murray Islands, Torres Strait, northern Queensland; Iredale, 1937b: 22; Smith, 1992: 129; Smith, 1992: 129.

Hadra webbi incallida Iredale, 1933: 43 - Atherton Tableland, north-eastern Queensland; Iredale, 1837b: 20; Smith, 1992: 131..

Hadra bipartita (Férussac) Iredale, 1937b: 20; Solem, 1979: 134-138, figs. 34-35; Richardson, 1985: 151-152; Smith, 1992: 130.

Hadra webbi (Pilsbry) Iredale, 1937b: 20; Richardson, 1985: 153; Smith, 1992: 131.

Hadra semicastanea (Pfeiffer, 1849) Iredale, 1937b: 20; Richardson, 1985: 152-153; Smith, 1992: 130

Hadra blighi Iredale, 1937b: 21 - Restoration Island, north eastern Queensland; Smith, 1992: 131.

Hadra (bartschi) quaesita Iredale, 1937b: 22 - Warrior Island, Torres Strait, northern Queensland; Smith, 1992: 129.

Hadra funiculata Iredale, 1937b: 22; Richardson, 1985: 152; Smith, 1992: 130.

Hadra waltoni (Marshall) Richardson, 1985: 153.

Hadra bartschi (Marshall) Richardson, 1985: 151; Smith, 1992: 129

Diagnosis

Shell medium to large, light to mid-brown above, dark brown to black below, lip white. Penis with two sphincters.

Description

Shell medium to very large, 22.4 to 68.3 mm (mean 46.9 mm) in diameter, and 15.8 to 57.3 mm (mean 37.5 mm) in height, with 5.00 to 7.125 (mean 6.157) whorls, H/D ratio 0.633 to 1.319 (mean 0.772). Apical sculpture worn smooth in all specimens examined, postapical sculpture of irregular wrinkles and radial growth ridges. Shell periphery rounded to sharply keeled, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening. Umbilicus deep. Shell usually light to mid-brown above, and dark brown to black below, divided sharply at periphery, sometimes by pale band. Occasionally a shell may be entirely yellow or light brown. Lip always white and porcellaneous. Shell solid to thin. Based on 385 measured adults.

Solem (1979) gave a detailed description of the genitalia of this species, based on a single specimen from the type locality. His description and illustrations agreed with material from other localities examined by me. No need exists to repeat the description, but Solem's illustration is reproduced here to allow direct comparison with other species (Fig. 6.4).

Discussion

Despite the glut of names which has filled the literature since the mid-1800s, all bipartite shells can be synonymised under *Hadra bipartita*. The species is extremely variable in size and shape, but is characterised conchologically by the colour pattern. Although workers were keen to raise individual bipartite specimens to the rank of species on the basis of size, spire height or gloss, this did not extend to the blond colour form, which was found to be widespread.

Dissection of material from a range of localities showed that the morphology of the male reproductive tract did not vary between populations, or between colour morphs. Solem (1979) illustrated a bipartite specimen from Cooktown (6.4), which Iredale (1937b) considered to be the type locality. His figure agreed with that of Pace (1901) of an individual from the tip of Cape York. Specimens from Lizard Island and islands in Torres Strait were examined during this study and judged to be conspecific on the basis of epiphallic and penial characters.

The confusion caused by intraspecific variation is explicable. Early workers dealt mainly with shells, erecting species on conchological evidence only. Iredale (1937b: 19) regarded the genus *Hadra* as being "a source of trouble for local conchologists who attempted to separate the species, using their special knowledge of the actual living conditions". He attacked Marshall, whose conclusions, he feels, were "tragical" (Iredale, 1937b: 19). Within the same paragraph, he pointed out that the geography of Torres Strait was of overriding importance, and that, if some of Marshall's new taxa were valid, it was likely that "many more [names] will also be necessary, as the colonies on each islet appear to differ a little" (Iredale, 1937b: 20).

MacGillivray (1851) reported that on Lizard Island individuals from the low scrub were solid and highly coloured, while those from the higher parts of the island are thin-shelled and dull. Ecological data are not available to examine this further, although specimens from island habitats tended to be much smaller than those from wet forest (Fig. 6.5), and the shells may also be quite thin. The keeled form, which Pilsbry (1900c) named *Thersites webbi*, was common on the Atherton Tableland, but was not confined to that area. Keeling may occur in any population and is not a useful character on which to base a species. The genitalia of keeled and round specimens from the Atherton Tablelands indicate that *T. webbi* is not a separate species from *Hadra bipartita.*

Hadra bipartita was shown to have the widest distribution of any hadroid camaenid, occurring from New Guinea to the Herbert River, a linear range of over 1000km. Its southern limit coincided approximately with that of *H. bellendenkerensis*, which may be significant biogeographically or an artefact of collecting regimes. Extralimital records from localities such as the Northern Territory, Hervey Bay, Qld, and Richmond River, NSW, were considered as either accidental introductions or the results of mistakes during labelling.

Range and habitat

Hadra bipartita is found on and coastally of the Great Dividing Range south to Mission Beach and north to the Torres Strait islands (Fig. 6.6). Extralimitally, it occurs in New Guinea. It is predominantly a rainforest species, but may be encountered anywhere where there is sufficient cover. It has been recorded from swamp at Daintree through a variety of rainforest types to coastal scrub and grass on Lizard Island. Populations on Flinders Island occur in open sclerophyll. A large altitudinal range is covered by this species: from sea level to the summit of Mt Bartle Frere (1586 m).

These snails rest by day in leaf litter where the brown apex of the shell is camouflaged against the forest debris. Pittas and mammalian predators often feed on this species. Damaged shells can be found in numbers indicating the presence of this species when no live animals can be located.

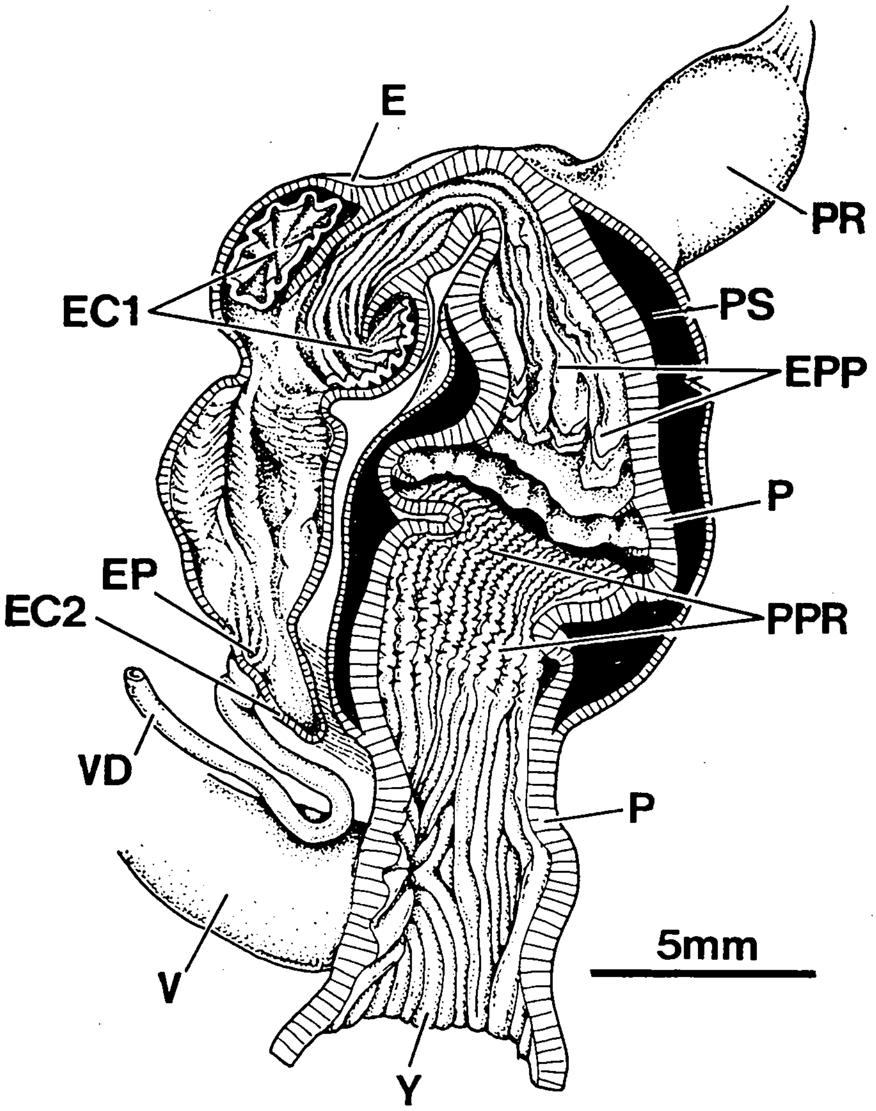
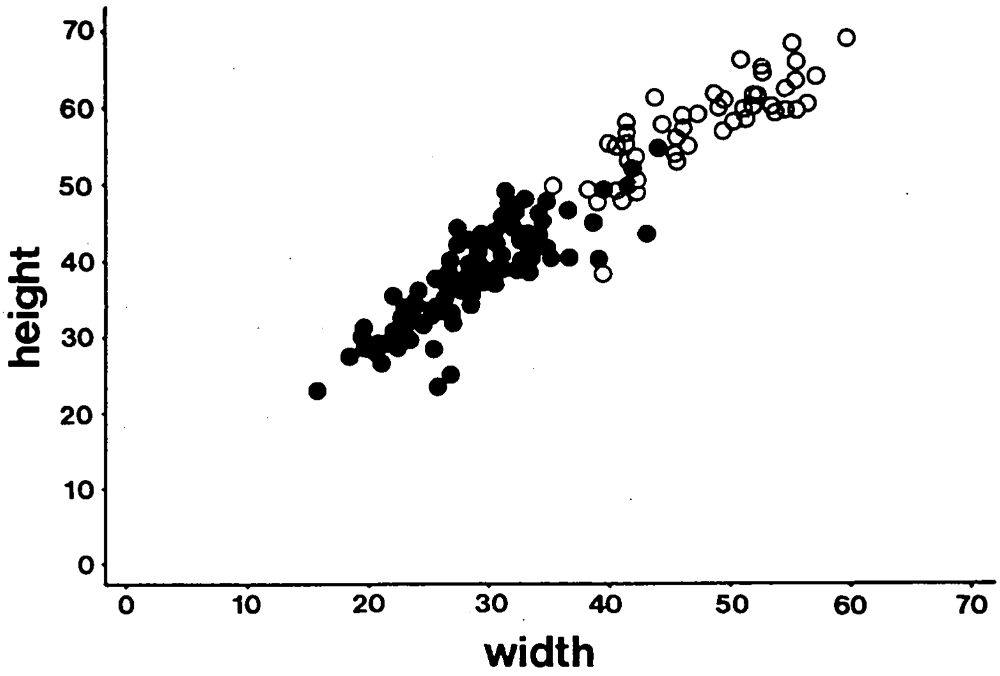


Fig. 6.4: Terminal genitalia of *Hadra bipartita* (Férussac) (labelled after Solem, 1979) (E = epiphallus; EC1 = distal epiphallic caecum; EC2 = proximal epiphallic caecum; EP = epiphallic pore; EPP = epiphallic pilasters; P = penis; PPR = penial ridges; PR = penial retractor muscle; PS = penial sheath; V = vagina; VD = vas deferens; Y = genital atrium) (redrawn from Solem, 1979)



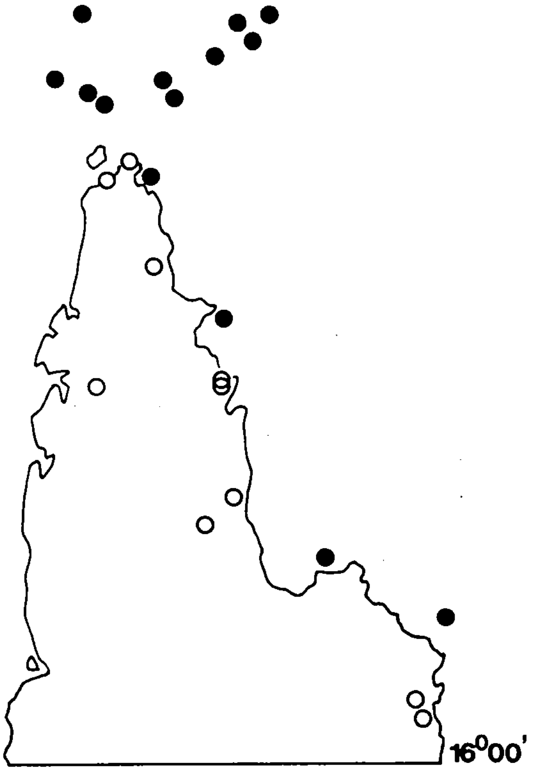


Fig. 6.5: Comparison of shell sizes of *Hadra bipartita* (Férussac) on Cape York Peninsula: ●, islands (n=118); ○, mainland (n=68).

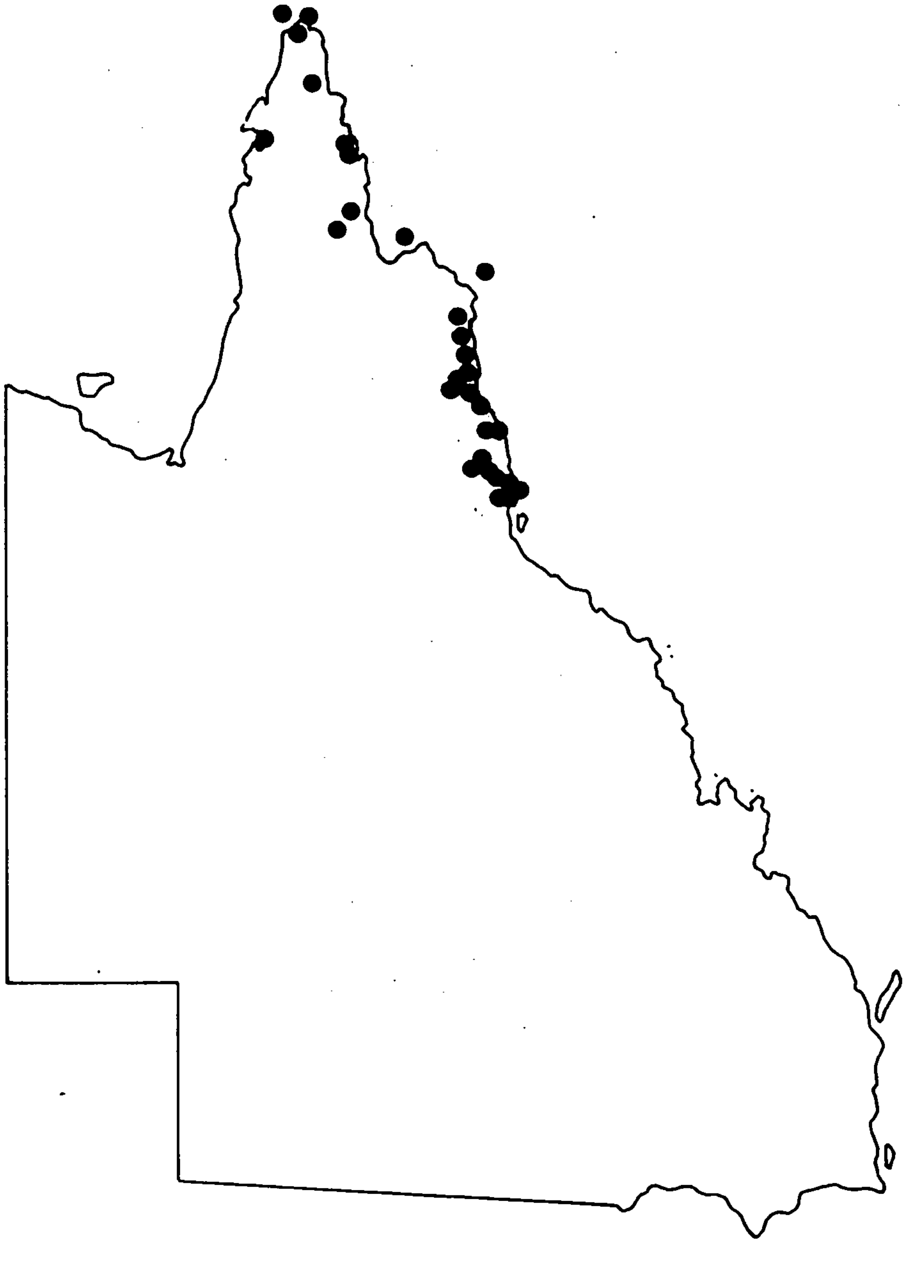


Fig. 6.6: Distribution of *Hadra bipartita* (Férussac).

***Hadra dunkiensis* (Forbes), comb. nov.**

Helix dunkiensis Forbes, 1851: 378, pl.ii, figs. 7a-b - Dunk Island, Queensland; Reeve, 1852: sp. 756; Pfeiffer, 1853: 224; Cox, 1864: 12; Cox, 1868: 43, pl. 8, fig. 9; Brazier, 1876: 122; Tryon, 1887: 215, pl. 50, figs. 22-24; Hedley, 1888: 54; Pilsbry, 1890: 134; Pilsbry, 1894: 130; Iredale, 1937b: 24; Smith, 1992: 160.

Helix (Hadra) coxenae Brazier, 1875a: 32 - Johnson River, Queensland; Hedley, 1888: 57; Pilsbry, 1890: 134; Pilsbry, 1894: 130; Iredale, 1937b: 24;.

Helix nicomede Brazier, 1878: 79, pl.8, fig.6 - Cardwell, Queensland; Hedley, 1888: 60; Pilsbry, 1890: 173, pl. 47, fig. 87; Pilsbry, 1894: 134; Iredale, 1933: 47; Iredale, 1937b: 24.

Spurlingia nicomede (Brazier) Iredale, 1933: 47; Iredale, 1937b: 24; Richardson, 1985: 290.

Spurlingia cadmus Iredale, 1937b: 25, pl. 2, fig. 6 - Goold Island, Queensland; Richardson, 1985: 290.

Spurlingia helga Iredale, 1937b: 25, pl. 2, fig. 4 - Hinchinbrook Island, Queensland; Richardson, 1985: 290.

Spurlingia portus Iredale, 1937b: 25, pl. 2, fig. 6 - Port Douglas, Queensland; Richardson, 1985: 290.

Diagnosis

Shell medium, rounded, pale yellow to horn, unbanded, lip white. Penis with single sphincter.

Description

Shell medium, 26.5 to 38.2 mm (mean 29.8 mm) in diameter, and 17.3 to 29.5 mm (mean 21.7 mm) in height, with 5.25 to 6.5 (mean 5.923) whorls, H/D ratio 0.665 to 0.847 (mean 0.721). Apical sculpture worn smooth in all specimens examined, postapical sculpture of irregular wrinkles and radial growth ridges. Shell periphery rounded to slightly keeled, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, not occluding umbilical opening. Umbilicus deep. Shell pale yellow to horn, lacking bands. Lip white and porcellaneous. Shell thin. Based on 30 measured adults.

Free oviduct short, less than 25% length of vagina, which is equal in length to penis. Free oviduct diverges from vagina at right angle and reflexes at right angle before entering uterus. Spermathecal shaft long, swollen at junction with vagina. Penial retractor muscle inserts on distal epiphallus, at junction with penis. Epiphallus has two caeca, one proximally at junction with vas deferens, the second at point of insertion of retractor muscle. Penis sculpture proximally of longitudinal folds overlain with shallow transverse furrows, gradually becoming irregular longitudinal ridges towards genital atrium (Fig. 6.7). Penis sheath thin near insertion of penial retractor, becoming thicker as it approaches atrium.

Discussion

The shell of *H. dunkiensis* is similar to the paler Torres Strait island forms of *H. bipartita*. Without reference to the anatomy, it may be impossible to distinguish between the two species.

At least two other species, probably closely-related to *H. dunkiensis*, occur in drier areas of North Queensland. *Spurlingia gemma* Iredale, 1937, and *S. excellens* Iredale, 1937, are both described from material collected in the Chillagoe/Almaden region. A possibly undescribed species is known from Yaramulla Station and Rosella Plains Station (Undara region), 150 km west of Cardwell.

Range and habitat

Hadra dunkiensis occurs in the southern portion of the Wet Tropics, from Hinchinbrook Island and Cardwell, north to Tinaroo in the central Atherton Tablelands. It also occurs on the smaller continental islands, including Goold Island and Dunk Island (Fig. 6.8). This species inhabits coastal rainforest.

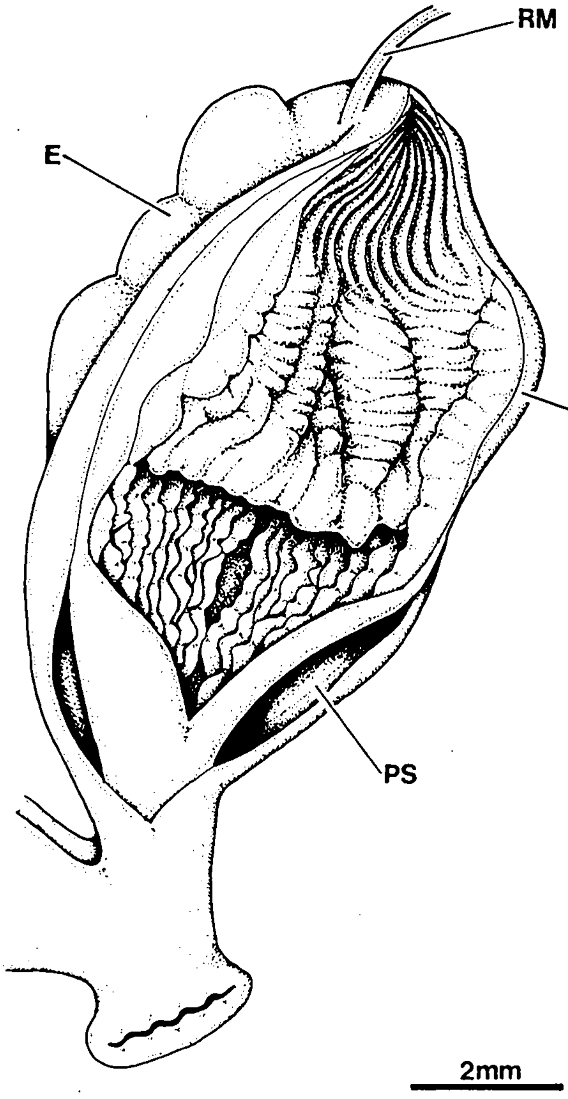


Fig. 6.7: Lining of penis of *Hadra dunkiensis* (Forbes) (Mt Carbine) (E = epiphallus, RM = penial retractor muscle, P = penis, PS = penial sheath)

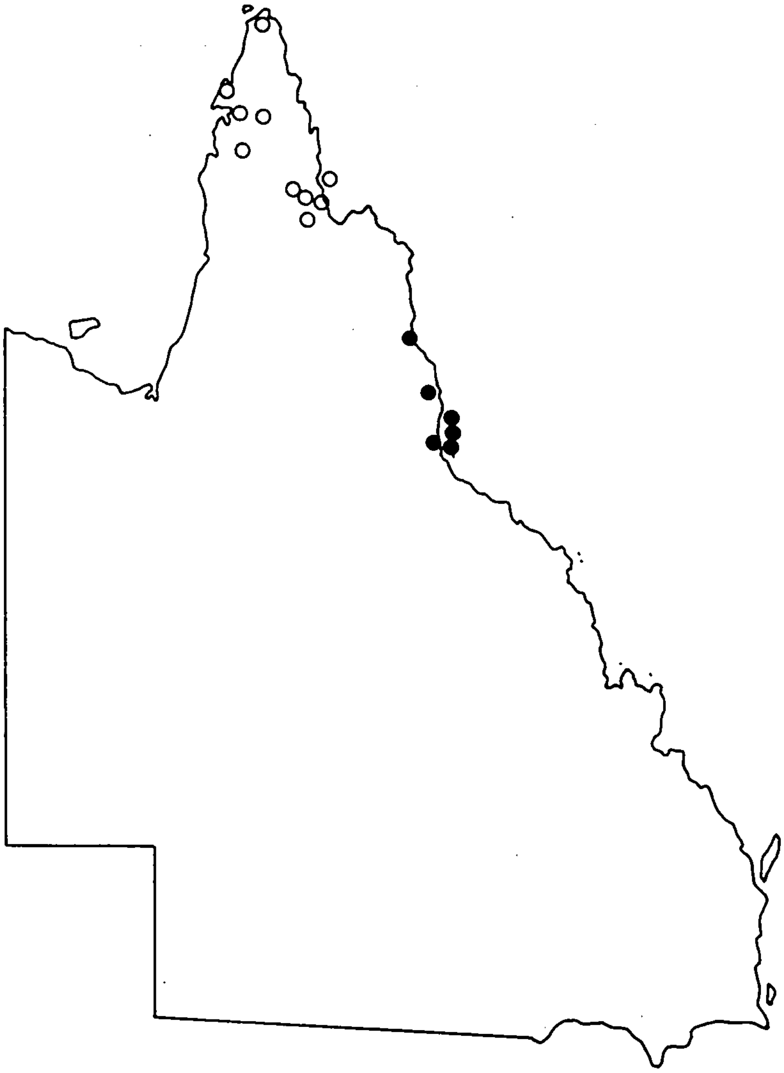


Fig. 6.8: Distribution of *Hadra dunkiensis* (Forbes) (●) and *H. barneyi* (Cox) (○). (Cox)

***Hadra barneyi* (Cox)**

Helix (Camaena) barneyi Cox, 1873a: 148, pl. 16, fig. 2 - Barney Island, Torres Strait; Pfeiffer, 1876: 365; Brazier, 1880: 305; Hedley, 1888: 56; Iredale, 1937b: 37; Solem, 1979: 138-139, figs. 33a-c.

Helix (Hadra) barneyi (Cox) Pilsbry, 1890: 165, pl. 34, fig. 6.

Thersites (Sphaerospira) barneyi (Cox) Pilsbry, 1894: 133.

Micardista barneyi (Cox) Iredale, 1933: 47; Iredale 1937b: 37.

Hadra barneyi (Cox) Solem, 1979: 138-139, figs. 33a-c; Richardson, 1985: 150; Smith, 1992: 129.

Diagnosis

Shell large, yellow to pale brown, light peripheral band, dark umbilical patch, dark lip. Penis with single sphincter and a flap of tissue.

Description

Shell large, 32.3 to 46.3 mm (mean 39.9 mm) in diameter, and 25.1 to 40.8 mm (mean 29.6 mm) in height, with 5.125 to 6.625 (mean 5.991) whorls, H/D ratio 0.74 to 0.927 (mean 0.794). Apical sculpture worn smooth in all specimens examined. Postapical sculpture of thick wrinkles and pustules. Shell periphery rounded, body whorl descending sharply behind lip. Lip is expanded and moderately flared, reflected over umbilical opening. Umbilicus deep. Shell yellow to pale brown with dark circum-umbilical patch and pale peripheral band. Lip dark and porcellaneous. Based on 32 measured adults.

Free oviduct moderately short, swollen at junction with vagina. Vagina short, about 50% length of penis and epiphallus. Spermathecal shaft long, swollen and curved at junction with vagina. Penial retractor muscle inserts distally on bend in epiphallus. Epiphallus complicated with two small caeca proximally. Proximal caecum short, lined with longitudinal ridges and grooves, minutely pustulate. Distal caecum shallow with multiple longitudinal folds. Distal epiphallus equal in width to penis, but junction marked externally by slight constriction. Epiphallus and penis separated internally by single high sphincter. The epiphallus and upper surface of sphincter are lined with irregular longitudinal ridges. Below this lies a flap of tissue, similar in size to the sphincter, but not wholly annular. Longitudinal ridges extend onto this flap. Penis short, not folded within thin penis sheath. Below sphincter the penial chamber is lined with a herringbone pattern of fine ridges which disappear into the genital atrium as longitudinal ridges (Fig. 6.9).

Discussion

This species occurs sympatrically with *Hadra bipartita*, but little is known of its ecology. Despite specimens of *Hadra barneyi* being comparatively rare in museum collections, Roth (1901) recorded that it was common item in the diet of the Nggerikudi people of the Pennefather and Batavia Rivers. The Nggerikudi name for the species is *tó-ri*.

Range and habitat

Hadra barneyi is found throughout inland Cape York Peninsula, as far south as Ebagoolah (14^{0}15'S) (Fig. 6.8). Records from the Torres Strait islands seem doubtful, but much of its probable range is poorly known. No records can be found of this species occurring in New Guinea.

Hadra barneyi occurs in isolated patches of vine thicket, under bark, under or in logs, or among rocks on vegetated outcrops. It may bury itself in friable soil under forest debris.

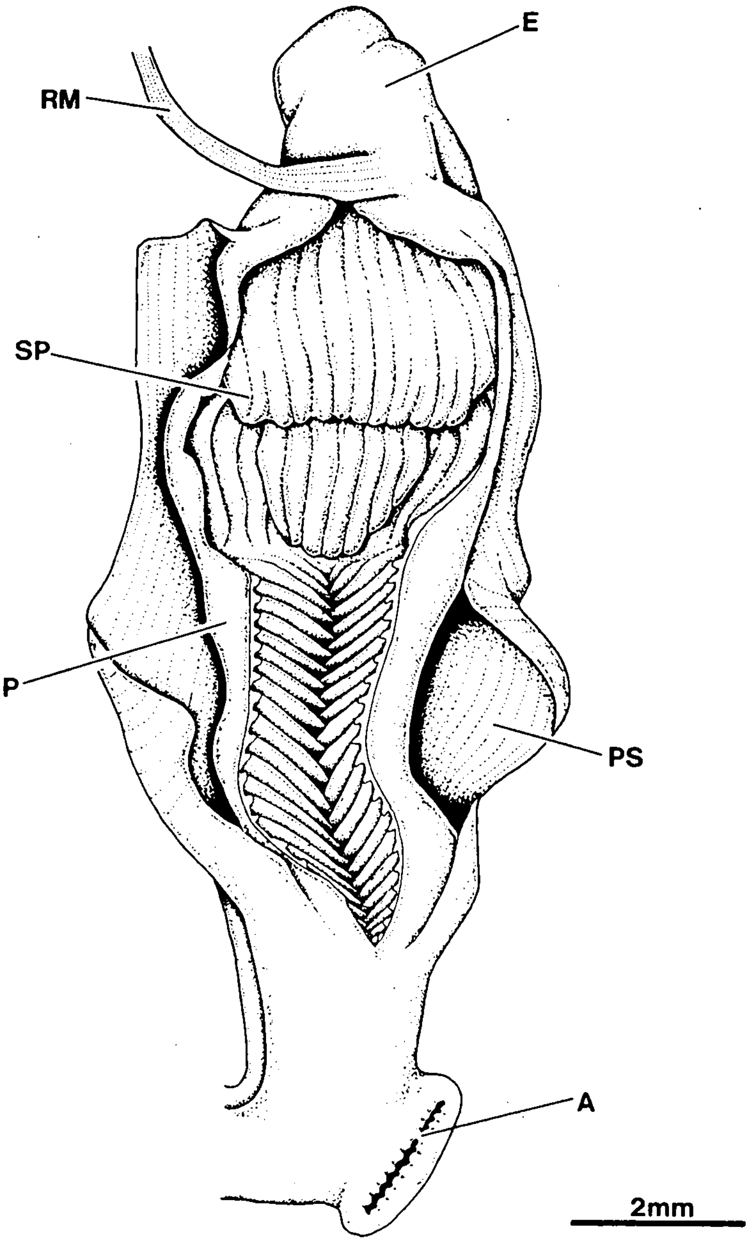


Fig. 6.9: Lining of penis of *Hadra barneyi* (Cox) (Lankelly Creek) (A = atrium, E = epiphallus, RM = penial retractor muscle, P = penis, PS = penial sheath, SP = penial sphincter)

***Hadra bellendenkerensis* (Brazier)**

Helix bellendenkerensis Brazier, 1875a: 32, pl. 4, fig. 4 - Bellenden Ker Mountains, North Queensland; Hedley, 1888: 57 (as *Helix bellenden-kerrensis*); Iredale, 1937b: 25.

Helix beddomae Brazier, 1878: 80, pl. 8, fig. 6 - Cardwell, Queensland; Iredale, 1937b: 25.

Thersites castanea Odhner, 1917: 87, pl. 3, figs. 97-98, textfig. 44 - Cedar Creek, Bellenden Ker Mountains, North Queensland; Iredale, 1937b: 26.

Gnarosophia bellendenkerensis (Brazier) Iredale, 1933: 46; Richardson, 1985: 148.

Gnarosophia beddomae (Brazier) Iredale, 1937b: 25; Richardson, 1985: 148.

Gnarosophia castanea (Odhner) Iredale, 1937b: 26; Richardson, 1985: 148.

Gnarosophia humoricola Iredale, 1937b: 26, pl. 2, fig 17 - Innisfail, Queensland; Richardson, 1985: 148.

Thersites pterinus Clench & Archer, 1938: 21 - Lake Barrine, Queensland; Richardson, 1985: 293.

Hadra bellendenkerensis (Brazier) Smith, 1992: 130

Diagnosis

Shell large, dark brown with paler bands, dark lip. Flagellum large. Penis with single sphincter.

Description

Shell very large, 37.5 to 56.3mm (mean 46.8mm) in diameter, and 30.6 to 46.7mm (mean 37.1mm) in height, with 5.125 to 6.375 (mean 5.737) whorls, H/D ratio 0.729 to 1.0 (mean 0.828). Apical sculpture of weakly irregular pustules and interrupted ridges, postapical sculpture of very shallow irregular wrinkles and radial growth ridges. Shell periphery rounded to mildly angular, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over the umbilical opening. Umbilicus deep. Shell dark brown with paler peripheral band and one or more other paler bands, dark subsutural band, dark radial band behind lip. Lip brown, glossy. Shell relatively solid. Based on 62 measured adults.

Free oviduct short, less than 25% length of vagina, which is equal in length to penis sheath, but is much shorter than penis. Proximally and distally free oviduct is narrow, median section distinctly swollen. Spermathecal shaft broad, diverging from vagina at an acute angle. Epiphallus complicated with two well-developed caeca proximally (Fig. 6.10a). Distal caecum lined with longitudinal ridges and grooves, proximal caecum with multiple longitudinal folds. Distal epiphallus mostly smooth, but may be thrown into longitudinal ridges by preservation techniques. Distal epiphallus equal in width to penis, but junction marked externally by slight constriction. Penis long, folded in penis sheath, which is very thin. Epiphallus and penis separated internally by single high sphincter, which may be constricted in preserved specimens giving impression of a penial papilla (Fig. 6.10b). Below the sphincter the penial chamber is lined with regular lozenge-shaped papillae (Fig. 6.11). Papillae fade out distally and are replaced by longitudinal ridges towards atrium.

Discussion

Odhner (1917) described *Thersites castanea* from Cedar Creek and other areas in the southern Atherton Tablelands. He made no reference to *H. bellendenkerensis*, although his specimens were almost topotypic. He examined the sculpture and interpreted it as demonstrating affinities between *T. castanea* and the southern *T. richmondiana* (Pfeiffer) and *T. novaehollandiae* (Gray).

Collecting around Innisfail produced *Gnarosophia humoricola* Iredale, 1937. The type locality was close to Bellenden Ker (approximately 30km south of the peak), but Iredale invoked the complex geological history of the area to allow specific status for a number of forms. Clench and Archer (1938) described a new species, *Thersites pterinus*, from Lake Barrine, on the Atherton Tablelands. They referred to it as "one of the rarest finds in *Thersites*" (1938: 21), and suggested an affinity with *Helix rainbirdi* Cox.

The types of *Thersites castanea*, *Gnarosophia humoricola* and *T. pterinus* resemble those of *Hadra bellendenkerensis* in colour, although the shape varies between shells. Examination of the genitalia of topotypic material confirmed Smith's (1992) opinion that these species should all be included in *H. bellendenkerensis*. A specimen of the bipartite *Helix beddomae* was dissected, demonstrating that this is a colour form of *Hadra bellendenkerensis*.

Hadra bellendenkerensis is distributed from Mt Pershouse on the Cardwell Range, north to the Endeavour River. Current evidence suggests that this species is restricted to the continuous block of vine forest which constitutes the Wet Tropics. So far, little collecting has been undertaken in the isolated patches of rainforest in the Seaview Range, south of the Herbert River.

Hadra bellendenkerensis and *H. bipartita* occur microsympatrically in the Wet Tropics, but *H. bellendenkerensis* appears to be much less abundant. Unlike *H. bipartita*, it is rarely found near pitta anvils.

The shell is variable in size and shape, but the colour pattern is stable over much of its range. Close to the southern limit, individuals sometimes have bipartite coloration: the top of the shell is dark brown, while the bands on the underside of the shell coalesce to form a solid black base. Juveniles of *H. bellendenkerensis* and *H. bipartita* may be confused, but the adults are distinguished by the difference in lip colour.

Range and habitat

Hadra bellendenkerensis is found mainly on the Atherton Tablelands, extending south to the Cardwell region and north to Cooktown (Fig. 6.12). This species is occurs exclusively in vine forest.

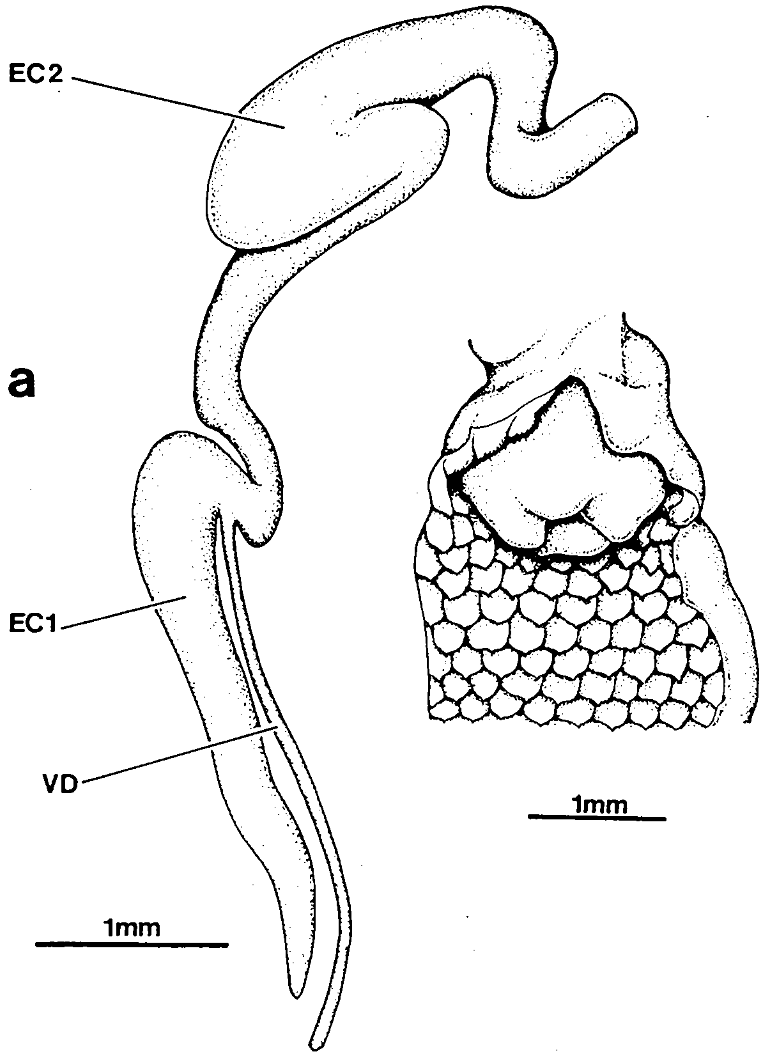


Fig. 6.10: Terminal male genitalia of *Hadra bellendenkerensis* (Brazier) (Jarrah Creek): **a** epiphallic caeca (EC1, EC2 = epiphallic caeca, VD = vas deferens), **b** penial sphincter constricted.

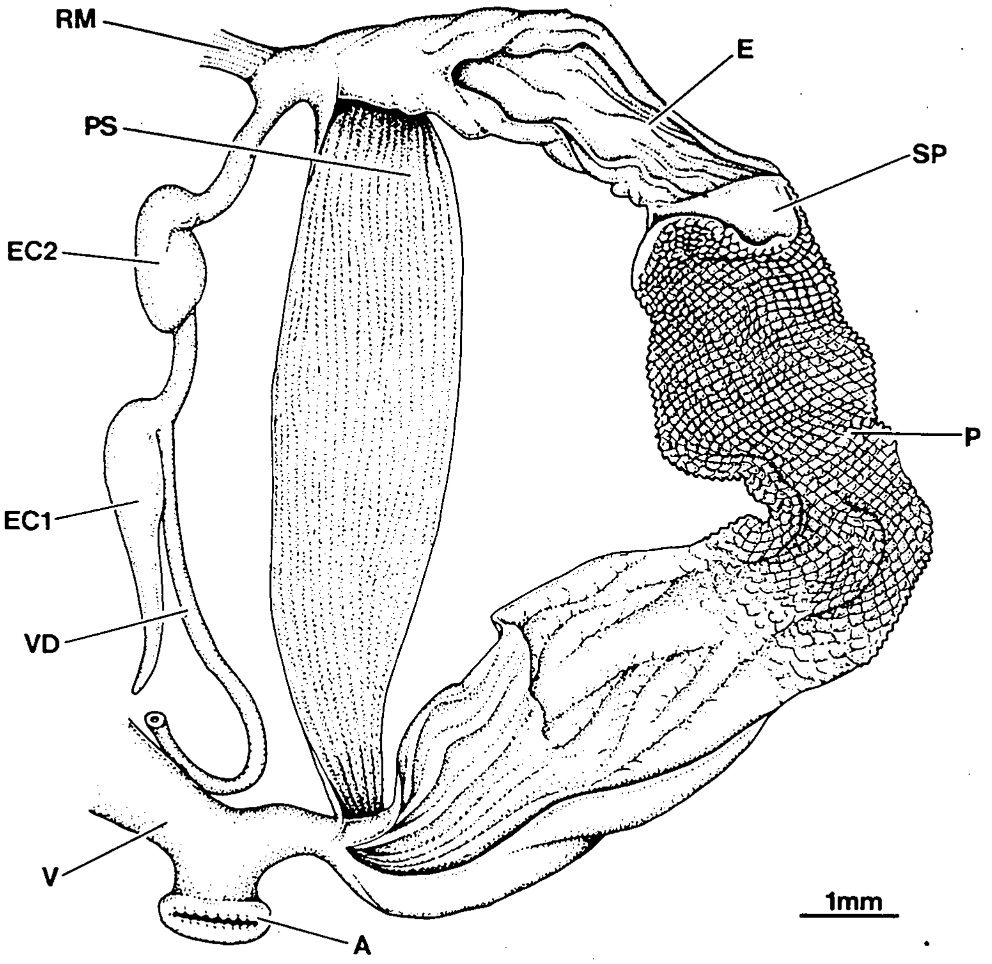


Fig. 6.11: Lining of penis of *Hadra bellendenkerensis* (Brazier) (Jarrah Creek) (A = atrium, E = epiphallus, EC1, EC2 = epiphallic caeca, RM = penial retractor muscle, P = penis, PS = penial sheath, SP = sphincter, V = vagina, VD = vas deferens).

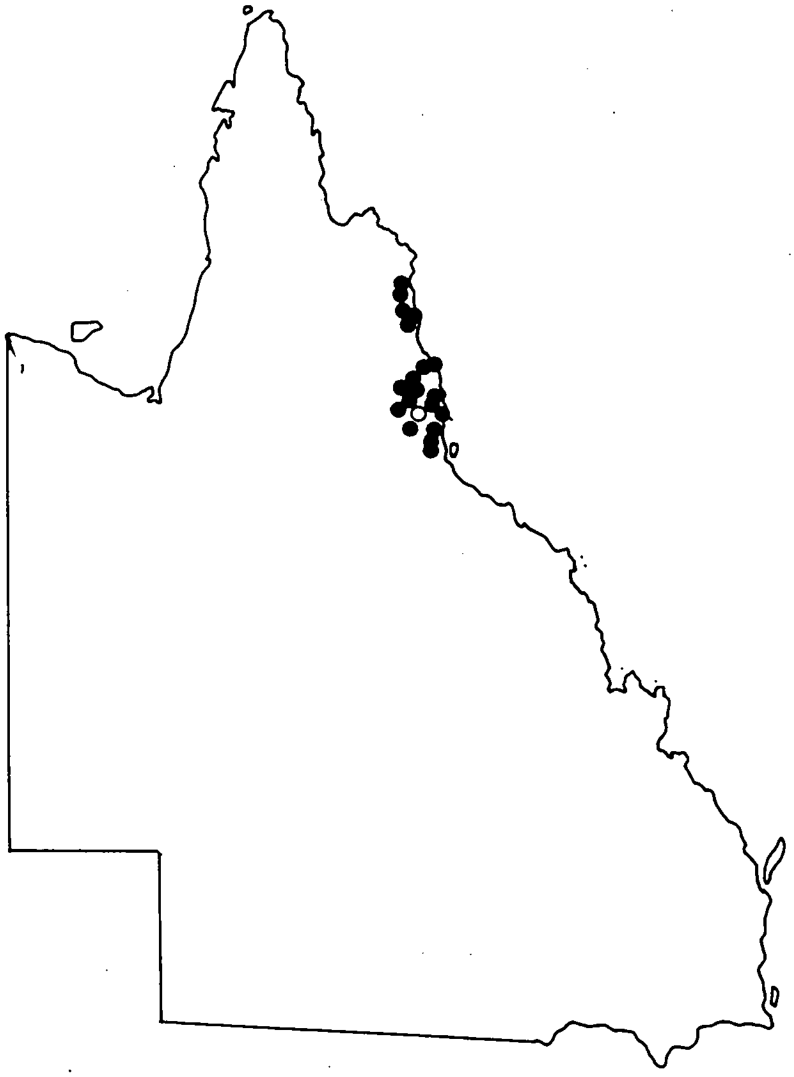


Fig. 6.12: Distribution of *Hadra bellendenkerensis* (Brazier) (●) and *H. rudis* (Hedley) (○).

Hadra rudis (Hedley), comb. nov.

Planispira rudis Hedley, 1912: 258 - Tinaroo Scrubs, SW of Cairns, Queensland; Iredale, 1937b: 22.

Jacksonena rudis (Hedley) Iredale, 1937b: 22; Richardson, 1985: 163; Smith, 1992: 131.

Diagnosis

Shell medium, sharply keeled, subdiscoidal. Penis with single sphincter.

Description

Shell medium, 26.0 to 35.1 mm (mean 29.87 mm) in diameter, and 11.7 to 17.0 mm (mean 16.37 mm) in height, with 6.75 to 5.25 (mean 5.00) whorls, H/D ratio 0.45 to 0.538 (mean 0.481). Apical sculpture worn smooth in all specimens examined, postapical sculpture of thick ropy wrinkles above keel overlain by growth ridges and other irregularities, finer typically hadroid wrinkles below keel. Shell periphery sharply keeled, body whorl descending slowly behind lip. Lip is expanded and moderately flared. Umbilicus open, wide and deep. Shell pale yellow to horn, lacking bands. Lip white and porcellaneous. Shell solid. Based on 3 measured adults.

Free oviduct short, less than 25% length of vagina, which is equal in length to penis. Free oviduct diverges from vagina at right angle and reflexes at right angle before entering uterus. Spermathecal shaft long and broad, not swollen at junction with vagina. Penial retractor muscle inserts on distal epiphallus, near junction with penis. Epiphallus long and not folded within penis sheath. Epiphallus has two caeca, one proximally at junction with vas deferens, the second at point of insertion of retractor muscle (Fig. 6.13). Penis sculpture of regular longitudinal zigzag ridges leading to the genital atrium.

Discussion

Although the shell of *Hadra rudis* does not resemble those of congeneric species, there are a number of reproductive characters which connect this and other *Hadra*. *Hadra rudis* has both the epiphallic caeca and the sphincter typical of the genus. In addition, the shell sculpture is similar to that of other *Hadra*.

Range and habitat

This species has been recorded from the Atherton Tableland, between Tinaroo and Palmerston National Park (Fig. 6.12). It is only known from vine forest.

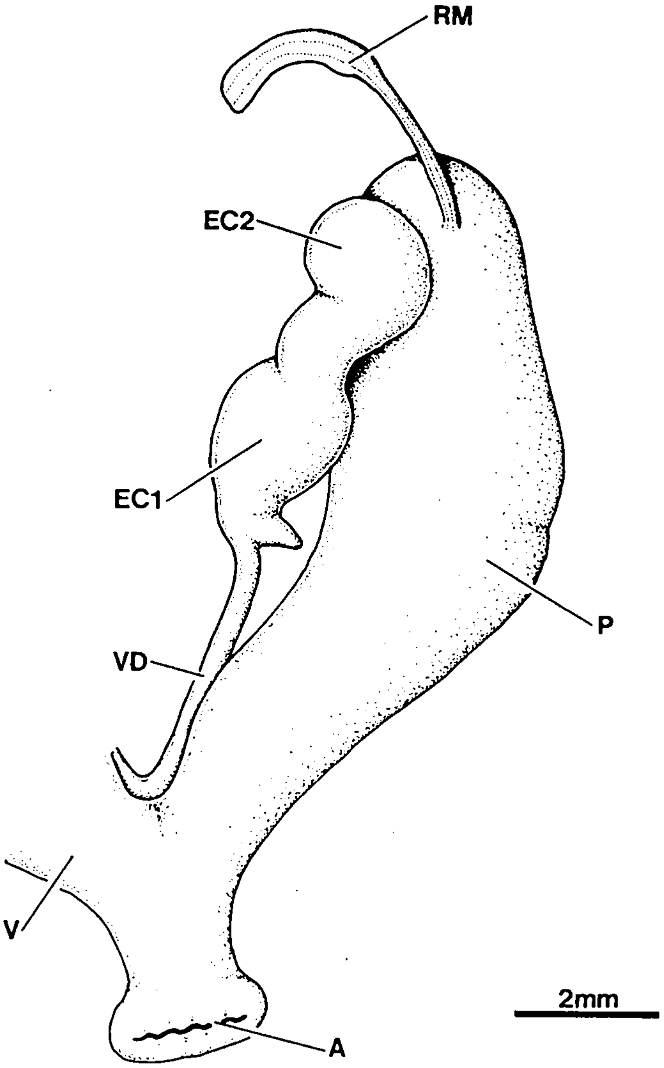


Fig. 6.13: Terminal male genitalia of *Hadra rudis* (Hedley) (Mt Bellenden Ker) (A = atrium, EC1, EC2 = epiphallic caeca, P = penis, RM = penial retractor muscle, V = vagina, VD = vas deferens).

Sphaerospira Mörch

Sphaerospira Mörch, 1867: 256; Pilsbry, 1891: 306; Iredale, 1937b: 27; Bishop, 1978: 200-208; Richardson, 1985: 288; Smith, 1992: 153-154. Type species, by subsequent designation, *Helix fraseri* Griffith & Pidgeon 1833.

Sphoerospira Fulton, 1904: 2.

Diagnosis

Sphaerospira can be distinguished from related genera by the combination of medium to large banded or plain shell with a glossy light brown to black lip, grey foot and collar, short epiphallic flagellum and small pointed penial papilla.

Description

Shell medium to very large. Postapical sculpture of fine irregular wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and moderately flared, reflected over umbilical opening, partly (*fraseri, informis*, sp. nov.) to wholly occluding it (*fraseri, blomfieldi, informis*). Shell pale brown with numerous darker bands, including subsutural and peripheral bands, dark radial line behind lip (*fraseri, informis*) or wholly brown with paler apex, sometimes with faint banding (*blomfieldi, informis,* sp. nov.). Lip light brown (sp. nov.) mid brown to dark purple to black (*fraseri, blomfieldi, informis*), glossy. Shell solid. Foot colour grey.

Free oviduct short, 25% or less length of vagina, which is roughly equal to penis sheath (*fraseri, blomfieldi, informis*) or shorter (sp. nov.). Free oviduct joins vagina smoothly (*fraseri*, sp. nov.) or diverges from it at right angles (*blomfieldi, informis*). Vagina swollen proximally, narrowing toward genital atrium. Spermathecal shaft broad, swollen at base (blomfieldi, informis, sp. nov.) or joining vagina smoothly (*fraseri*).

Small flagellum on epiphallus at junction with vas deferens with internal papilla marking entrance of vas deferens into epiphallus (*fraseri*) or flagellum and papilla absent (*blomfieldi*, *informis*, sp. nov.). Proximal epiphallus distinct from vas deferens. Penial retractor inserts proximally on bend in epiphallus (*fraseri*, *blomfieldi*, sp. nov.) or midway (*informis*). Penial papilla relatively small, ejaculatory opening subterminal. Penis lining of ridges (*fraseri*), ridges and papillae (*blomfieldi*, sp. nov.), or papillae (*informis*).

Species of *Sphaerospira*

Four species of *Sphaerospira* are found in eastern Queensland, of which one extends into northern New South Wales

- *Sphaerospira fraseri* (Griffith and Pidgeon, 1833) - type species
- *Sphaerospira blomfieldi* (Cox, 1864)
- *Sphaerospira informis* (Mousson, 1869)
- *Sphaerospira* sp. nov.

Discussion

Mörch erected the genus *Sphaerospira* in 1867, but failed to identify the type species. Pilsbry (1891) designated *Helix fraseri* Gray 1836. However, the species had already been described and figured by Griffith and Pidgeon (1833) from Gray's manuscript. Iredale initially considered *fraseri* and *informis* to be "so closely related they may be merely geographical representatives" (1933: 44). Later (1937) he separated them and recorded the variability of both species by assigning subspecific status to certain populations. He failed to recognise that *fraseri* and *informis*, like many other species of Camaenidae, vary continuously in size, shape and colour pattern.

Fulton (1904) had synonymised *mossmani* with *fraseri*, but Iredale (1937b) removed it from synonymy, because Brazier's original illustration (1875) showed it to be "a very distinct form" (1937b: 28). He preferred to leave it as a valid species until further study provided more solid evidence for synonymising it.

Iredale received a shell collected at Palmwoods, South Queensland, which he recognised as a *Sphaerospira*. He could not place it in *fraseri*, because of its large size, nor in *informis*, because of its location. He examined further material from Nambour and North Pine River, and decided to erect a new species, *parallela*, to cover the large shells of the Blackall Range.

King (1975) and Bishop (1978a) examined *Sphaerospira fraseri* from Cooloola and Kenilworth. King investigated aspects of reproductive behaviour and ecology, while Bishop studied the anatomy as a prelude to a taxonomic revision of the genus. No further taxonomic work was published on the genus until Smith (1992) synonymised *Bentosites* Iredale, 1933, *Varohadra* Iredale, 1933, *Temporena* Iredale, 1933, and Gen. nov. A (= *Figuladra* of Iredale, 1933, which is a *nomen nudum*) with *Sphaerospira*.

Key to the species of *Sphaerospira* in eastern Queensland rainforests

Genitalia

1. Flagellum at junction of vas deferens and epiphallus, with corresponding papilla in epiphallus..*fraseri*
   No flagellum..2
2. Penis lined with papillae only..*informis*
   Penis lined with ridges and papillae, or ridges only..3
3. Longitudinal ridges leading to genital atrium, penis folded in penis sheath..*blomfieldi*
   Oblique ridges leading to genital atrium, penis unfolded in penis sheath..sp. nov.

***Sphaerospira fraseri* (Griffith and Pidgeon)**

Helix fraseri Griffith & Pidgeon, 1833: pl. 36, fig. 6 (reversed); Gray, 1834: 64; Griffith & Pidgeon, 1836: pl. 36, fig. 6 (corrected); Griffith & Pidgeon, 1836: 597 - New Holland; Cox, 1868: 64, pl. 10, fig. 6; Iredale, 1937b: 27-28 - corrected type locality to Hay's Peak = Toowoomba, South Queensland.

Helix fraseri var. *flavescens* Hedley, 1888: 151 - Currumbin Creek, Queensland; Iredale, 1837b: 28. Not *Helix flavescens* Pfeiffer, 1848: 337.

Thersites (Sphoerospira) frazeri (sic) Fulton, 1904: 5.

Sphaerospira fraseri (Griffith & Pidgeon) Pilsbry, 1891: 304; Iredale, 1937b: 27-28; Richardson, 1985: 288; Smith, 1992: 155.

Sphaerospira parallela Iredale, 1937b: 27 - Blackall Range, Queensland; Richardson, 1985: 290.

Sphaerospira fraseri permuta Iredale, 1937b: 28, pl. 2, fig. 13 - Clarence River, New South Wales.

Sphaerospira fraseri feriarum Iredale, 1937b: 28, pl. 2, fig. 14 - Stradbroke Island.

Diagnosis

Medium to large banded or plain shell with mid-brown to black lip. Epiphallus with short flagellum, sometimes reduced to a small lump. Penis lined with numerous fine longitudinal ridges coalescing to form fewer, thicker longitudinal ridges at genital atrium.

Description

Shell medium to large, 38.2 to 58.7mm (mean 45.07mm) in diameter, and 32.9 to 42.6mm (mean 38.75mm) in height, with 5.5 to 6.5 (mean 5.772) whorls, H/D ratio 0.710 to 0.994 (mean 0.864). Apical sculpture worn smooth in all specimens examined, postapical sculpture of fine irregular wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and moderately flared, reflected over umbilical opening, partially to wholly occluding it. Shell pale brown with numerous darker bands, including subsutural and peripheral bands, dark radial line behind lip. Lip mid brown to dark purple to black, glossy. Shell solid. Based on 12 adults.

Free oviduct short, approximately 25% length of vagina which is equal in length to penis sheath. Free oviduct broad, joins vagina smoothly. Spermathecal shaft broad, not swollen at base. Small flagellum on epiphallus at junction with vas deferens. Internal papilla marks entry of vas deferens into epiphallus. Proximal epiphallus distinct from vas deferens. Penial retractor muscle inserts proximally on bend in epiphallus. Junction of epiphallus and penis marked externally by swelling, which is sometimes quite large, internally by pointed penial papilla, with basal ejaculatory opening. Penis lining simple, numerous fine parallel longitudinal ridges flanking sperm gutter (Fig. 6.14). Ridges sometimes broken and contracted into papillae proximally. Ridges break up into papillae opposite gutter. Ridges coalesce distally to form fewer, thicker longitudinal ridges leading to genital atrium.

Discussion

Sphaerospira fraseri is a very variable species with a wide range. Despite this, most workers recognised that the large snails of south east Queensland and north east New South Wales belonged to a single species. Iredale (1937b) identified a further species, *parallela*, from the Blackall Range, which is at the northern end of the *fraseri* distribution. Specimens of *parallela* were much larger than those of *fraseri* found to the south. Iredale selected North Pine River as the type locality, but this is very close to Brisbane and some distance from the Blackall Range. The holotype, which is a shell, almost certainly belongs to *fraseri*, so *parallela* is a junior synonym of *fraseri* (Smith, 1992).

Intraspecific variation in the penial lining is a possible source of confusion. Specimens from the D'Aguilar Range usually have a large outpocketing in the wall of the penis near the penial papilla. The ridges in the penial wall are fine and are rarely thrown into folds. In northern New South Wales, near the southern limit of the species, specimens lack the outpocketing. In the Mary River valley and Blackall Range, where shells are quite large, the penis is folded, and proximal ridges are frequently distorted into tiny papillae. It may be that several species exist within this area. If this is so, they cannot be distinguished reliably from reproductive anatomy alone, and may require further investigation using molecular techniques.

The shells of *fraseri* vary in size, shape and colour. Striped and brown shells are the most common, but blond individuals occur regularly. Hedley (1888) found a single blond specimen at Currumbin, which he named var. *flavescens*. The shell was yellow with a white lip, but the animal was not a true albino for the body was the normal grey colour. The colour of the mantle was not recorded.

Range and habitat

Mary River region, Queensland, to Clarence River, New South Wales (Fig. 6.15). *Sphaerospira fraseri* is found in a wide variety of habitats including vine forest, vine thicket; sclerophyll woodland, parks and gardens.

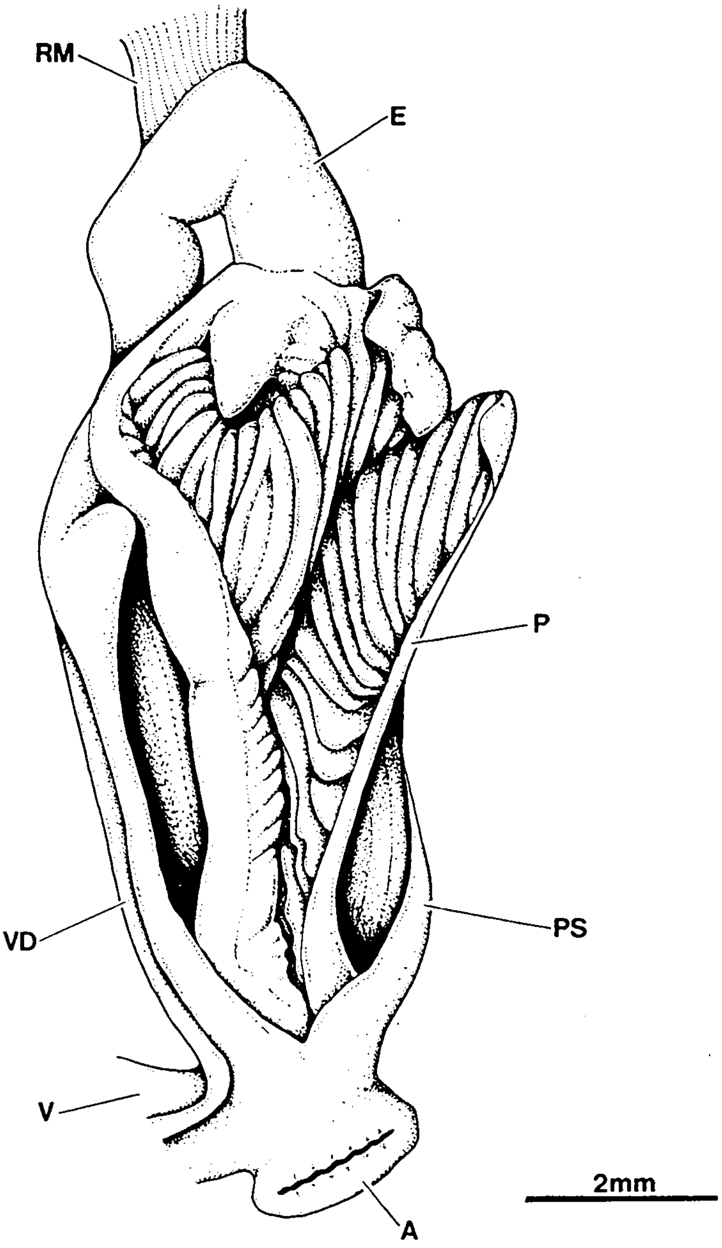


Fig. 6.14: Lining of penis of *Sphaerospira fraseri* (Griffith and Pidgeon) (Mt Glorious) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle, V = vagina, VD = vas deferens).

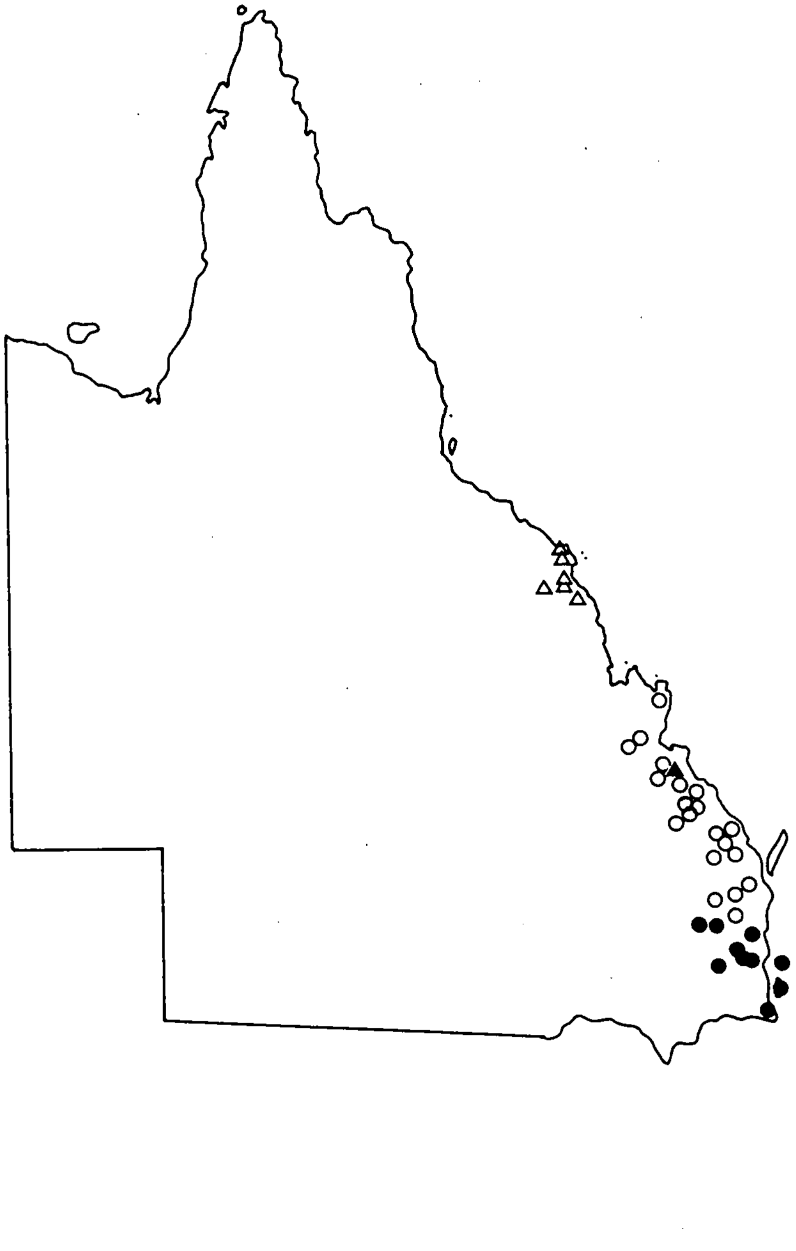


Fig. 6.15: Distribution of *Sphaerospira fraseri* (Griffith and Pidgeon) (●), *S. blomfieldi* (Cox) (○), *S. informis* (Mousson) (△), and *S.* sp. nov. (▲).

Sphaerospira blomfieldi **(Cox)**

Helix blomfieldi Cox, 1864b: 19 - Miriam Vale, Port Curtis, Queensland; Cox, 1868: 57, pl. i, fig. 1; Hedley, 1888: 57; Iredale, 1937b: 30.

Helix mossmani Brazier, 1875a: 33, pl. iv, fig. 6 - Dawson River, Queensland; Hedley, 1888: 60; Iredale, 1937b: 28.

Hadra blomfieldi var. *warroensis* Hedley & Musson, 1892: 556 - Warro, near Port Curtis; Iredale, 1937b: 30.

Thersites (Sphoerospira) blomfieldi (Cox) Fulton, 1904: 8.

Hadra mortenseni Iredale, 1929: 292 - Queensland; Iredale, 1937b: 33 - restricted type locality to Parnassus Range, north of Byfield, Queensland; Smith, 1992: 157.

Bentosites blomfieldi (Cox) Iredale: 1937b: 30; Richardson, 1985: 65.

Bentosites blomfieldi sidneyi Iredale, 1933: 45 - Coolabunia, Kingaroy, South Queensland; Iredale, 1937b: 30, pl. ii, fig. 23.

Bentosites blomfieldi latior Iredale, 1933: 45 - Mary River, Queensland; Iredale, 1937: 30, pl. ii, fig. 26.

Bentosites mortenseni (Iredale) Richardson, 1985: 308.

Sphaerospira blomfieldi (Cox) Smith, 1992: 154

Sphaerospira mortenseni (Iredale) Smith, 1992: 157.

Diagnosis

Vas deferens without flagellum. Proximal epiphallus with villi. Penis very long, folded within penis sheath, without pouch. Shallow penial papilla. Penis lined with anastomosing papillate ridges proximally merging into longitudinal ridges distally.

Description

Shell medium to large, 31.7 to 46.3 mm (mean 38.51) in diameter, and 29.3 to 46.2 mm (mean 38.17 mm) in height, with 5.125 to 7.0 (mean 5.678) whorls, H/D ratio 0.918 to 1.087 (mean 0.991). Apical sculpture worn smooth in all specimens examined, postapical sculpture of fine subparallel wrinkles, commonly arranged longitudinally, and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and moderately flared, reflected over umbilicus, wholly occluding it. Shell dark brown, sometimes with faint banding, apex paler than body whorl, light subsutural band. Lip dark, glossy.

Free oviduct less then 25% length of vagina, swollen at base, diverging from vagina at right angle. Vagina swollen proximally, narrowing towards genital atrium, approximately equal in length to penis sheath. Spermathecal shaft long and broad, swollen at base. Penial retractor muscle inserts proximally on bend of epiphallus. Epiphallus with numerous villi and papillae. Epiphallus and penis folded within penis sheath. Epiphallus with high pilaster which terminates in shallow penial papilla, with basal ejaculatory opening. Penis lining simple, with anastomosing papillate ridges proximally merging into longitudinal ridges towards genital atrium (Fig. 6.16).

Discussion

The shell of this large species is most frequently brown with a paler apex, but striped specimens are widespread. Both *Helix mossmani* and *Hadra mortenseni* are striped forms from the northern edge of the range. The holotype of *Helix mossmani* could not be located, but Brazier's illustration (1875a, pl. iv, fig. 6) and comments indicate that this belongs in *S. blomfieldi*. The Dawson River (type locality of *H. mossmani*) is a tributary of the Fitzroy River, which flows through Rockhampton.

The distributions of *S. blomfieldi* and *S. fraseri* do not appear to overlap, although the southern and northern limits respectively come very close together. Intensive collecting in the Mary River valley and mountain ranges to the east would define the limits. In the discussion of *S. fraseri*, it was noted that individuals from the north differ from those in the centre and south of the distribution, in both reproductive anatomy and shell size. It may be that these represent a hybrid zone, stretching from Mt Bauple coastally to Kenilworth. This is purely conjecture as insufficient specimens are available for examination at this time.

Range and habitat

Sphaerospira blomfieldi is found from the Parnassus Range, north-east of Rockhampton, to Wondai, inland from Gympie (Fig. 6.15). It occurs in all types of rainforest from mesophyll and notophyll vine forest to semi-evergreen vine thicket. Its large size precludes it from climbing, but it is commonly found in leaf litter and rotting logs.

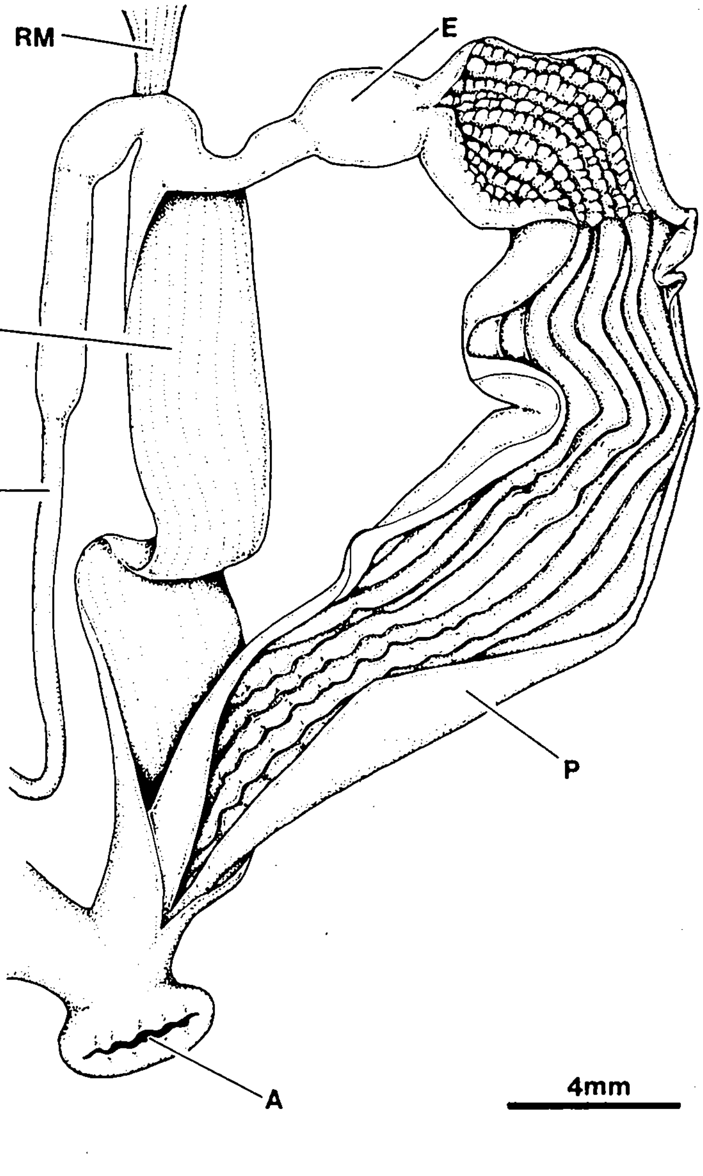


Fig. 6.16: Lining of penis of *Sphaerospira blomfieldi* (Cox) (Raglan) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens).

***Sphaerospira informis* (Mousson)**

Helix informis Mousson, 1869: 59, pl. iv, fig. 3 - Port Mackay Queensland; Tenison-Woods, 1875: 52; Hedley, 1988: 59; Iredale, 1937b: 28.

Helix infurius Tenison-Woods, 1875: 52 - typographical error only.

Thersites (Sphoerospira) informis (sic) (Mousson) Fulton, 1904: 8.

Sphaerospira informis (Mousson) Iredale, 1933: 44; Richardson, 1985: 290; Smith, 1992: 157.

Sphaerospira informis fringilla Iredale, 1937b: 28, pl. ii, fig. 12 - Finch Hatton, 50 miles W of Mackay.

Sphaerospira informis dietrichae Iredale, 1937b: 28, pl. ii, fig. 11 - Mt Dryander, Port Denison.

Diagnosis

Vas deferens without flagellum. Proximal epiphallus without papilla. Penis very long, folded within penis sheath, without pouch. Shallow penial papilla. Penis lined with numerous large square papillae.

Description

Shell large to very large, 41.2 to 63.5 mm (mean 53.45 mm) in diameter, and 37.6 to 65.4 mm (mean 52.7 mm) in height, with 5.25 to 7.25 (mean 5.942) whorls, H/D ratio 0.868 to 1.129 (mean 0.988). Apical sculpture worn smooth in all specimens examined, postapical sculpture of densely-packed subparallel wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and moderately flared, reflected over umbilicus, wholly or partially occluding it. Shell light to dark with numerous dark bands, dark radial line behind lip. Lip dark, glossy. Shell solid. Based on 51 measured adults.

Free oviduct short, less than 25% length of vagina, which is very long and folded many times. Free oviduct diverges from vagina at right angle. Spermathecal shaft long, swollen at base. Junction of vas deferens and epiphallus obvious, but no caecum or internal papilla. Penial retractor muscle inserts on bend in epiphallus. Epiphallus with high pilaster terminating in shallow penial papilla, with basal ejaculatory opening. Penis very long, coiled and folded within much shorter penis sheath. Penis lined with large square papillae, flattened and organised loosely in longitudinal rows toward genital atrium (Fig. 6.17). A narrow groove continues from base of penial papilla to atrium.

Discussion

Sphaerospira informis is one of the largest snails in Australia, and is the second largest native camaenid, exceeded only by *Hadra bipartita*. Individuals from montane rainforest are generally larger than those from lowland forests. Shells smashed by pittas are common in Eungella National Park, but live snails are rarely seen, except after rain. They hide under rocks and in and under logs, feeding at night on the ground and low down on the trunks of trees.

This species is the only wholly tropical *Sphaerospira*. Its northern limit is the isolated rainforest on Mt Dryander (J. Stanisic and D. Potter, pers. comm.), while the southernmost record is at Bell's Gap, south of Sarina. It is confined to vine forest, but frequently strays into rainforest gardens where its appearance is met with horror. The distribution of this species coincides roughly with that of *Bentosites yulei*, *B. gavisa* and *Varohadra oconnellensis*, suggesting that the Bowen and St Lawrence dry gaps to the north and south respectively may present a real barrier to these species (Bishop, 1981).

Range and habitat

Sphaerospira informis occurs in mid-east Queensland from Mt Dryander to south of Sarina (Fig. 6.15). This species occurs principally in vine forest, but is found occasionally well-watered parks and gardens.

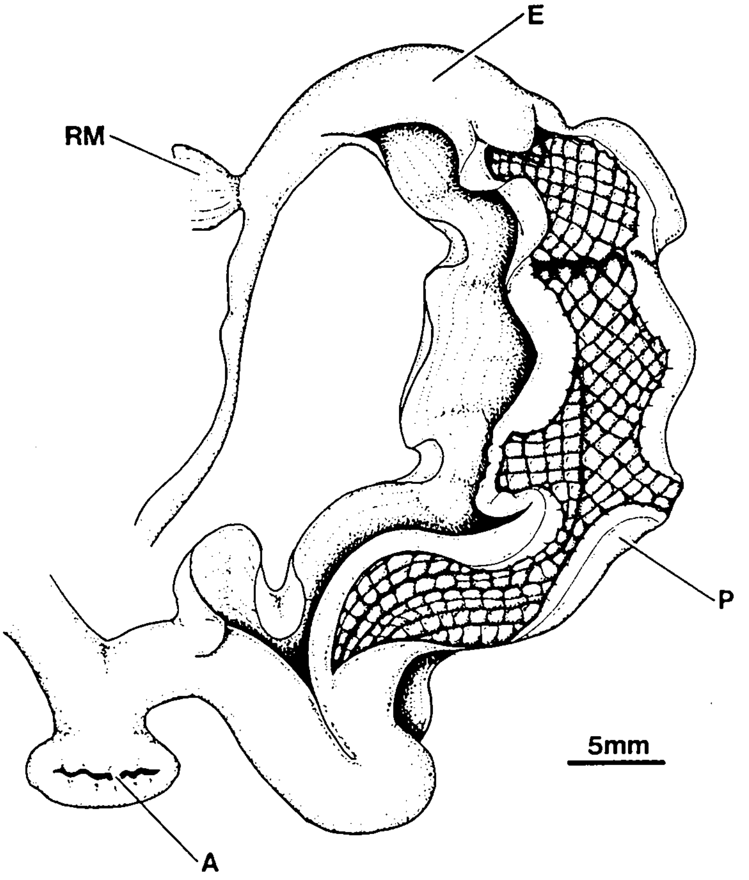


Fig. 6.17: Lining of penis of *Sphaerospira informis* (Mousson) (Eungella) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle).

Sphaerospira sp. nov.

Diagnosis

Vas deferens very thin, without flagellum. Epiphallus much longer than penis, unfolded. Penis very short, unfolded within penis sheath, without pouch. Shallow penial papilla. Penis lined with minute papillae proximally, merging into oblique ridges distally.

Description

Shell large, 33.0 to 33.1 mm (mean 33.05 mm) in diameter, and 31.0 to 32.2 mm (mean 31.60 mm) in height, with 6.25 to 6.5 (mean 6.375) whorls, H/D ratio 0.93 to 0.97 (mean 0.95) (Fig. 6.18). Apical sculpture worn smooth in all specimens examined, postapical sculpture of fine subparallel wrinkles, commonly arranged longitudinally, and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and moderately flared, reflected over umbilicus, partially occluding it. Shell mid-brown with light subsutural band and faint darker banding on body whorl, apex much paler than body whorl with distinct fine banding. Lip light brown, glossy.

Free oviduct short, less than 25% length of vagina, which is 50 - 66% length of penis sheath. Vagina swollen proximally, narrowing distally. Spermathecal shaft long, swollen at base. Junction of vas deferens and epiphallus obvious, but no caecum or internal papilla. Proximal epiphallus lined with numerous tall villi. Penial retractor muscle inserts proximally on bend in epiphallus. Distal epiphallus with elongate papillae terminating in shallow penial papilla, with basal ejaculatory opening. Penis short, swollen proximally, tapering gradually towards atrium. Penis lined with broad ridges, asymmetrically disposed (Fig. 6.19), which are quite distinct when penis is everted.

Discussion

This species has been confused with *Sphaerospira fraseri*, which it resembles conchologically. It occurs well to the north of *S. fraseri*, the northernmost record of which is Cooloola. *Sphaerospira* sp. nov. has a restricted distribution in the Boyne Valley at Dan Dan Scrub, an area of semi-evergreen vine thicket and araucarian microphyll vine forest which has been extensively logged.

I was cautious about recognising this species, as morphology of the reproductive tract is similar to that of *S. blomfieldi*. However, the proportions are different, and the disposition of ridges in the penis is distinct. The morphological differences between *S.* sp. nov. and *S. blomfieldi* are less than those between either species and *S. informis*., but there is no less a difference in penial morphology between *S.* sp. nov. and *S. blomfieldi* than there is between *Bentosites yulei* and *B. macleayi*, which are also sympatric, yet conchologically dissimilar.

Range and habitat

Known only from rainforest at Dan Dan Scrub, near Gladstone (Fig. 6.15).

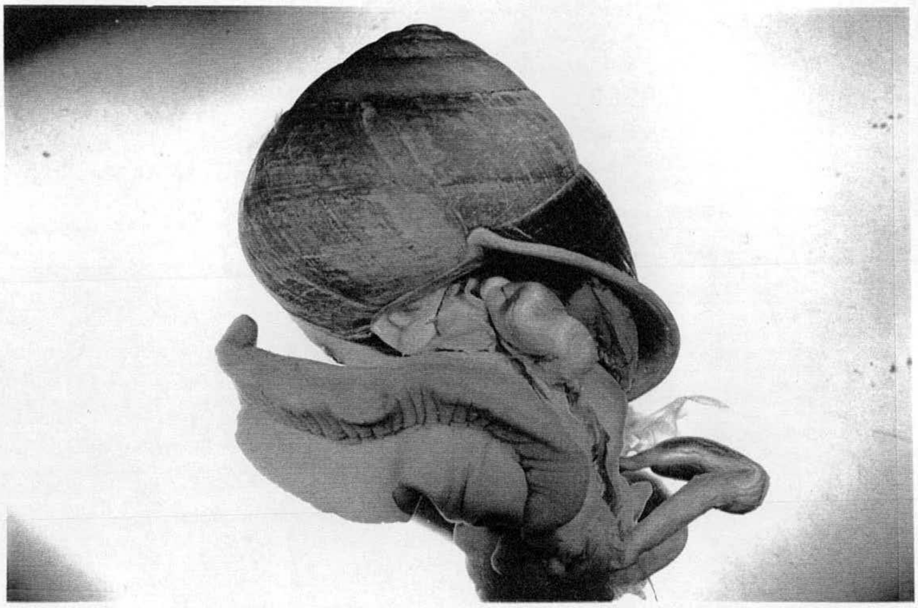


Fig. 6.18: *Sphaerospira sp. nov.* (DanDan Scrub)

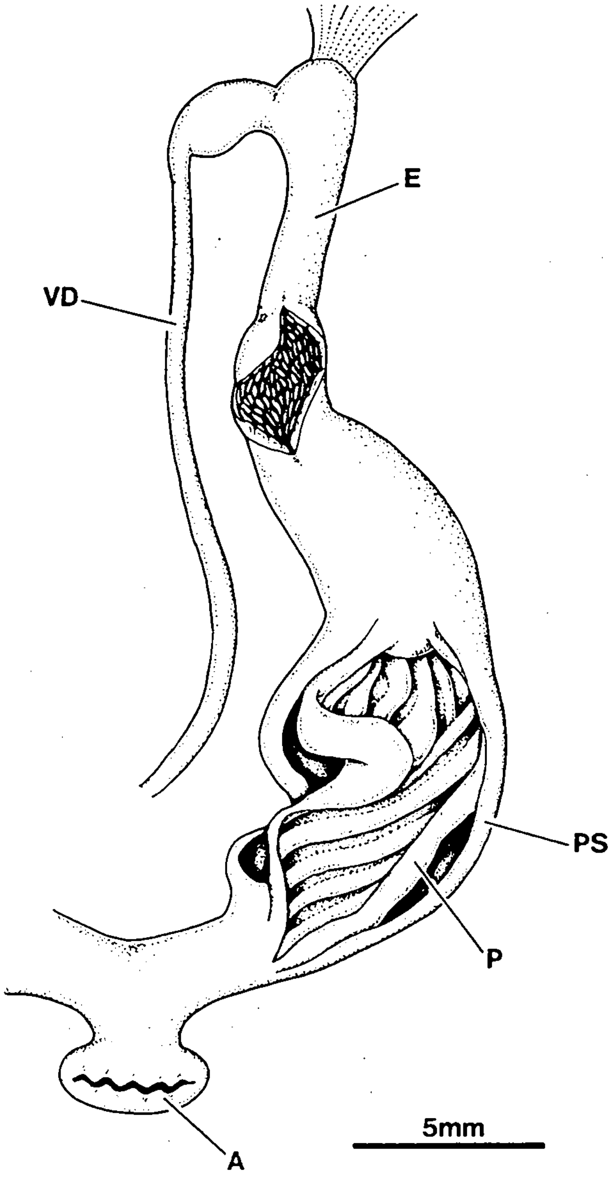


Fig. 6.19: Lining of penis of *Sphaerospira* sp. nov. (DanDan Scrub) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens).

Bentosites Iredale

Bentosites Iredale, 1933: 44; Iredale, 1937b: 29; Richardson, 1985: 65; Smith, 1992: 153. Type species *Helix macleayi* Cox 1865 by original designation.

Diagnosis

Bentosites can be distinguished from related genera by the combination of orange foot and collar, lack of muscle fibres in the epiphallic-penial bend, a flagellum on the vas deferens, and presence of a penial papilla.

Description

Shell medium. Post apical sculpture of fine wrinkles overlain by radial growth ridges (*macleayi, yulei, mulgravensis, rawnesleyi, mazee, gavisa*, sp. nov.) or rectangular pustules sometimes coalescing to form thick irregular wrinkles (*zebina*). Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and slighlty flared. Lip reflected over umbilicus which is open and excavated (*yulei*), partly occluded (*mulgravensis, rawnesleyi, mazee*) or wholly occluded (*macleayi, mulgravensis, rawnesleyi, zebina, mazee, gavisa*, sp. nov.). Shell with single peripheral band (*macleayi*), two or more bands (*yulei, mulgravensis, rawnesleyi, zebina, mazee, gavisa*, sp. nov.) or of single colour (*mulgravensis, rawnesleyi, mazee*). Dark radial band behind lip present (*macleayi, yulei, mulgravensis, mazee*, sp. nov.) or absent (*rawnesleyi, zebina, gavisa*). Lip dark (*macleayi, yulei, mulgravensis, rawnesleyi, mazee, gavisa*, sp. nov.) or with banding visible on inside (*zebina, gavisa*).

Foot colour orange.

Free oviduct short, between 25% length of vagina (all species except sp. nov.) and 35% length of vagina (sp. nov.), which is shorter than penis sheath (*macleayi, yulei, mazee*, sp. nov.) or equal to penis sheath (*mulgravensis, rawnesleyi, zebina, gavisa*). Spermathecal shaft narrow (*macleayi, yulei, zebina, gavisa*) to broad (*mulgravensis, rawnesleyi, mazee*).

Vas deferens with short to medium flagellum (*yulei, mulgravensis, rawnesleyi, mazee*, sp. nov.) or no flagellum (*macleayi, zebina, gavisa*). Vas deferens not contained within penis sheath, but it and proximal epiphallus are bound to it by mesenteries. Penis sheath of equal thickness along its length. Proximal epiphallus indistinguishable from vas deferens. Penial retractor muscle inserts midway on bend of epiphallus. Distal epiphallus expanded, equal in width to penis. Junction of epiphallus and penis indistinguishable externally (*zebina*, sp. nov.) or marked externally by a pouch (*macleayi, yulei, mulgravensis, rawnesleyi, mazee, gavisa*). Penial papilla relatively large, without sculpture. Basal ejaculatory opening. Sculpture of papillae and ridges (*macleayi, yulei, mulgravensis, rawnesleyi, mazee*, sp. nov.) or ridges only (*zebina, gavisa*).

Species of *Bentosites*

Eight species of *Bentosites* are found in mid-eastern Queensland:

- *Bentosites macleayi* (Cox, 1865) - type species
- *Bentosites yulei* (Forbes, 1851)
- *Bentosites mulgravensis* (Brazier, 1872)
- *Bentosites rawnesleyi* (Cox, 1873)
- *Bentosites zebina* (Brazier, 1878)
- *Bentosites mazee* (Brazier, 1878)
- *Bentosites gavisa* Iredale, 1933
- *Bentosites* sp. nov.

Previous studies and nomenclature

Iredale (1933) introduced the name *Bentosites* to cover a series of shells with a round base and closed umbilicus. The type was *H. macleayi* Cox 1865, from the Whitsunday Islands. The series included *gratiosa* Cox and *etheridgei* Brazier, which were thought to be closely related, and the more distantly related *croftoni* Cox, *coxi* Crosse, and *blomfieldi* Cox. *Bentosites* was a subgeneric name, but Iredale never specified to which genus it belonged (1933: 44). Immediately after introducing it, he used it as a full generic name when describing a new subspecies, *Bentosites macleayi wardiana* Iredale. The term "subgeneric" may have been a typographical error. Iredale (1937b) included seven species in *Bentosites*. As well as the six originally placed in this genus, he described a new species, *Bentosites birchi*, from the Proserpine River (1937b: 29). With the exception of *blomfieldi*, *Bentosites* as delineated by Iredale, was confined to mid-east Queensland.

Smith (1992) synonymised *Bentosites* with *Sphaerospira*, but an investigation of the anatomy of both genera in this study indicates that the they are not the same genus.

Key to species of *Bentosites*

Shells

1.	Shell flattened with excavated umbilicus	*yulei*
	Shell with wholly or partially occluded umbilicus	2
2.	Shell pale with dark lip and single dark band	*macleayi*
	Shell with more than one band	3
3.	Shell pale with several dark bands and thin white subsutural band	*gavisa*
	Shell banded or dark, no white subsutural band	4
4.	Shell colour and bands strongly contrasting	sp. nov.
	Shell and band colours similar	5
5.	Shell with predominantly pustulose microsculpture	*zebina*
	Shell with wrinkled microsculpture	6
6.	Dark radial line behind lip	7
	Dark radial line absent in striped shells	*rawnesleyi*
7.	Coastally north of Cardwell	*mulgravensis*
	Paluma Range and adjacent ranges	*mazee*

Genitalia

1. Flagellum at junction of vas deferens and epiphallus (may be no more than a tiny bump) 2

Flagellum absent 6

2. Penis unfolded in penis sheath 3

Penis folded or kinked near genital atrium 4

3. Penis with longitudinal pilaster .... sp. nov.

Penis lacking pilaster .... *yulei*

6. Penis folded proximally .... *mazee*

Penis folded or kinked near atrium 5

5. Penis long, folded near atrium, flagellum reduced to tiny bump .... *mulgravensis*

Penis short, kinked near atrium, flagellum distinct .... *rawnesleyi*

6. Penis lined with papillae proximally and distally .... *macleayi*

Penis lined with longitudinal ridges only 7

7. Penis unfolded in penis sheath .... *zebina*

Penis folded in penis sheath .... *gavisa*

Bentosites macleayi (Cox)

Helix macleayi Cox, 1865: 486, textfig. - Port Denison, Queensland; Cox, 1868: 45, pl. 8, fig. 3; Hedley, 1889: 101, restricted type locality to Whitsunday Islands; Iredale, 1937b: 29.

Bentosites macleayi (Cox) Iredale, 1933: 46; Iredale, 1937b: 29; Richardson, 1985: 67; Smith, 1992: 157.

Bentosites macleayi wardiana Iredale, 1933: 44 - Hayman Island, Whitsunday Group, Queensland; Iredale, 1937b: 29, pl. 2, fig. 22.

Sphaerospira macleayi (Cox) Smith, 1992: 157

Diagnosis

Shell medium, globose with raised spire, pale with dark peripheral band and dark lip. Very short flagellum on vas deferens, penial scupture of papillae and few longitudinal ridges. Whitsunday Islands only.

Description

Shell medium, 23.4 to 33.4 mm (mean 27.75 mm) in diameter, 20.0 to 31.6 mm (mean 26.41 mm) in height, with 5.0 to 6.125 (mean 5.659) whorls, H/D ratio 0.828 to 1.072 (mean 0.948). Apical sculpture worn smooth in all specimens examined, postapical sculpture of fine wrinkles overlain by radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and slightly flared. Lip reflected over umbilicus, totally occluding it. Shell colour pale yellow with dark peripheral band and dark radial band behind lip. Lip dark. Shell solid. Based on 133 measured adults.

Free oviduct short, less than 30% length of vagina, which is 65-75% length of penis. Spermathecal shaft thin, swollen at base. Vas deferens with very short flagellum. Junction of vas deferens and epiphallus indistinguishable externally. Penial retractor muscle inserts on bend of epiphallus. Epiphallus narrow proximally, but greatly expanded distally, equal in width to penis. Lumen of epiphallus very narrow. Junction of epiphallus and penis marked externally by pouch, internally by rounded penial papilla, with basal ejaculatory opening. Complex sculpture on lining of penis chamber (Fig. 6.20). Proximally, a broad fan of ridges dissected into flattened papillae surrounds the epiphallic papilla. This gives way to four high longitudinal ridges, two either side of a wide channel which originates beneath epiphallic papilla and persists into genital atrium. Distally, irregular high papilla occur opposite the channel just above genital atrium.

Discussion

Bentosites macleayi is the least variable member of the genus. Its occurrence only on the Whitsunday Islands is interesting, and is currently under investigation by the author.

This shell of this species most closely resembles that of *B. gavisa*, but the anatomy of the male reproductive tract is similar to that of *B. yulei*. *Bentosites macleayi* is sympatric with both species on Whitsunday Island, but nothing is known of the ecology. It is interesting that the two species with almost identical penial sculpture should differ so markedly in shell form. Whether this is a product of ecological factors, important in mate recognition or simply coincidence is as yet unknown.

Range and habitat

Despite early records from "Port Denison", this species is confined to islands of the Whitsunday Group (Fig. 6.21). Extensive collecting by the Queensland Museum, James Cook University, and the Queensland National Parks and Wildlife Service has failed to turn up any evidence that *B. macleayi* occurs on the mainland.

This species is largely arboreal and is found in gullies with vine thicket or isolated patches of vine forest on the islands. It has also been recorded from open forest on Hook Island. The lush "rainforest" gardens of the island resorts may support sizeable colonies.

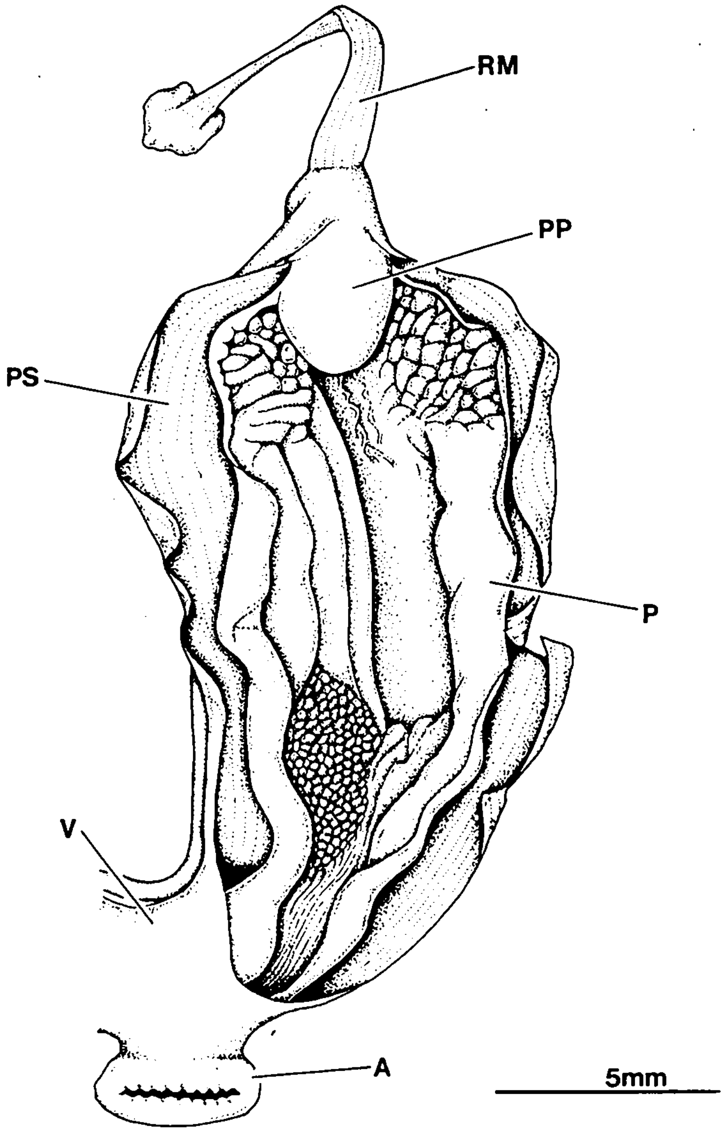


Fig. 6.20: Lining of penis of *Bentosites macleayi* (Cox) (Hook Island) (A = atrium, P = penis, PP = penial papilla, PS = penial sheath, RM = retractor muscle, V = vagina).

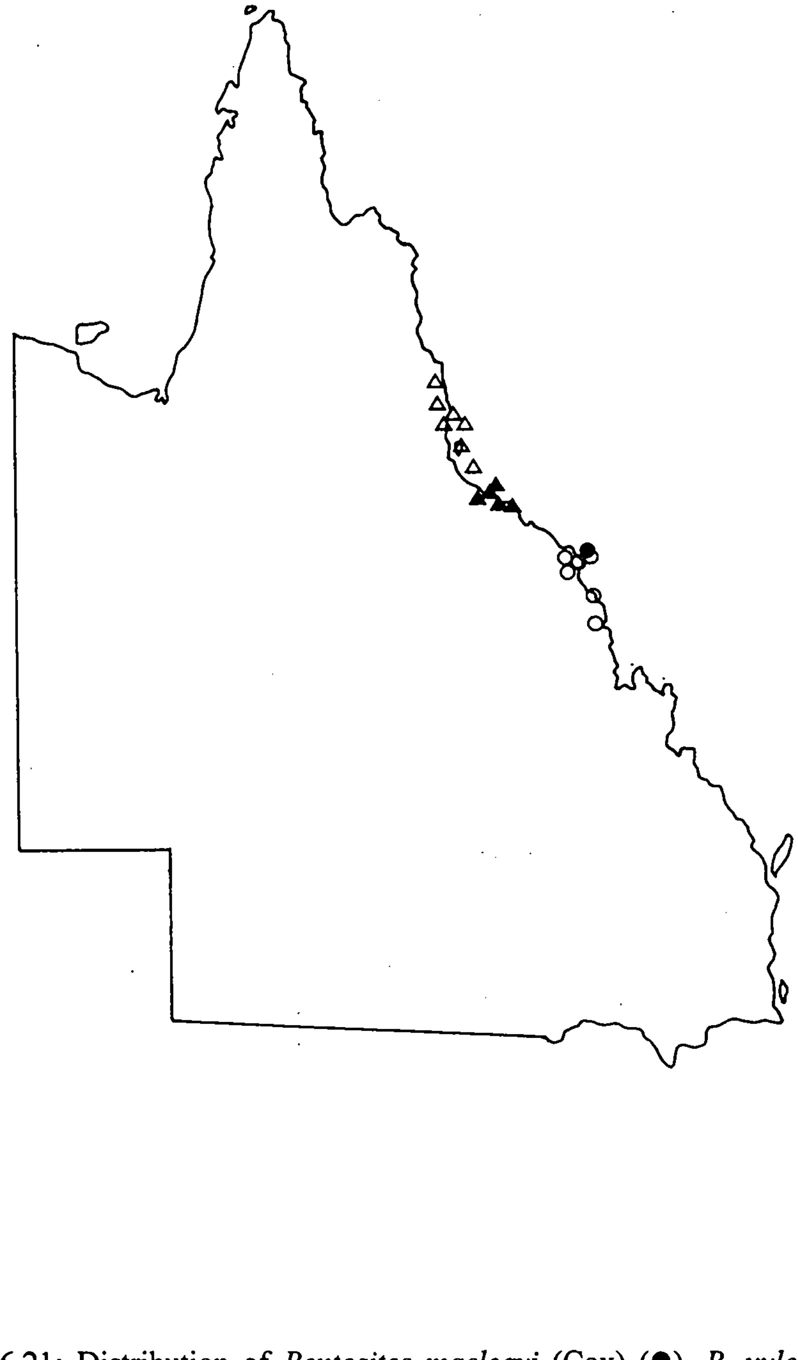


Fig. 6.21: Distribution of *Bentosites macleayi* (Cox) (●), *B. yulei* (Forbes) (○), *B. mulgravensis* (Brazier) (Δ) and *B. rawnesleyi* (Cox) (▲).

***Bentosites yulei* (Forbes)**

Helix yulei Forbes, 1851: 377, pl. ii, figs. 6a-6b - Port Molle, Queensland; Hedley, 1888: 62; Iredale, 1937b: 30.

Helix rainbirdi Cox, 1870: 170, pl. xvi, fig. 1 - Mt Dryander, Port Denison, Queensland; Hedley, 1888: 61; Iredale, 1937b: 30.

Helix rainbirdi variety Pilsbry, 1890: 158, pl. 35, figs. 6-7 - type locality unknown; Iredale, 1937b: 31 - corrected type locality to Proserpine and O'Connell River.

Helix basalis Pilsbry, 1890: 158, pl. 39, figs. 84-85 - Port Mackay, Queensland; Iredale, 1937b: 31. Not *H. basalis* Schmeltz, 1869.

Thersites (Sphoerospira) yulei (sic) (Forbes) Fulton, 1904: 6.

Varohadra yulei (Forbes) Iredale, 1933: 45; Iredale, 1937b: 30; Richardson, 1985: 311.

Varohadra yulei rainbirdi Iredale, 1933: 45.

Varohadra rainbirdi (Cox) Iredale, 1937b: 30; Richardson, 1985: 309.

Varohadra starena Iredale, 1937b: 31, pl. iii, fig. 1 - Whitsunday Island; Richardson, 1985: 310 (as *storena*).

Varohadra findera Iredale, 1937b: 31, pl. iii, fig. 2 - new name for *Helix basalis* variety Pilsbry, 1890; Richardson, 1985: 307.

Varohadra thorogoodi Iredale, 1937b: 31, pl. iii, fig. 3 - new name for *H. rainbirdi* variety Pilsbry, 1890; Richardson, 1985: 310.

Sphaerospira yulei (Forbes) Smith, 1992: 159

Diagnosis

Shell medium, depressed, dark with two to three lighter bands, dark umbilical patch, dark lip. Umbilicus excavated. Short flagellum on vas deferens. Pointed penial papilla. Penial sculpture of papillae and longitudinal ridges.

Description

Shell medium, 28.8 to 42.7 mm (mean 35.15 mm) in diameter, and 20.2 to 36.5 mm (mean 27.07 mm) in height, with 6.25 to 6 (mean 6.99) whorls, H/D ratio 0.664 to 0.893 (mean 0.767). Apical sculpture worn smooth in all specimens examined, postapical sculpture of fine wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending sharply behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, which is partially occluded. Umbilicus deep, excavated. Shell dark with two to three lighter bands, dark radial band behind lip, dark band around umbilicus. Lip brown, glossy. Shell relatively solid. Based on 87 measured adults.

Free oviduct short, less than 25% of vagina, which is shorter than penis sheath. Spermathecal shaft narrow, swollen at base. Vas deferens with short flagellum. Penial retractor muscle inserts on bend of epiphallus. Epiphallus simple, with thick pilaster which terminates in pointed penial papilla, with basal ejaculatory opening. Penis lining complicated, with small papillae proximally, near penial papilla. Main sculpture of longitudinal ridges, forming a sperm gutter opposite papillae. Distally, ridges are thrown into broad papillae, leading down to genital atrium (Fig. 6.22).

Discussion

Iredale (1937b) split this species on differences in shell shape, but examination of a large series of shells (87 adults) showed continuous variation with no definite limits to each 'form' (Fig. 6.23). The genitalia are consistent among individuals from all type localities, so *Helix rainbirdi*, *Varohadra starena*, *V. findera* and *V. thorogoodi* are considered junior synonyms of *B. yulei.* Smith (1992) included these species and *Varohadra macneilli* Iredale, 1937, in the synonymy of *Sphaerospira yulei*.

Bentosites yulei is the commonest *Bentosites* in mid-east Queensland, its abundance reflected in the large number of names given to it by earlier authors. It maintains roughly the same shell shape throughout its range. Most specimens are depressed, but occasional individuals are quite globose. There is a superficial resemblance to *Temporena macneilli*, but *B. yulei* always has an excavated umbilicus.

It occurs sympatrically with several other species: *Bentosites macleayi, B. gavisa, Temporena etheridgei, Sphaerospira informis, and Varohadra oconnellensis.* Whether it is found microsympatrically with any of these is not known at this stage. Conchologically, *B. yulei* resembles *V. oconnellensis*, and anatomically it resembles *B. macleayi.*

Range and habitat

Bentosites yulei occurs from Mt Dryander to the Seaforth region, north of Mackay, and also the Whitsunday Islands (Fig. 6.21). This species is found under logs and rocks in lowland vine forest. It has been recorded from open forest on Hook Island, and on trees behind the foredunes on Whitsunday Island.

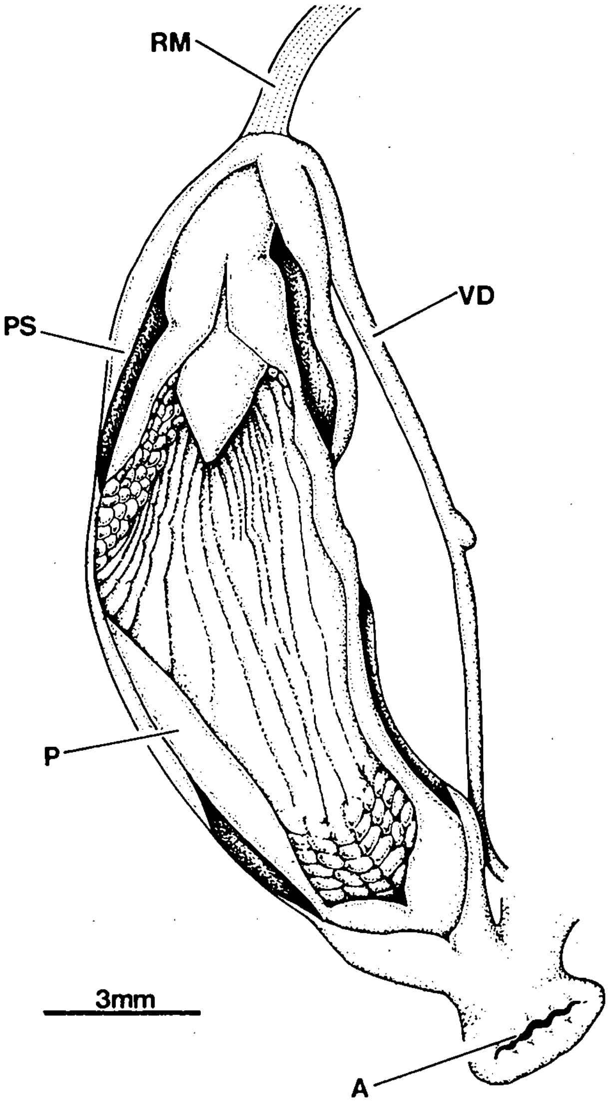


Fig. 6.22: Lining of penis of *Bentosites yulei* (Forbes) (Kelsey Creek) (A = atrium, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens).

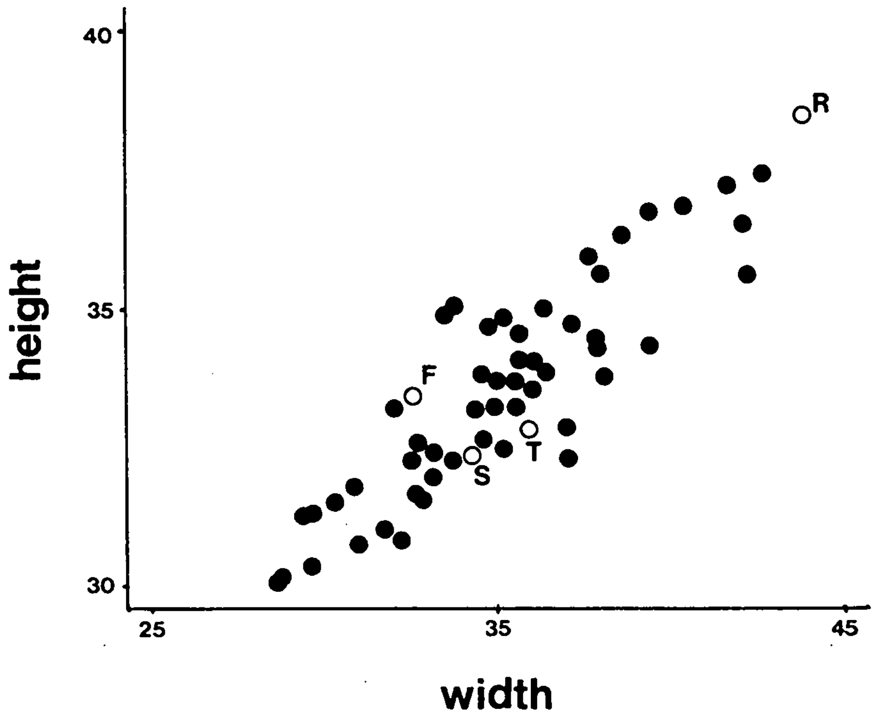


Fig. 6.23: Shell shape of *Bentosites yulei* (Forbes) (F = holotype of *findera*, R = holotype of *rainbirdi*, S = holotype of *starena*, T = holotype of *thorogoodi*)

***Bentosites mulgravensis* (Brazier)**

Helix (Camaena) mulgravensis Brazier, 1872a: 21 - Mulgrave Island, Queensland; Hedley, 1888: 60; Iredale, 1937b: 26 - corrected type locality to probably Mulgrave River.

Helix (Hadra) cookensis Brazier, 1875b: 17 - Cooktown; Hedley, 1888: 57; Iredale 1937b: 35, pl. iii, fig. 18 - corrected type locality to Brooke Island, Rockingham Bay, Queensland.

Helix (Hadra) palmensis Brazier, 1876a: 105 - Palm Island, Queensland; Hedley, 1888: 60; Fulton, 1904: 7, pl. i, figs. 5-6; Iredale, 1937b: 26 - corrected type locality to Great North Palm Island.

Helix bebias Brazier, 1878: 78 - Garden Island, Rockingham Bay, Queensland; Hedley, 1888: 57; Iredale, 1937b: 35.

Helix palmensis meridionalis Brazier, 1881b: 458 - Large South Palm Island, Queensland; Iredale, 1937b: 26.

Gnarosophia palmensis austrina Iredale, 1933: 46 - nom. nov. for *palmensis meridionalis*; Iredale, 1937b: 26.

Gnarosophia bellaria Iredale, 1937b: 36, pl. ii, fig. 16 - Hinchinbrook Island, Queensland; Richardson, 1985: 148.

Varohadra russelli Iredale, 1937b, p. 36, pl. iii, fig. 19 - North Barnard Island, Queensland; Richardson, 1985: 310.

Varohadra hubbardi Iredale, 1937, p. 36, pl. iii, fig. 20 - Johnstone River district, Queensland; Richardson, 1985: 308.

Varohadra banfieldi Iredale, 1937b, p. 36, pl. iii, fig. 17 - Dunk Island, Queensland; Richardson, 1985: 306; Smith, 1992: 159.

Diagnosis

Shell medium to large, striped, dark umbilical patch, dark lip. Umbilicus partially to wholly occluded. Short flagellum on vas deferens. Pointed penial papilla in pouch. Penis folded near genital atrium. Penis lining of large papillae and longitudinal ridges.

Description

Shell small to large, 32.0 to 49.3mm (mean 39.67mm) in diameter, and 25.7 to 49.1mm (mean 33.27mm) in height, with 5.325 to 5.75 (mean 5.422) whorls, H/D ratio 0.788 to 0.995 (mean 0.833). Apical sculpture worn smooth in all specimens examined, postapical sculpture of weak irregular wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, partially to almost wholly occluding it. Shell mid-brown with darker peripheral band and numerous other darker bands, dark subsutural band, dark radial band behind lip, dark circum-umbilical patch. Lip mid- to dark brown, glossy. Shell light to solid. Based on 18 measured adults.

Free oviduct broad, less than 25% length of vagina. Vagina narrow, equal in length to penis sheath. Spermathecal shaft broad and long, base of shaft swollen at junction with vagina. Vas deferens with short flagellum. Penial retractor muscle inserts proximally on bend of epiphallus. Proximal epiphallus slightly enlarged, but distal epiphallus greatly swollen. Junction of epiphallus and penis marked externally by distinct "pouch". Internally, "pouch" encloses broad flattened penial papilla with basal ejaculatory opening. Penis folded near genital atrium. Penis lining complicated with large, lozenge-shaped papillae proximally, coalescing into thick longitudinal ridges, which become beaded near genital atrium (Fig. 6.24).

Discussion

At least eight species are included in *Bentosites mulgravensis*. The type locality of *Helix mulgravensis* was originally said to be Mulgrave Island, Torres Strait (Brazier, 1872a), but Iredale (1937b) corrected it to Mulgrave River, near Gordonvale, north-east Queensland. The holotype of *H. mulgravensis* is a medium-sized, heavily-banded shell with a dark subsutural band, a dark radial band behind the lip, and a dark umbilical patch. It most closely resembles the types of *Helix (Hadra) cookensis*, *Gnarosophia bellaria*, *Varohadra hubbardi* and *V. banfieldi*. The type locality of *G. bellaria* is Hinchinbrook Island, that of *V. hubbardi* is the Johnstone River, near Innisfail, and that of *V. banfieldi* is Dunk Island. The type locality of *Helix (Hadra) cookensis* was listed as Cooktown by Brazier (1875b), but Iredale (1937b) amended it to Brooke Island, Rockingham Bay.

The large species *Helix (Hadra) palmensis* and its subspecies from the Palm Group of islands are much larger than any of the preceding forms, but otherwise agree with them.

The holotype of *Varohadra russelli*, from North Barnard Island, is a small shell, which lacks the dark subsutural band, dark radial band behind the lip, and dark umbilical patch. The lip is pale and banded. No topotypic wet material has been examined, but the variation demonstrated by this specimen from the previously mentioned types is no greater than that shown by individuals in other species (*e.g. Bentosites gavisa, Figuladra incei*). North Barnard Island is also in the middle of the range of *B. mulgravensis*, so it is reasonable to include this species. Unfortunately, the holotype of the remaining species, *Helix bebias*, could not be located. Brazier's description and illustration (1878) agree with the preceding forms, and the type locality, Garden Island in Rockingham Bay, places it within the range of *B. mulgravensis*.

The plethora of names attributed to *B. mulgravensis* is probably due less to the variability of the species than to the large number of continental islands along the coast between Cairns and Townsville. Naming island populations as separate species was *de* *rigueur* for conchologists (*cf.* Marshall, 1927, *Hadra bipartita*), irrespective of the proximity of the mainland or the recency of isolation.

Although populations have been recorded on the mainland adjacent to Dunk Island northwards, information about the species' range to the south is patchy. It occurs on Hinchinbrook Island, which is very close to the mainland for its entire length, but the habitat here is drastically different to that to the north. South of Cardwell, the eastern edge of the Cardwell Range sweeps down to extensive stands of mangroves continuing to the mouth of the Herbert River. This appears to be unsuitable habitat for *B. mulgravensis*. Further south, the swamps and coastal vegetation of Halifax Bay are also probably unihabited by this species, while rainforests on the Palm Group sustain a population with very large shells (*Helix (Hadra) palmensis* Brazier).

This species, with *Bentosites rawnesleyi* (see below), and the synonyms of both, were included in the synonymy of *Sphaerospira sardalabiata* (Cox, 1871) by Smith (1992). Evidence from this study suggests they are separate species, but the type of *Helix sardalabiata* is a blond shell, so it is impossible to determine its affinities.

Range and habitat

Bentosites mulgravensis occurs in north-eastern Queensland, from at least the Mulgrave River, near Gordonvale, to the Palm Group, east of Ingham (Fig. 6.21). This species is found in vine forest, vine thicket, parks and gardens.

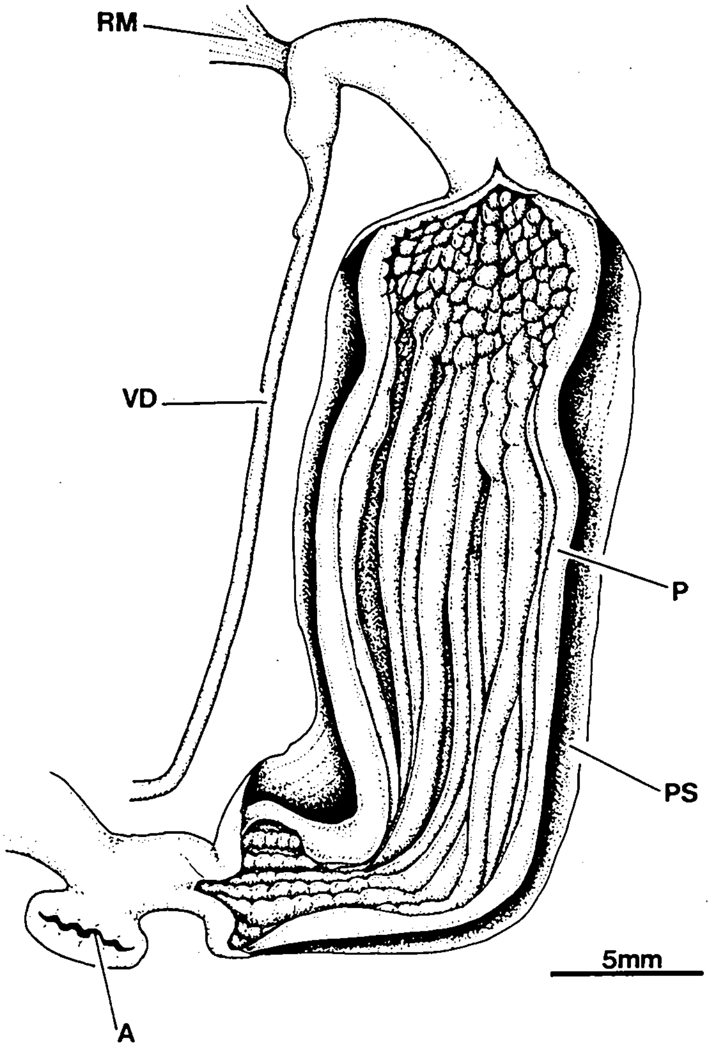


Fig. 6.24: Lining of penis of *Bentosites mulgravensis* (Brazier) (Kurrimine Beach) (A = atrium, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens).

Bentosites rawnesleyi **(Cox)**

Helix (Camaena) rawnesleyi Cox, 1873b: 564, pl. xlviii, fig. 2 - Mt Elliot, Queensland; Hedley, 1888: 61; Iredale, 1937b: 27.

Helix bala Brazier, 1878: 78, pl. 8, fig. 4 - Magnetic Island, Queensland; Hedley, 1888: 56; Hedley, 1889: 101; Iredale, 1937b: 32.

Gnarosophia rawnesleyi (Cox) Richardson, 1985: 149.

Diagnosis

Shell medium, depressed to globose, dark or striped. Lip mid-to pale brown. Umbilicus occluded. Short flagellum on vas deferens. Pointed penial papilla in pouch. Penial sculpture of minute densely-packed papillae and longitudinal ridges. Penis folded near genital atrium.

Description

Shell small to large, 26.8 to 45.2 mm (mean 33.92 mm) in diameter, and 20.8 to 41.3 mm (mean 28.31 mm) in height, with 6.5 to 6.25 (mean 5.257) whorls, H/D ratio 0.719 to 0.956 (mean 0.829). Apical sculpture worn smooth in all specimens examined, postapical sculpture of weak irregular wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, partially to almost wholly occluding it. Shell mid-brown with darker peripheral band and numerous other darker bands, dark subsutural band, with or without dark circum-umbilical patch; sometimes shell is wholly brown with paler spire. Lip pale to mid-brown, glossy. Shell light to solid. Based on 44 measured adults.

Free oviduct broad, less than 25% length of vagina. Vagina narrow, equal in length to penis sheath. Spermathecal shaft broad and long, base swollen at junction with vagina. Vas deferens with short flagellum. Penial retractor muscle inserts proximally on bend of epiphallus. Proximal epiphallus slightly enlarged, distal epiphallus greatly swollen. Junction of epiphallus and penis marked externally by distinct "pouch". Internally, "pouch" encloses broad flattened penial papilla with basal ejaculatory opening. Penis folded near genital atrium. Penis lining complicated, with numerous small densely-packed papillae around penial papilla, changing to broad longitudinal ridges in mid-section. Distally, ridges coalesce to form irregular horizontal bands near genital atrium (Fig. 6.25).

Discussion

Bentosites rawnesleyi is a very variable species. Specimes are usually striped or dark brown with a brown lip. Brazier's *bala* is unusual, as it is brown with a white lip, similar to *Figuladra incei* (Philippi). This colour form was first recorded from Magnetic Island. It also occurs on Cape Cleveland, but is not found on Castle Hill, Townsville, as Iredale (1937b) suggests.

Bentosites rawnesleyi has been referred to by the specific epithet *stephensoniana* Brazier 1872 (Bishop, 1981: 945). I have examined the holotype of this species: it is probably an albino, as it has yellow whorls and a white lip. The sculpture is irregularly wrinkled. The type locality is Port Denison, an old name for the Bowen region, which covers a large area of mid-eastern Queensland from Mt Elliot to Mackay. From this evidence (if the locality is correct) it is reasonable to assume it belongs to either *Bentosites* or *Temporena*. However, it is unreasonable to place it in synonymy, particularly if it is to be the senior synonym. The name is valid but as the taxonomic position is uncertain, *Helix stephensoniana* is treated here as species incertae sedis (ICZN, 1985).

Two other names might possibly be attributed to this species: *Helix hilli* Brazier 1875 and *Helix tomsoni* Brazier 1876. The types cannot be located, but the illustrations suggest that they belong to either *B. rawnseleyi* or *B. mulgravensis*. The locality given for both specimens is Mt Elliot, but this may be erroneous (see under *Gnarosophia* in *Previous studies and nomenclature* of genus *Hadra*). Once again, it is apposite to omit these names from synonymy until further information is available.

Bentosites rawnesleyi occurs sympatrically, but apparently not microsympatrically, with *B. zebina* over a large part of its range. In Townsville, for instance, *B. rawnesleyi* occurs in vine thicket on granite talus at Many Peaks Range, Pallarenda, where *B. zebina* is absent. Conversely, *B. zebina* is abundant in the well-watered gardens on Melton Hill, a granite outcrop in the heart of Townsville, but *B. rawnesleyi* is not found there. They do occur together at the Haughton River, Giru, which marks the southern limit of their coastal distribution. Both reach much further south in the vine thickets of the Burdekin Basin.

Range and habitat

Bentosites rawnesleyi is found in north-eastern Queensland, from Hervey's Range, east of Townsville, to Giru, south of Ayr. It also occurs on Magnetic Island (Fig. 6.21). It has been recorded from a variety of habitats, including vine forest, vine thicket, parks and gardens.

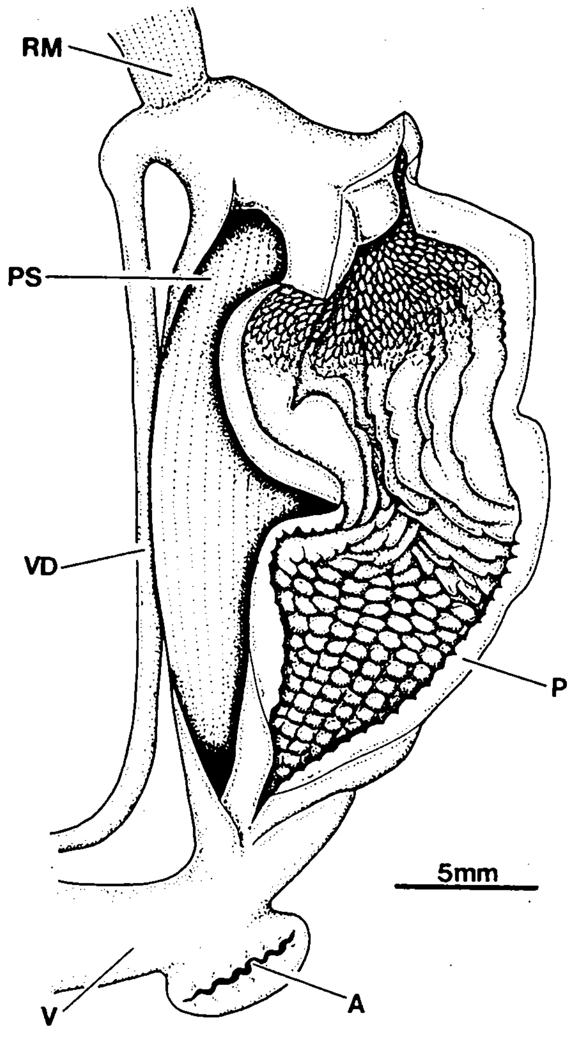


Fig. 6.25: Lining of penis of *Bentosites rawnesleyi* (Brazier) (Many Peaks Range) (A = atrium, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens).

***Bentosites zebina* (Brazier), comb. nov.**

Helix zebina Brazier, 1878: 78, pl. 8, fig. 2 - Douglas River, Queensland; Hedley, 1888: 62; Iredale, 1937b: 34.

Varohadra zebina (Brazier) Iredale, 1937b: 34; Richardson, 1985: 311 (as *zelina*).

Sphaerospira zebina (Brazier) Smith, 1992: 160.

Diagnosis

Shell with rectangular pustules. Penis with pointed penial papilla, sculpture of single long pilaster and numerous longitudinal ridges.

Description

Shell medium, 30.7 to 36.8mm (mean 33.94mm) in diameter and 23.3 to 31.6mm (mean 25.63mm) in height, with 5.125 to 6.125 (mean 5.481) whorls, H/D ratio 0.680 to 0.858 (mean 0.755). Postapical sculpture of rectangular pustules with their long axes lying parallel to the suture, sometimes coalescing into thick anastamosing wrinkles on the body whorl. Shell periphery rounded, body whorl descending gradually behind lip. Lip is expanded and moderately flared, reflected over the umbilical opening, totally occluding it. Shell pale horn, always with brown peripheral and subsutural bands plus numerous finer parallel bands. Lip glossy, shell pattern visible on outer lip, but lip dark brown where it covers umbilicus. Based on 77 measured adults.

Free oviduct short, less than 25% of vagina, which is roughly equal in length to penis. Free oviduct swollen at base. Spermathecal shaft long. Vas deferens lacking flagellum. Proximal epiphallus indistinguishable from vas deferens. Penial retractor muscle inserts on bend in epiphallus. Proximal epiphallus simple, distal epiphallus with thick pilaster which terminates in pointed penial papilla, with basal ejaculatory opening. Penis long, unfolded. Penis with single longitudinal pilaster and numerous finer parallel ridges, continuing to genital atrium (Fig. 6.26).

Discussion

Bentosites zebina has a curious sculpture which sets it apart from its congeners. The apical whorls bear regularly-spaced rectangular pustules which generally persist on the body whorl. In some individuals the pustules coalesce to form thick irregular wrinkles, more typical of the sculpture expected from this genus. It is similar to the pattern found on *Hadra barneyi*, also a vine thicket species.

Conchologically, it resembles *B. rawnesleyi* more than any other species, but anatomically it is similar to *B. gavisa*. All other species of *Bentosites* have papillae as part of the penial sculpture, but both *B. zebina* and *B. gavisa* have longitudinal ridges only.

This is the only species of *Bentosites* to penetrate far inland. The most westerly record is Wando Vale, over 200km WSW of Townsville. Museum specimens are mainly from localities on the Flinders Highway, so the northern and southern limits are unknown. Mt Fox on the western edge of the Seaview Range is the northernmost record, while Rishton Scrub, south east of Charters Towers is the southernmost.

The type locality is Douglas River, but there are two rivers by that name within the range of *B. zebina*, and both drain into the Burdekin. One is near Ayr, and the other is near Kangaroo Hills and Mt Fox. It is likely that this species extends on to the Clarke River limestone to the west, and may possibly reach the Einasleigh River.

It is hardy and occurs where there is little cover and daytime temperatures are high. I have found specimens under logs on limestone outcrops and in hollow fence posts, exposed to the midday sun.

Range and habitat

Bentosites zebina is found in north-eastern Queensland, from the Burdekin delta inland to Wando Vale (Fig. 6.27). It occurs principally in vine thicket, in logs, and at the base of rock piles.

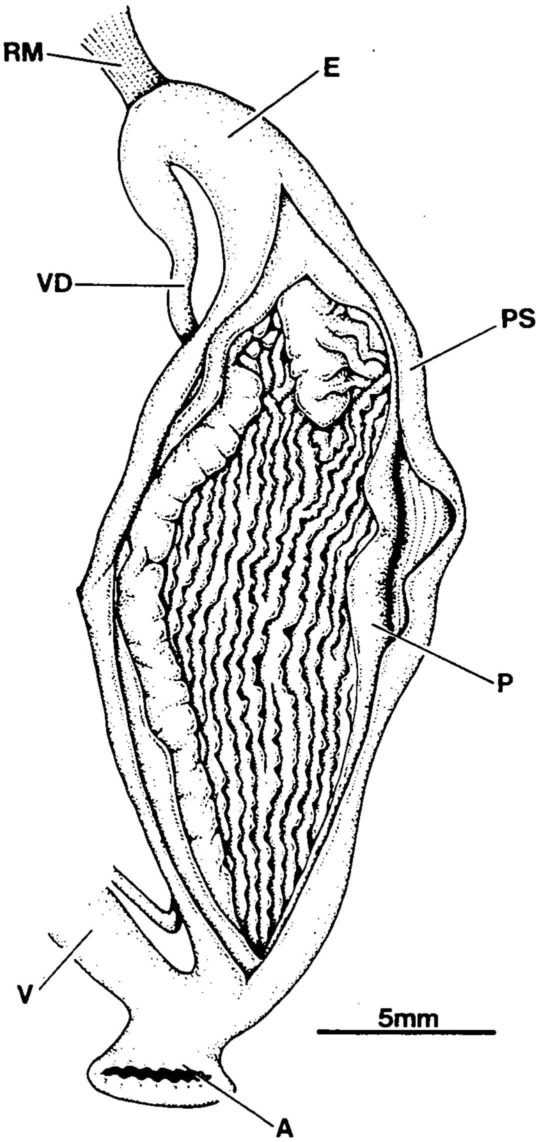


Fig. 6.26: Lining of penis of *Bentosites zebina* (Brazier) (Calcium) (A = atrium, P = penis, PS = penial sheath, RM = penial retractor muscle, V = vagina, VD = vas deferens).

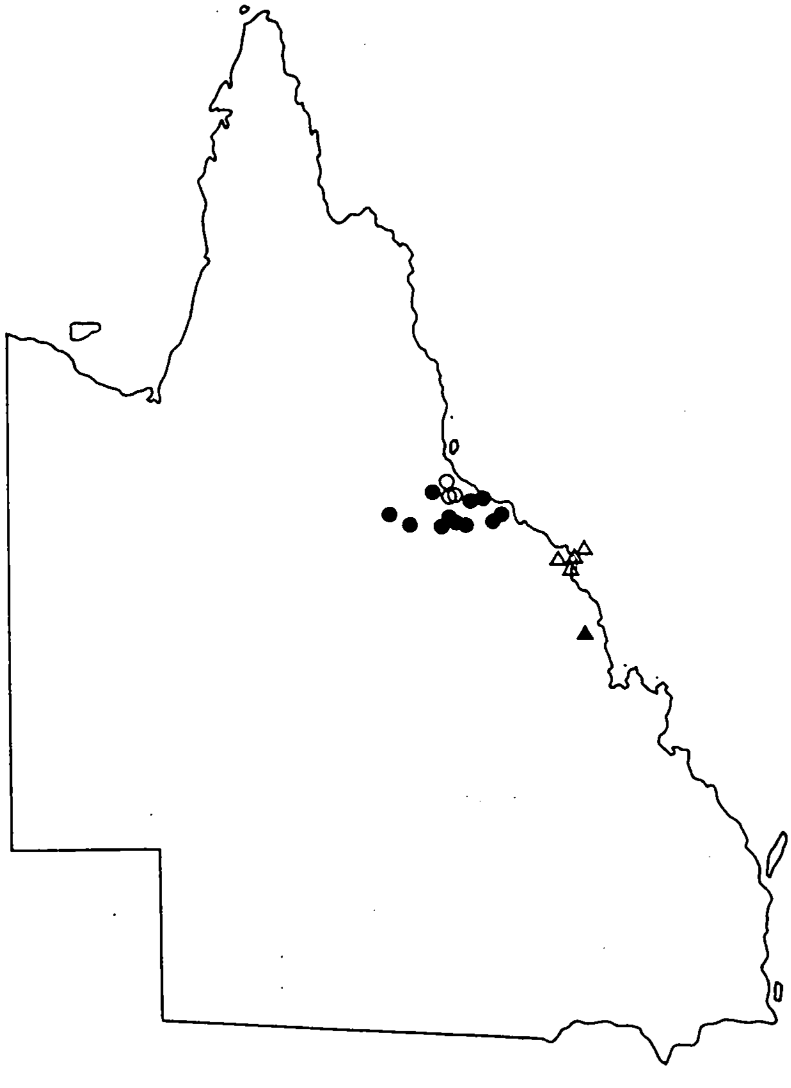


Fig. 6.27: Distribution of *Bentosites zebina* (Brazier) (●), *B. mazee* (Brazier) (○), *B. gavisa* (Iredale) (Δ) and *B*. sp. nov. (▲).

Bentosites mazee (Brazier)

Helix mazee Brazier, 1878: 79 - Waterview (= Seaview) Range Scrubs, Cardwell, Queensland; Hedley, 1888: 60; Iredale 1937b: 26.

Gnarosophia mazee (Brazier) Iredale 1937b: 26; Richardson, 1985: 148.

Diagnosis

Shell large, globose. Shell dark, light, or striped. Dark umbilical patch. Dark line behind lip. Umbilicus occluded. Short flagellum on vas deferens. Pointed penial papilla with penial pouch. Penis folded. Penial sculpture of tiny papillae and longitudinal ridges.

Description

Shell large, 41.8 to 46.8mm (mean 43.03mm) in diameter, and 46.1 to 49.0mm (mean 46.46mm) in height, with 5.125 to 6.5 (mean 5.875) whorls, H/D ratio 0.984 to 1.172 (mean 1.081). Apical sculpture worn smooth in all specimens examined, postapical sculpture of very shallow irregular wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over the umbilical opening, partially to almost wholly occluding it. Shell pale, striped or entirely brown, with dark subsutural band, dark circum-umbilical patch, and dark radial line behind lip. Lip brown to black, glossy. Shell solid. Based on 5 measured adults.

Free oviduct swollen at base, less than 25% length of vagina. Vagina swollen proximally, narrow towards atrium, approximately 75% length of penis sheath. Spermathecal shaft broad, swollen at base. Proximal epiphallus virtually indistinguishable from vas deferens. Penial retractor muscle inserts proximally on epiphallus. Junction of epiphallus and penis marked externally by pouch, internally by large pointed penial papilla, with basal ejaculatory opening. Penis folded in penis sheath. Penis lining of tiny papillae near penial papilla, changing abruptly to short longitudinal ridges, which break down into elongate papillae towards genital atrium (Fig. 6.28).

Discussion

Smith (1992) included this species in the synonymy of *Sphaerospira sardalabiata* (Cox), together with *B. mulgravensis* and *B. rawnesleyi.*

Bentosites mazee appears to have a limited distribution, but this may be a function of the paucity of study in this area. Despite their proximity to Townsville, the Seaview and Paluma Ranges are poorly known. Although several undescribed helicarionids are abundant on Mt Spec, *B. mazee* is rarely collected. It has been found under logs by me and other workers in wet sclerophyll to the west of Mt Spec National Park, but never more than one specimen at a time. Dead juveniles are relatively common, but adults dead or alive are scarce.

Range and habitat

Bentosites mazee occurs in north-eastern Queensland, from the Seaview Range, south east of Ingham, to the Paluma Range, north east of Townsville (Fig. 6.27). It is found in vine forest and wet sclerophyll.

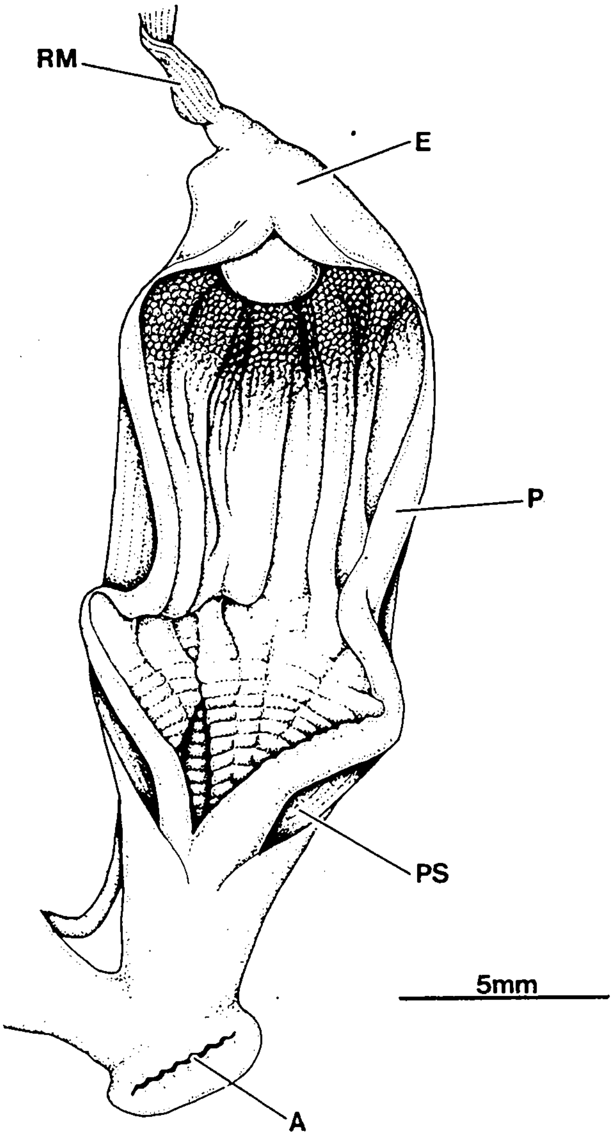


Fig. 6.28: Lining of penis of *Bentosites mazee* (Brazier) (Paluma) (A = atrium, P = penis, PS = penial sheath, RM = penial retractor muscle).

***Bentosites gavisa* Iredale**

Helix gratiosa Cox, 1871: 53, pl. iii, fig. 1 - Whitsunday Island, Queensland; Hedley, 1888: 58; Iredale, 1937b: 29. Not *H. gratiosa* Studer, 1820: 87.

Bentosites birchi Iredale, 1933: 44 - Proserpine River, Queensland; Iredale, 1937b: 29, pl. ii, fig. 21; Richardson, 1985: 65.

Bentosites gavisa Iredale, 1933: 46. - nom. nov. for *Helix gratiosa* Cox; Iredale, 1937b: 29; Richardson, 1985: 67.

Diagnosis

Shell medium, globose. Shell pale with a white subsutural bands and one or more dark bands. Umbilicus occluded. Lip dark or showing body whorl banding. No flagellum on vas deferens. Penis folded. Penis lining of longitudinal ridges, comprised on plates proximally.

Description

Shell medium, 30.6 to 35.7mm (mean 33.01mm) in diameter, and 29.7 to 36.9mm (mean 33.06mm) in height, with 5.0 to 5.625 (mean 5.438) whorls, H/D ratio 0.902 to 1.070 (mean 1.001). Apical sculpture worn smooth on all specimens examined, postapical sculpture of fine subparallel wrinkles and radial growth ridges. Shell periphery rounded to very slightly angular, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, wholly occluding it. Shell pale with thin white subsutural band, and one or more darker bands, sometimes very wide and often running together to give an entirely dark shell. Lip brown or showing body whorl banding, never white. Shell relatively solid. Based on 14 measured adults.

Free oviduct short, less than 25% of vagina, which is roughly equal in length to penis sheath. Free oviduct swollen. Spermathecal shaft long. Penial retractor muscle inserts proximally on bend of epiphallus. Proximal epiphallus barely distinguishable from vas deferens. Junction of epiphallus and penis marked internally by rounded penial papilla, with basal ejaculatory opening. Penis folded within sheath. Penis lining of fine longitudinal ridges composed initially of irregular plates, becoming smooth toward genital atrium. A high pilaster persists along the length of the penis (Fig. 6.29).

Discussion

This enigmatic species has long been confused with *Temporena etheridgei* (e.g. Smith, 1992), but is separable conchologically on the lip colour. Some specimens of *B. gavisa* are dark (*B. birchi* Iredale), superficially resembling *T. etheridgei*, but the lip of *B. gavisa* is either dark or shows the banding on the body whorl, while the lip of *T. etheridgei* is always white.

The shell of this species is similar to *B. macleayi*, which shares its habitat on the Whitsunday Islands. Its reproductive anatomy is most like that *B. zebina*, occurring to the north-east of *B. gavisa.*

Range and habitat

Bentosites gavisa is found in mid-eastern Queensland, in the Conway Ranges, east of Proserpine, and on the Whitsunday Islands (Fig. 6.27). It is largely arboreal, and occurs in a variety of forest types, including the landward edge of mangroves (J. Worsfold, J. LeRoi, pers. comm.).

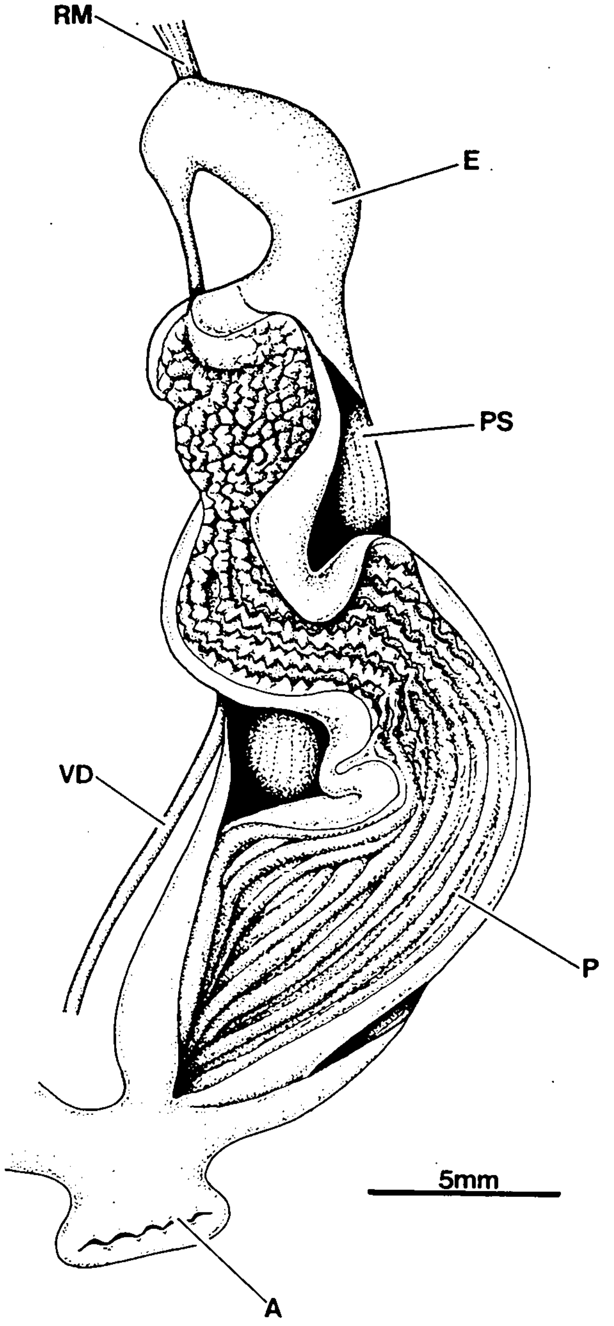


Fig. 6.29: Lining of penis of *Bentosites gavisa* Iredale (Wilson's Beach) (A = atrium, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens).

Bentosites sp. nov.

Diagnosis

Shell medium, globose. Shell pale always with dark subsutural and supraperipheral bands. Umbilicus occluded. Lip dark. Flagellum on vas deferens. Penis not folded. Penial papilla large and pointed with warty growth on surface.

Description

Shell medium, 28.6 to 31.8mm (mean 30.72mm) in diameter, and 28.6 to 33.6mm (mean 30.47mm) in height, with 5.75 to 6.25 (mean 6.017) whorls, H/D ratio 0.9 to 1.174 (mean 1.003) (Fig. 6.30). Apical sculpture worn smooth on all specimens examined, postapical sculpture of fine subparallel wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, wholly occluding it. Shell pale, always with subsutural and supraperipheral dark bands, sometimes with additional finer bands. Lip brown. Shell relatively solid. Based on 15 measured adults.

Free oviduct medium, approximately 35% of vagina, which is less than 50% length of penis sheath. Free oviduct swollen at base. Spermathecal shaft long. Penial retractor muscle inserts proximally on bend of epiphallus. Proximal epiphallus barely distinguishable from vas deferens, medium flagellum at junction of vas deferens and epiphallus. Junction of epiphallus and penis marked internally by pointed penial papilla, with basal ejaculatory opening. The surface of the penial papilla bears one or more warty growths. Penis not folded within sheath. Penis lining of longitudinal ridges covered with papillae, becoming smooth toward genital atrium. A high pilaster persists along the length of the penis (Fig. 6.31).

Discussion

The shell of this species is very similar to that of *Bentosites gavisa*, but lacks the subsutural white band.

Range and habitat

Known only from the type locality (Fig. 6.27), which is south of Pine Mountain, approximately 50 km SW of Sarina, mid-east Queensland.

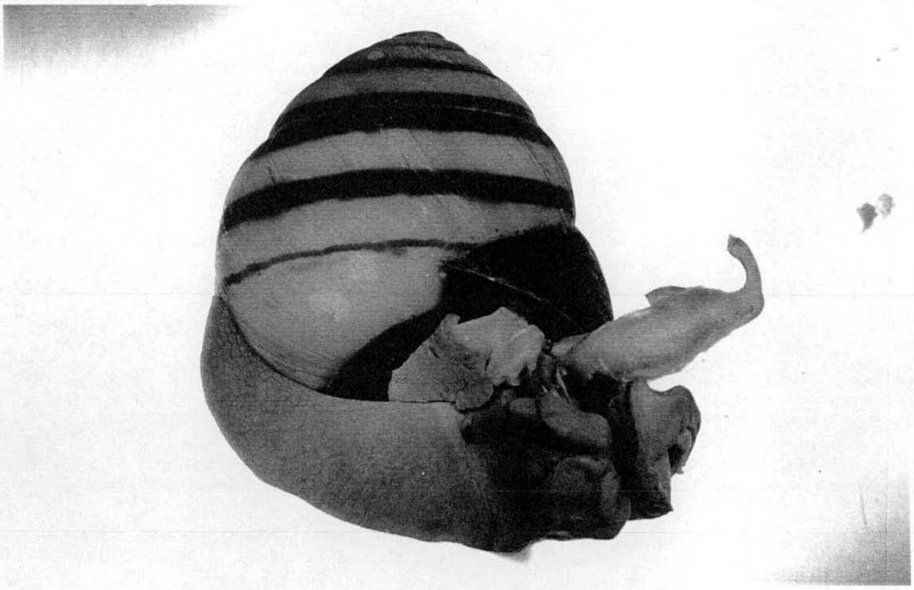


Fig. 6.30: *Bentosites sp. nov.* (Denham Range)

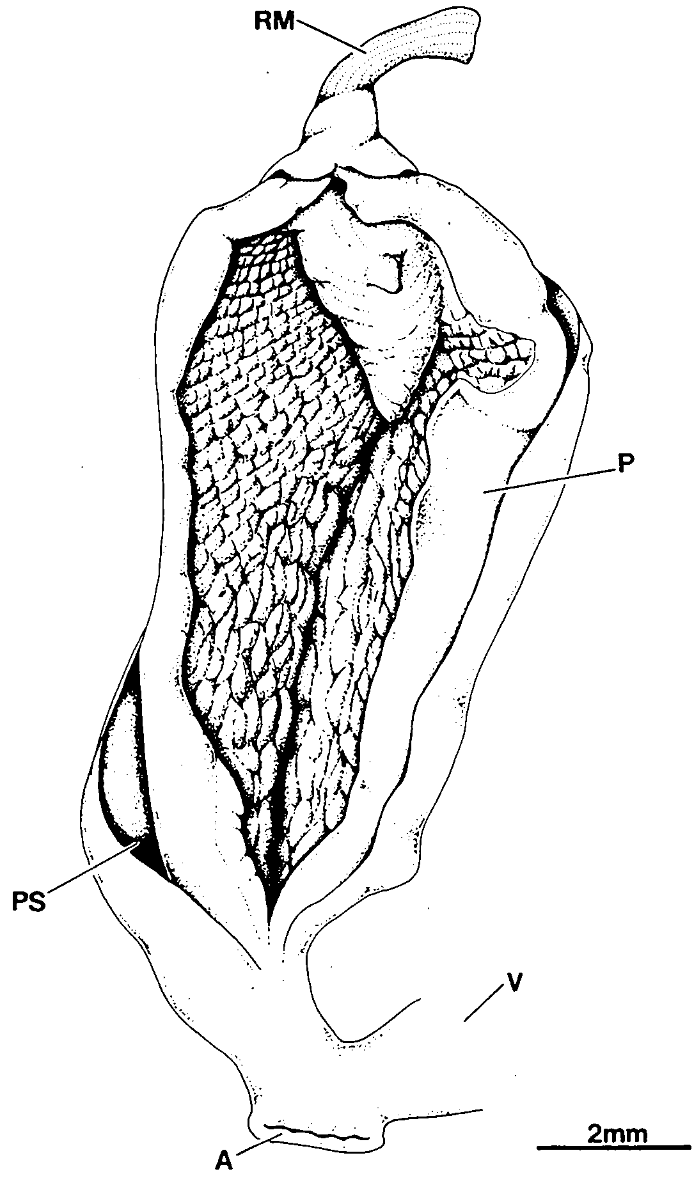


Fig. 6.31: Lining of penis of *Bentosites* sp. nov. (Denham Range) (P = penis, PS = penial sheath, RM = penial retractor muscle, V = vagina).

Varohadra Iredale

Varohadra Iredale, 1933: 45; Iredale, 1937b: 30; Richardson, 1985: 305; Smith, 1992: 153-154. Type species *Helix oconnellensis* Cox, 1871, by original designation.

Diagnosis

Varohadra can be distinguished from related genera by the combination of flattened shell, grey foot and collar, and lack of penial papilla.

Description

As for species.

Species of Varohadra

There is a single species of *Varohadra.*

Varohadra oconnellensis (Cox, 1871) - type species

***Varohadra oconnellensis* (Cox)**

Helix albofilata Schmeltz, 1869: 73 - nom. nud.; Iredale, 1937b: 30.

Helix oconnellensis Cox, 1871: 55, pl. 3, fig. 4 - O'Connell River, near Port Denison, Queensland; Hedley, 1888: 60; Iredale, 1937b: 30.

Helix oconnelli Schmeltz, 1874: 96; Iredale, 1937b: 30.

Helix albomarginata Schmeltz, 1874: 94 - nom. nud.; Iredale, 1937b: 30

Varohadra oconnellensis (Cox) Iredale, 1933: 45; Iredale, 1937b: 30; Richardson, 1985: 309.

Varohadra oconnellensis jacksoni Iredale, 1933: 45 - Finch Hatton, 50 miles west of Mackay, Queensland; Iredale, 1937b: 30, pl. 2, fig. 20.

Varohadra oconnellensis caroli Iredale, 1933: 45 - Lindeman Island, Whitsunday Group, Queensland; Iredale, 1937b: 30, pl. 2, fig. 19.

Sphaerospira oconnellensis (Cox) Smith, 1992: 157.

Diagnosis

Shell medium, chocolate brown with white subsutural band. Umbilicus excavated. Short flagellum at junction of vas deferens and epiphallus. No penial papilla, but gross thickening of penis wall at junction with epiphallus.

Description

Shell medium, 26.4 to 36.3mm (mean 28.31 mm) in diameter, and 16.3 to 29.8mm (mean 21.19 mm) in height, with 6.375 to 5.5 (mean 6.983) whorls, H/D ratio 0.629 to 1.114 (mean 0.7531). Apical sculpture worn smooth in all material examined.

Postapical sculpture of broad, shallow ridges overlain by minute subparallel wrinkles, regular longitudinal ridges on upper part of whorls give faintly reticulated appearance. Shell periphery keeled, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening. Umbilicus deep. Shell chocolate brown with pale subsutural band. Lip same colour as shell. Shell solid. Based on 83 measured adults. Foot colour grey.

Free oviduct short, about 25 - 35% length of vagina, which is equal in length to penis. Free oviduct swollen at junction with vagina. Spermathecal shaft long, swollen at junction with vagina. Small flagellum at junction of vas and epiphallus. Penial retractor muscle inserts on bend of epiphallus. Epiphallus about 50% length of penis. Junction of epiphallus and penis marked externally by slight constriction and internally by extreme thickening of wall, rather than separate penial papilla. Penis lining of papillae fusing to form regular oblique to horizontal ridges, which thicken towards genital atrium (Fig. 6.32).

Discussion

Varohadra oconnellensis is widespread in mid-eastern Queensland, but live specimens are rarely collected. This monotypic genus differs markedly from the other genera and species with which it is wholly or partially sympatric. Only one species approaches it conchologically: *Bentosites yulei*. Both *V. oconnellensis* and *B. yulei* have an excavated umbilicus, and in some localities the shells are very similar in size. The reproductive tracts are distinct, *B. yulei* possessing a large pointed penial papilla, which is absent in *V. oconnellensis*, while the penis wall of *V. oconnellensis* is considerably thicker than that of *B. yulei.*

Range and habitat

Varohadra oconnellensis occurs in mid-eastern Queensland, coastally from the O'Connell River near Mt Dryander to Hatfield's Gap, south of Sarina (Fig. 6.33). It is found in vine forest, where it is semi-arboreal. At Cape Hillsborough it occurs in scree slopes in vine forest and sclerophyll forest and woodland, and has also been collected in grassy patches in open forest.

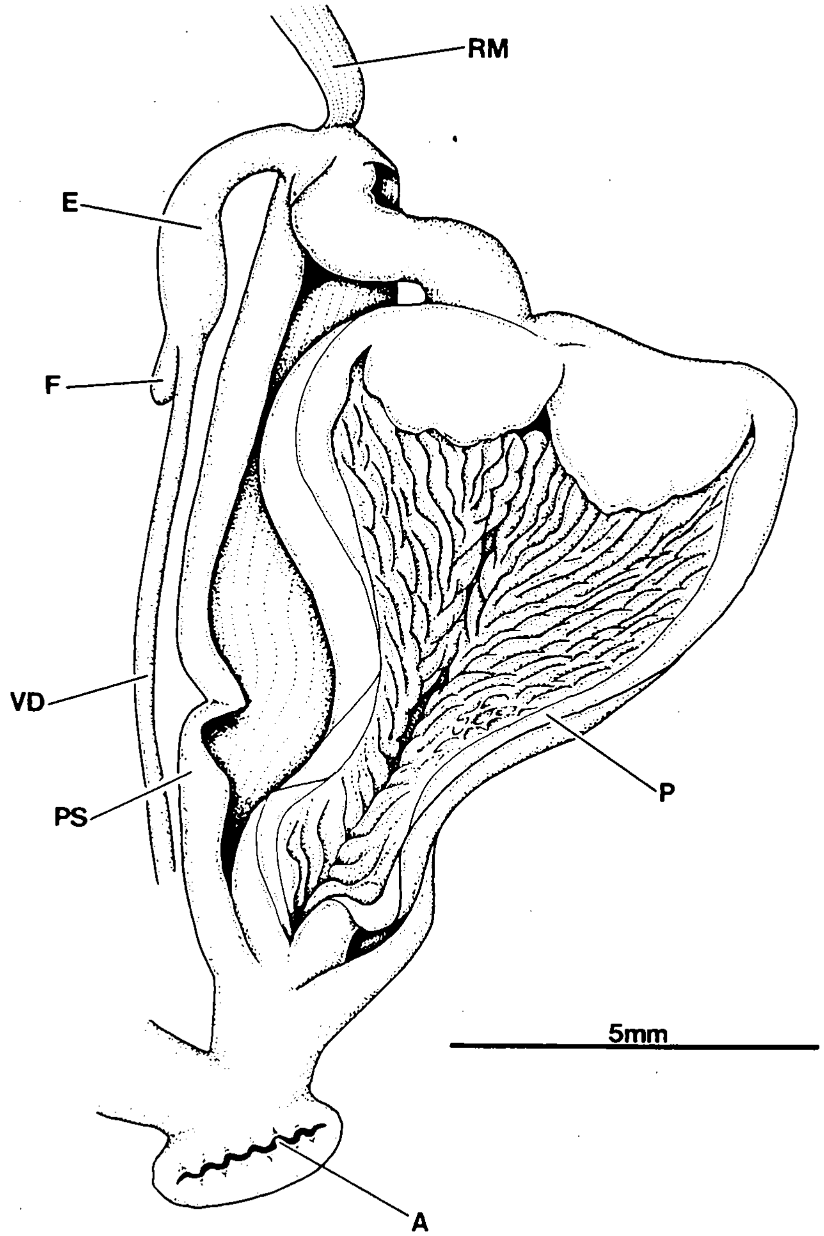


Fig. 6.32: Lining of penis of *Varohadra oconnellensis* (Cox) (Proserpine) (A = atrium, E = epiphallus, F = epiphallic flagellum, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens)

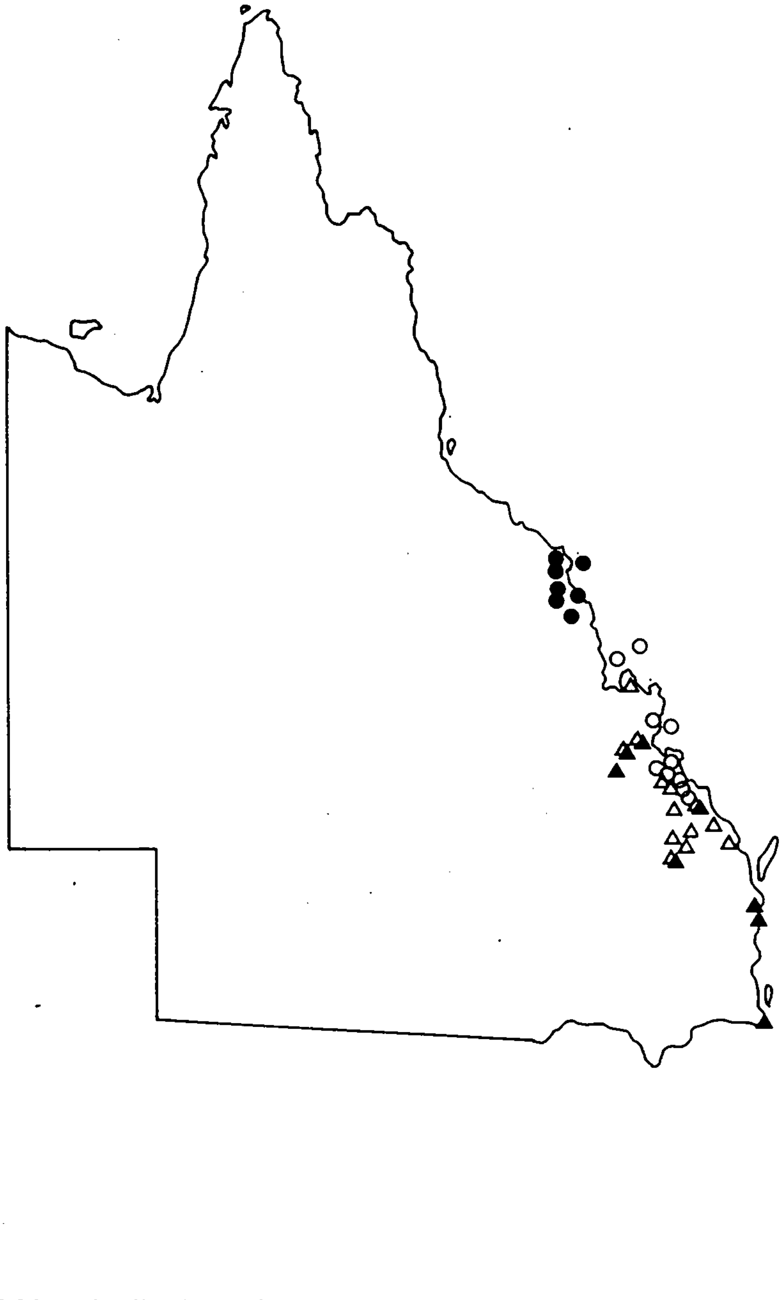


Fig. 6.33: Distribution of *Varohadra oconnellensis* (Cox) (●) and Gen. nov. *incei* (Philippi) (○), Gen. nov. A *appendiculata* (Reeve) (△), and Gen. nov. A *mattea* (Iredale) (▲).

Gen. nov. A

Figuladra Iredale, 1933: 45 - nom. nud.; Iredale, 1937b: 30; Richardson, 1985: 305; Smith, 1992: 154. Type species *Helix curtisiana* Pfeiffer, 1864, by original designation.

Diagnosis

Gen. nov. A can be distinguished from related genera by the combination of orange foot and collar, flagellum on the vas deferens, swollen distal epiphallus and presence of muscles in the epiphallic-penial bend.

Description

Shell small to medium. Postapical sculpture of radial growth ridges only. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and moderately flared, reflected over umbilicus, partially occluding it (*incei, mattea*). Shell light with numerous darker bands, dark subsutural band, dark band around umbilicus, lacking dark radial band behind lip (*incei, mattea*), banded with dark radial band behind lip (*appendiculata*), dark brown with yellow band around umbilicus (*incei*) or wholly brown (*incei*), or any combination. Lip white (*incei, appendiculata*), light (*mattea*), sometimes dark (*appendiculata*), usually glossy. Shell thin to solid.

Foot colour orange.

Ovotestis and albumen gland typical, hermaphrodite duct entering laterally on small talon. Free oviduct short, less than 25% length of vagina, which is approximately 50% length of penis. Free oviduct obtusely reflexed, swollen at junction with vagina. Spermathecal shaft long, swollen at junction with vagina. Spermathecal head lies near base of albumen gland.

Vas deferens with short (*incei*) to long (*appendiculata, mattea*) flagellum, not contained within penis sheath, but bound to it by mesenteries. Very long penial retractor muscle inserts on bend of epiphallus. Muscle fibres on inside of epiphallic-penial bend (*incei*), muscle fibres envelope part of distal epiphallus and bind it to penis (*appendiculata*), or epiphallus and penis folded within penis sheath and bound by muscle fibres (*mattea*). Distal epiphallus with pilaster terminating in large penial papilla at junction with penis. Penis very long, unfolded (*incei*) or folded (*appendiculata, mattea*) within penis sheath. Sculpture on penis lining complicated. Papilla on lining of epiphallic chamber coalesce to form parallel ridges either side of a pilaster on penis wall, with pilaster distally breaking up into asymmetrically disposed ridges and finally, irregular papillae (*incei*), penis lined with numerous flattened interdigitating papillae, giving way in one section to anastomosing longitudinal ridges close to genital atrium (*appendiculata*), close to epiphallus, flanking longitudinal pilaster, penis lined with lozenge-shaped papillae partially fused in oblique rows, which halfway along penis, become thickened ridges leading to genital atrium (*mattea*).

Species of Gen. nov. A

There are three species of Gen. nov. A in eastern Australia:

- Gen. nov. A *incei* (Philippi, 1846) - type species
- Gen. nov. A *appendiculata* (Reeve, 1854)
- Gen. nov. A *mattea* (Iredale, 1933)

Discussion

Iredale (1933) introduced *Figuladra* as a subspecies of *Varohadra*, with *Helix curtisiana* Pfeiffer, 1864, designated as type species. No description or definition was provided to distinguish this subgenus from the nominate subgenus, so under Article 13 of the International Code of Zoological Nomenclature (ICZN, 1985), *Figuladra* is not an available name. Smith (1992) synonymised *Figuladra* with *Sphaerospira.*

Key to species of Gen. nov. A

Genitalia

1. Short flagellum at junction of vas deferens and epiphallus .... *incei*

   Long flagellum at junction of vas deferens and epiphallus 2

2. Penis with longitudinal ridges toward atrium .... *appendiculata*

   Penis with oblique ridges toward atrium .... *mattea*

Gen. nov. A *incei* (Philippi)

Helix incei Philippi, 1846: 83, pl. vii, fig. 3 - Australia; Iredale, 1937: 33 - restricted type locality to Percy Islands, South Queensland.

Helix lessoni Pfeiffer, 1846: 71 - Australia; Iredale, 1937: 32 - restricted type locality to Percy Islands, South Queensland.

Helix curtisiana Pfeiffer, 1864: 528 - Port Curtis, Queensland; Cox, 1868: pl. 20, fig. 9; Iredale, 1937b: p. 32 - corrected type locality to Mount Larcom.

Helix incei var. *depressior* Schmeltz, 1869: 73 - nom. nud.

Helix aureedensis Brazier, 1872b: 640 - Aureed Island, Torres Strait; Iredale, 1937b: 32 - corrected type locality to Port Denison.

Helix (Camaena) challisi Cox, 1873: 565 - L. Island, Torres Strait; Iredale, 1937b: 33 - corrected type locality to L.Island, Broad Sound, Queensland.

Helix yeppoonensis Beddome, 1897: 123 - Yeppoon, Queensland.

Thersites (Sphoerospira) incei (Philippi) Fulton, 1904: 2.

Thersites (Sphoerospira) incei var. *yeppoonensis* Fulton, 1904: 3.

Thersites (Sphoerospira) lessoni (Pfeiffer) Fulton, 1904: 3.

Thersites (Sphoerospira) lessoni var. *aureedensis* Fulton, 1904:3.

Varohadra bernhardi Iredale, 1933: 45; Iredale, 1937b: 32, pl. iii, fig. 7; Richardson, 1985: 306.

Varohadra curtisiana (Pfeiffer) Iredale, 1933: 45; Richardson, 1985: 306.

Varohadra curtisiana exedra Iredale, 1933: 45 - Boyne Island, Port Curtis, Queensland; Iredale, 1937b: 32, pl. 3, fig. 6.

Varohadra yeppoonensis Iredale, 1937b: 31; Richardson, 1985: 311.

Varohadra lessoni (Pfeiffer) Iredale, 1937b: 32; Richardson, 1985: 308.

Varohadra aureedensis (Brazier) Iredale, 1937b: 32; Richardson, 1985: 305.

Varohadra incei (Philippi) Iredale, 1937b: 33.

Varohadra challisi (Cox) Iredale, 1937b: 33; Richardson, 1985: 306.

Varohadra keppelensis Iredale, 1937b: 33, pl. iii, fig. 8 - North Keppel Island, Queensland; Richardson, 1985: 308.

Varohadra keppelensis degener Iredale, 1937b: 33, pl. iii, fig. 9 - South Keppel Island.

Sphaerospira incei (Philippi) Richardson, 1985: 289; Smith, 1992: 156

Sphaerospira incei curtisiana Smith, 1992: 156

Sphaerospira incei lessoni Smith, 1992: 156.

Diagnosis

Short flagellum on vas deferens. Muscle fibres on inside of epiphallic-penial bend. Penis lined with oblique ridges proximally, asymmetrical ridges and irregular pustules distally.

Description

Shell medium to large, 26.1 to 40.0mm (mean 29.03mm) in diameter, and 18.6 to 32.5mm (height 23.29mm) in height, with 5.0 to 6.0 (mean 5.36) whorls, H/D ratio 0.684 to 0.932 (mean 0.794). Apical sculpture worn smooth in all specimens examined, postapical sculpture of radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, partially occluding it. Shell in several colour forms, grading into one another, from pale yellow or brown with thin bands, to brown with large yellow circumumbilical patch, to wholly brown. Lip white, sometimes glossy. Shell thin to solid. Based on 56 measured adults.

Free oviduct short, less than 25% length of vagina, which is approximately 50% length of penis. Free oviduct obtusely reflexed, swollen at junction with vagina. Spermathecal shaft long, swollen at junction with vagina. Sheath enclosing proximal epiphallus. Very long penial retractor muscle inserts on bend of epiphallus. Muscle fibres on inside of epiphallic-penial bend (Fig. 6.34). Distal epiphallus with pilaster terminating in large penial papilla at junction with penis. Papilla on lining of epiphallic chamber coalesce to form parallel ridges either side of a pilaster on penis wall. Distally, pilaster breaks up into asymmetrically disposed ridges and finally, irregular papillae (Fig. 6.35). Penis very long, unfolded within penis sheath.

Discussion

This is an extremely variable species, which is reflected in the number of names attributed to it. The striped shell, *Helix incei*, was originally described from "Australia", but Iredale (1937b) restricted the type locality to the Percy Islands. Pfeiffer (1846) named another species, *Helix lessoni*, the type locality of which was also simply "Australia". Iredale (1937b) decided that this material had probably been collected by the H.M.S. Fly, and amended the type locality to the Percy Islands. The three syntypes of *lessoni*, held at the British Museum (Natural History), exhibit two colour patterns: "typical" *lessoni* (brown with yellow umbilical patch) and "typical" *incei* (banded) (J. Stanisic and D. Potter, pers. comm.). A third colour form, *H.*

curtisiana, was described by Pfeiffer (1864) from Port Curtis. This was a chestnut brown shell with a white lip. Smith (1992) splits this species into three subspecies based on the colour patterns mentioned above. The holotype of *H. aureedensis* is a pale brown, faintly banded shell, with a yellow umbilical patch and white lip. Iredale (1937b) corrected the original type locality of "Aureed Island, Torres Strait" to Port Denison, which is vague and also probably incorrect. No shell with this colour pattern has been collected since in the Bowen region, which is the site of Port Denison.

The *lessoni* colour pattern also occurs in *Varohadra bernhardi* from Rockhampton, while *H. challisi* and *V. keppelensis* are both striped like *incei*. These patterns are not discrete and intermediates are found in most parts of the species' range. The reproductive tract morphology varies to much lesser extent.

Range and habitat

Gen. nov. A *incei* is found in mid-eastern to south-eastern Queensland, from the Northumberland Islands to Curtis Island, off Gladstone (Fig. 6.33). It occurs in vine thicket, often on limestone.

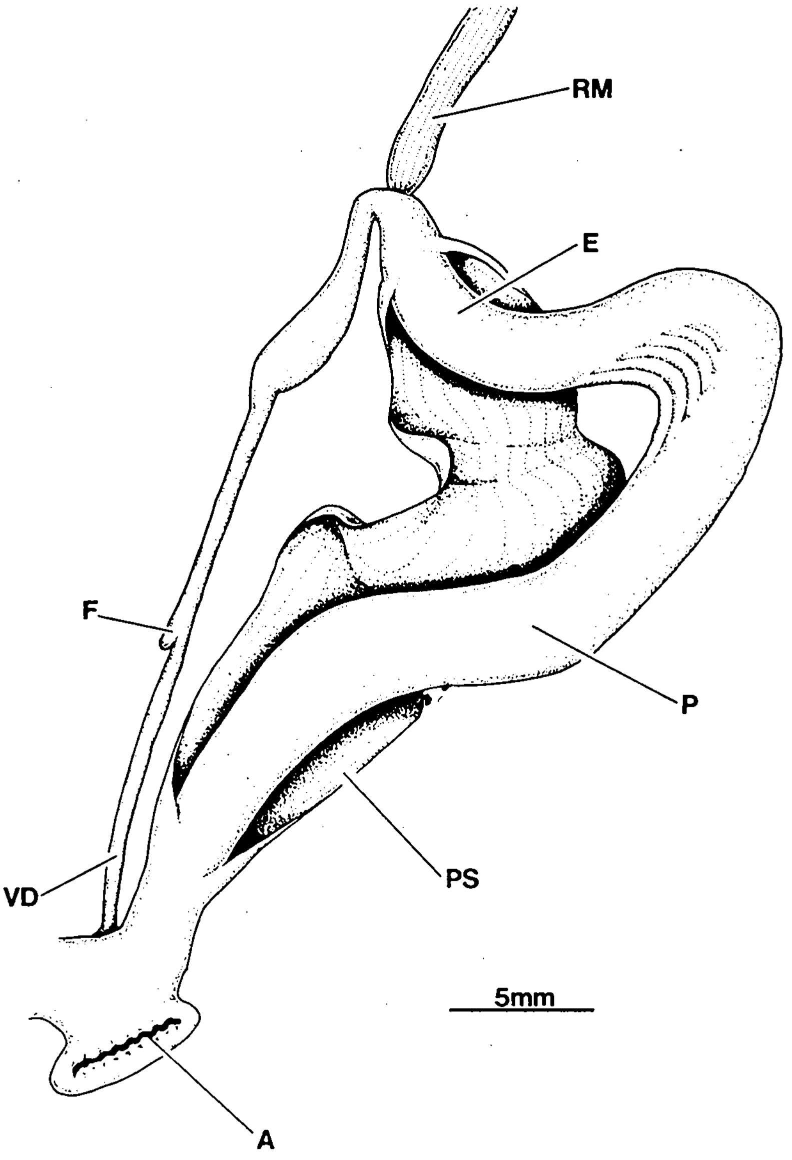


Fig. 6.34: Muscle fibres on terminal male genitalia of Gen. nov. A *incei* (Philippi) (Eurimbula) (A = atrium, E = epiphallus, F = epiphallic flagellum, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens)

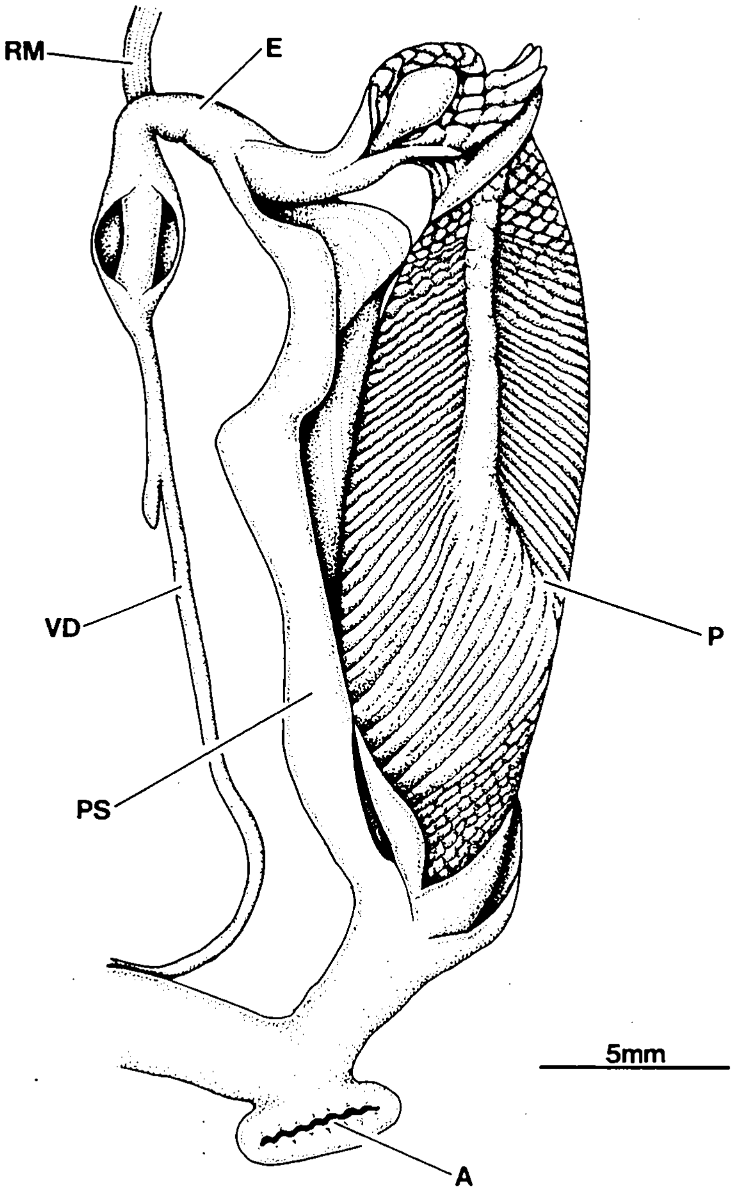


Fig. 6.35: Lining of penis of Gen. nov. A *incei* (Philippi) (Eurimbula) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens)

Gen. nov. A *appendiculata* (Reeve)

Helix appendiculata Reeve, 1854: 193, sp. 1353 - Australia; Pfeiffer, 1854: 149; Iredale, 1937b: 34 - restricted type locality to Bersaker Range, near Rockhampton.

Helix thatcheri Cox, 1870: 170, pl. xvi, fig. 2 - Mt Bersaker, Rockhampton, South Queensland.

Helix (Hadra) bayensis Brazier, 1875c: 2 - Wide Bay, Queensland; Iredale, 1937b: 34, pl. iii, fig. 16.

Varohadra bayensis (Brazier) Iredale, 1937b: 36; Richardson, 1985: 306.

Varohadra bayensis reducta Iredale, 1937b: 34, pl. iii, fig. 15 - Tenningering (Mt Perry), Bundaberg, Queensland.

Varohadra appendiculata (Reeve) Iredale, 1937b: 34; Richardson, 1985: 305.

Sphaerospira appendiculata (Reeve) Smith, 1992: 156.

Diagnosis

Vas deferens with long flagellum. Muscle fibres on epiphallic-penial bend enveloping epiphallus. Penial lining with flattened interdigitating papillae and longitudinal ridges.

Description

Shell medium, 31.9 to 36.2mm (mean 36.14mm) in diameter, and 26.0 to 26.9mm (mean 25.48mm) in height, with 5.25 to 6.0 (mean 5.48) whorls, H/D ratio 0.681 to 0.812 (mean 0.746). Apical sculpture worn smooth on all specimens examined, postapical sculpture of radial growth ridges only. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and moderately flared, reflected over umbilicus, partially occluding it. Shell light to dark, with numerous darker bands, dark subsutural band, dark radial band behind lip. Lip light to dark. Based on 339 measured adults.

Free oviduct short, less than 25% length of vagina. Free oviduct swollen at base, reflexed obtusely before entering uterus. Spermathecal shaft swollen slightly at junction with vagina, otherwise narrow. Vas deferens with long flagellum. Penial retractor muscle inserts on bend of epiphallus. Epiphallus swollen proximally. Muscle fibres envelop part of distal epiphallus and bind it to penis (Fig. 6.36). Distal epiphallus with pilaster termainating in large rounded penial papilla at junction with penis. Penis lining complicated, with numerous flattened interdigitating papillae, giving way in one section to anastomosing longitudinal ridges close to genital atrium (Fig. 6.37).

Discussion

The dark radial band behind the lip of Gen. nov. A *appendiculata* separates it from Gen. nov. A *incei* and Gen. nov. A *mattea.* The anatomy is quite distinct, with the development of the muscle fibres in the epiphallic-penial bend midway between that of Gen. nov. A *incei* and Gen. nov. A *mattea.*

No topotypic wet material of *thatcheri* was available, but examination of the holotype suggests it is a depressed form of Gen. nov. A *appendiculata*, as suggested by Iredale (1937b).

Range and habitat

Gen. nov. A *appendiculata* is found in mid-eastern to south-eastern Queensland, from Berserker Range near Rockhampton, to Gayndah, inland of Maryborough (Fig. 6.33). This species has been recorded mainly from semi-evergreen vine thicket and related `dry' rainforest types in mid-east Queensland from Mt Morgan to Coalstoun Lakes. It is associated with limestone at Ambrose, Bracewell and Mt Larcom. It occurs in riverine rainforest at Colosseum and Builyan, in suburban gardens at Rockhampton, an in *Acacia* regrowth on sand at Woodgate NP.

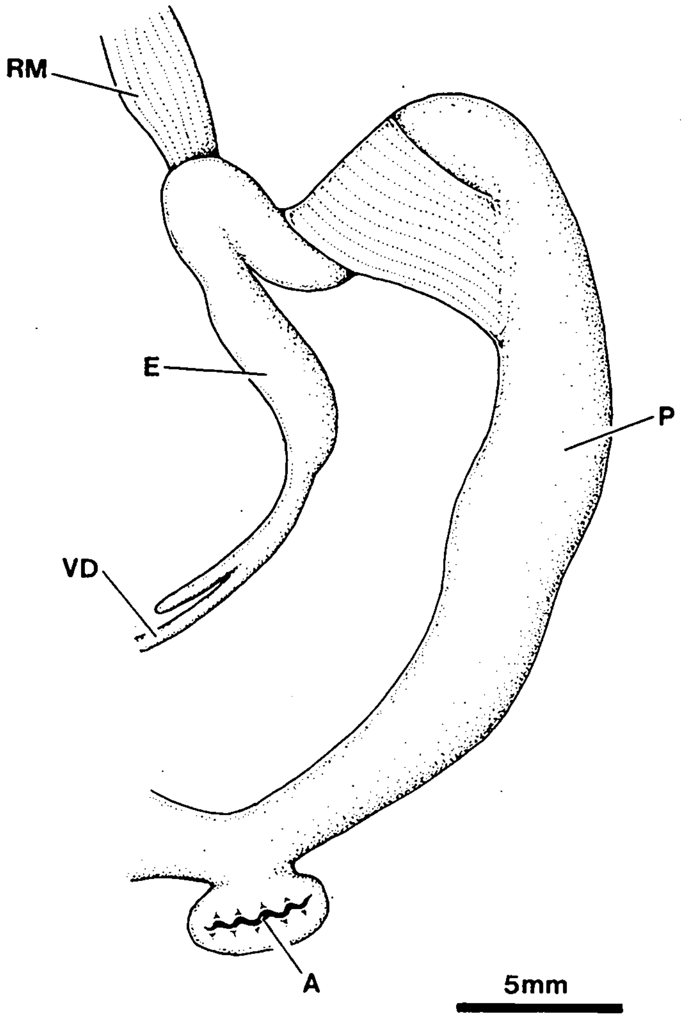


Fig. 6.36: Muscle fibres on genitalia of Gen. nov. A *appendiculata* (Reeve) (Ulam Ranges) (A = atrium, E = epiphallus, P = penis, RM = penial retractor muscle, VD = vas deferens)

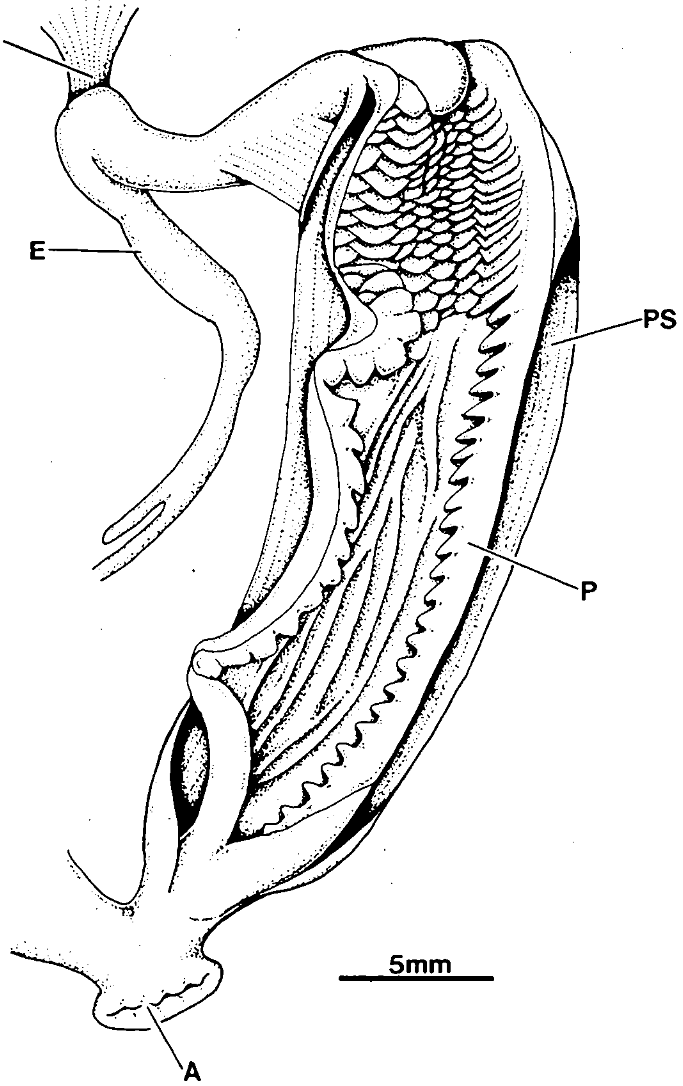


Fig. 6.37: Lining of penis of Gen. nov. A *appendiculata* (Reeve) (Ulam Range) (A = atrium, E = epiphallus, P = penis, RM = penial retractor muscle, VD = vas deferens)

Gen. nov. A *mattea* (Iredale) comb. nov.

Varohadra incei mattea Iredale, 1933: 46 - Rockhampton, Queensland.

Varohadra mattea Iredale, 1937b: 33, pl. iii, fig. 11; Richardson, 1985: 308.

Diagnosis

Vas deferens with long flagellum. Muscle fibres on inside of large epiphallic-penial bend. Penial lined proximally with papillae in oblique rows, becoming thickened ridges distally.

Description

Shell small to medium, 25.4 to 31.9mm (mean 28.52mm) in diameter, and 18.0 to 25.2mm (mean 21.58mm) in height, with 5.0 to 5.25 (mean 5.202) whorls, H/D ratio 0.656 to 0.826 (mean 0.756). Apical sculpture worn smooth on all specimens examined, postapical sculpture of radial growth ridges only. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and moderately flared, reflected over umbilicus, partly occluding it. Shell light with numerous darker bands, dark subsutural band, dark band around umbilicus. Lip light, glossy. Based on 57 measured adults.

Free oviduct short, less than 25% length of vagina. Free oviduct swollen at base, obtusely reflexed before junction with uterus. Spermathecal shaft narrow, swollen at base. Long flagellum on vas deferens. Penial retractor muscle inserts on bend of epiphallus. Epiphallus expanded proximally. Junction of ephiphallus and penis folded within penis sheath and bound by muscle fibres (Fig. 6.38). Distal epiphallus with pilaster terminating in large penial papilla at junction with penis. Pilaster continues along length of penis. Near epiphallus, penis lined with lozenge-shaped papillae partially fused in oblique rows. Halfway along penis, papillae become thickened ridges leading to genital atrium (Fig. 6.39).

Discussion

Gen. nov. A *mattea* can easily be mistaken for a small Gen. nov. A *incei* by referring to the shell alone. The reproductive anatomy is quite distinct. The junction of the epiphallic-penial complex is bound into an S-shape by muscle fibres which may be an extension of the penial retractor muscle.

Range and habitat

Gen. nov. A *mattea* occurs from Rockhampton, mid-eastern Queensland, to Tweed River, northern New South Wales (Fig. 6.33). This species is found in a wide range of habitats from open sclerophyll forest to vine thicket. It has been recorded from partly cleared sclerophyll woodland at Cooloola State Forest and unspecified sclerophyll growth at Mt Morgan. It is widespread in semi-evergreen vine thicket and related rainforest types such as Bottle-tree scrub from Mt Morgan to Gayndah. At Noosa Heads it occurs in *Casuarina* forest. It has been collected in suburban gardens in Rockhampton and Gladstone.

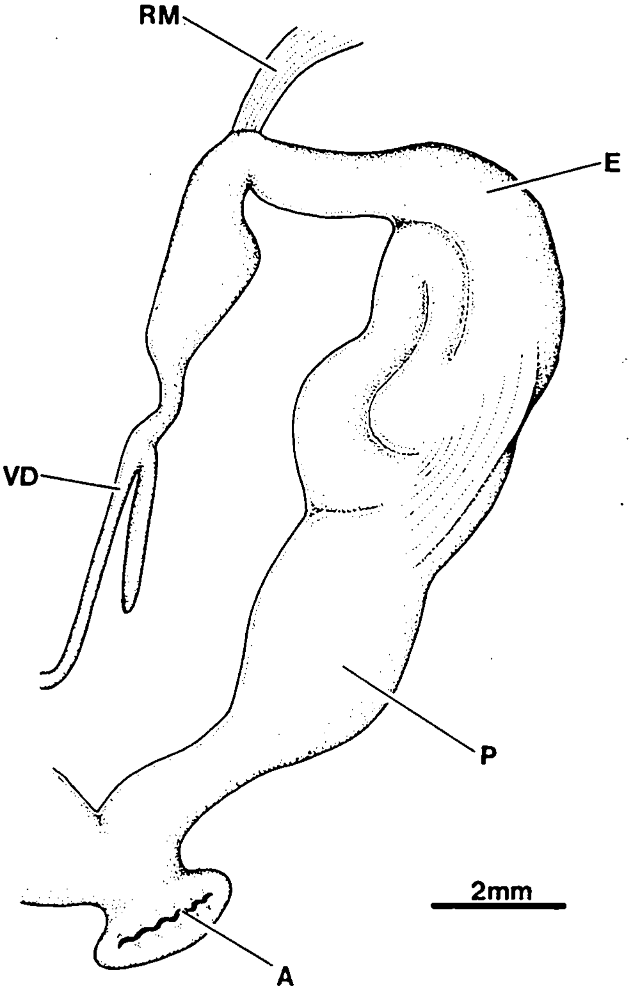


Fig. 6.38: Muscle fibres on genitalia of Gen. nov. A *mattea* (Iredale) (Rockhampton) (A = atrium, E = epiphallus, P = penis, RM = penial retractor muscle, VD = vas deferens).

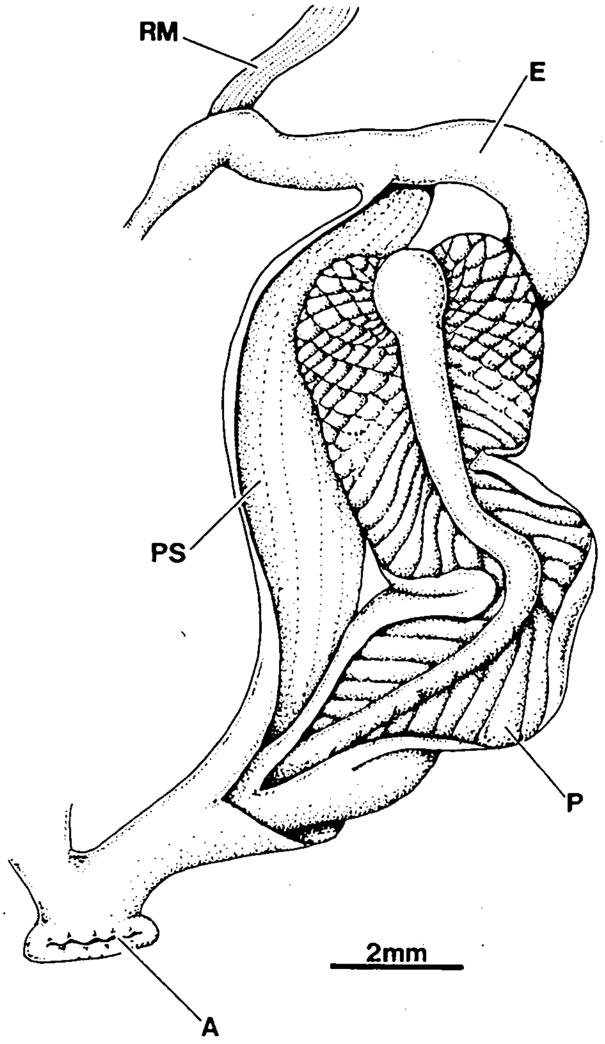


Fig. 6.39: Lining of penis of Gen. nov. A *mattea* (Iredale) (Rockhampton) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle)

Temporena Iredale

Temporena Iredale, 1933: 46; ; Richardson, 1985: 291; Smith, 1992: 153. Type species *Helix whartoni* Cox, 1871, by original designation.

Diagnosis

Temporena can be distinguished from related genera by the combination of orange foot and collar, lack of muscle fibres in the epiphallic-penial bend, short to long flagellum on vas deferens, presence of a shallow penial papilla, and penial sheath which is thin proximally and thick distally.

Description

Shell medium. Postapical sculpture of fine wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and slightly flared. Lip reflected over umbilicus which is partially (*whartoni, macneilli*) to wholly occluded (*coxi, etheridgei, macneilli*). Shell with light with dark banding (*whartoni, coxi, macneilli*) or dark with light banding (*etheridgei*). Dark umbilical patch present (*whartoni, coxi, etheridgei, macneilli*) or absent (*macneilli*). Lip white (*coxi, etheridgei*) or banding on body whorl visible (*whartoni, macneilli*). Shell thin (*whartoni, macneilli*) to solid (*coxi, etheridgei*).

Ovotestis and albumen gland typical, hermaphroditic duct entering laterally on small talon. Free oviduct short and broad, approximately 25% length of vagina, which is equal to penis sheath. Spermathecal shaft long and broad. Spermathecal head lies near base of albumen gland. Vas deferens with flagellum, very short (*etheridgei*), short (*macneilli*), medium (*whartoni*) to long (*coxi*), not enclosed within penis sheath but bound to it by mesenteries. Proximal epiphallus indistinguishable externally from vas deferens. Penial retractor muscle inserts on bend of epiphallus. Epiphallus with thick pilaster which terminates in a shallow pointed penial papilla, with subterminal ejaculatory opening. Penis long, folded within penis sheath (*whartoni, coxi, etheridgei*). Penis sheath thin proximally and slightly thicker distally. Lining of penis with longitudinal pilaster, and sculpture of fine diverging ridges near penial papilla, becoming large rounded papillae, and irregular longitudinal folds and ridges near genital atrium (*whartoni*), with tiny papillae extending onto proximal penis in subparallel rows, eventually coalescing to form irregular longitudinal ridges separated by small papillae towards genital atrium (*coxi*), with tiny papillae extending onto proximal penis in subparallel rows, merging into elongate papillae, eventually coalescing to form thick irregular longitudinal ridges towards genital atrium (*etheridgei*), or with coarse papillae extending onto proximal penis, eventually coalescing to form anastomosing ridges towards genital atrium (*macneilli*).

Species of *Temporena*

Four species of *Temporena* occur in Queensland:

- *Temporena whartoni* (Cox, 1871)
- *Temporena coxi* (Crosse, 1866)
- *Temporena etheridgei* (Brazier, 1877)
- *Temporena macneilli* (Iredale, 1937b)

Discussion

Temporena was introduced as a subgenus of *Gnarosophia*. The new subgenus was separated from the nominate subgenus by the thinness of the shell and its more flattened profile. *Helix whartoni* Cox was assigned type species.

Temporena was later raised to the level of genus (Iredale, 1937b). According to Iredale (1937b) it contained only two species: *T. whartoni* (Cox) and *T. mitifica* Iredale, 1933. Smith (1992) synonymised it with *Sphaerospira*.

Keys to the species of *Temporena* in eastern Queensland rainforests

Shells

1. Lip white 2
   Lip dark or banded 3
2. Shell generally dark with thin white subsutural band .... *etheridgei*
   Shell light with darker banding, but no white subsutural band .... *coxi*
3. Shell small, Bowen region .... *macneilli*
   Shell medium, Holbourne Island only .... *whartoni*

Genitalia

1. Flagellum at junction of vas deferens and epiphallus tiny, no more than a bump .... *etheridgei*
   Flagellum distinct 2
2. Penis with tiny regular papillae proximally .... *coxi*
   Penis with coarse papillae proximally 3
3. Penis with fine diverging ridges near penial papilla, irregular longitudinal ridges leading to atrium .... *whartoni*
   Penis with papillae near penial papilla, anastomosing longitudinal ridges leading to atrium .... *macneilli*

***Temporena whartoni* (Cox)**

Helix whartoni Cox, 1871: 55, pl. iii, figs. 5 5a - Port Denison, Queensland.

Gnarosophia (Temporena) whartoni (Cox) Iredale, 1933: 46. Iredale, 1937b: 27 - corrected type locality to Holbourne Island.

Temporena whartoni (Cox) Iredale, 1937b: 27; Richardson, 1985: 292.

Sphaerospira whartoni (Cox) Smith, 1992: 159.

Diagnosis

Shell medium, pale with numerous darker bands, dark band round umbilicus. Vas deferens with medium flagellum. Penial papilla pointed, penis lining with diverging longitudinal ridges and large papillae.

Description

Shell medium, 30.3 to 39.1mm (mean 36.56mm) in diameter, and 22.1 to 28.7mm (mean 25.19mm) in height, with 5.0 to 6.0 (mean 5.324) whorls, H/D ratio 0.646 to 0.829 (mean 0.729). Apical sculpture worn smooth in all specimens examined, postapical sculpture of fine subparallel wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilicus which is partially occluded. Shell pale with numerous dark bands, dark band around umbilicus. Lip glossy. Shell thin. Based on 87 measured adults.

Free oviduct short, less than 25% length of vagina, which is 75% length of penis. Free oviduct diverges from vagina at acute angle. Spermatheca shaft long, swollen at base. Vas deferens with medium flagellum. Proximal epiphallus indistinguishable externally from vas deferens. Penial retractor muscle inserts on bend of epiphallus. Epiphallus with thick pilaster which terminates in a shallow pointed penial papilla, with subterminal ejaculatory opening. Penis long, folded within penis sheath. Penis sheath thin proximally and slightly thicker distally. Lining of penis with longitudinal pilaster, and sculpture of fine diverging ridges near penial papilla, becoming large rounded papillae. Irregular longitudinal folds and ridges near genital atrium (Fig. 6.40).

Discussion

Holbourne Island is a small continental island, east of Cape Upstart (Fig. 6.41). It is built of young (Permian-Mesozoic) volcanics contemporary with outcrops at Cape Upstart, Cape Edgecumbe and Gloucester Island. The eastern part of the island is gabbro, diorite and dolerite, while the western part is mainly leucocratic adamelllite and granite (Paine et al, 1970). Although now protected, it was once mined for phosphate.

The presence of an endemic snail on an island so small and isolated has been questioned. There is a precendent in this area. *Bentosites macleayi* occurs only on the Whitsunday Group, even though some islands (e.g. the Molle Group) are very close to the mainland. Admittedly, the range of that species is much larger than that of *T. whartoni*, but it illustrates the point that some populations are easily isolated.

Nothing resembling *Temporena whartoni* has been recovered from the adjacent mainland, so until evidence to the contrary is produced it must be assumed that this species is confined to Holbourne Island.

Range and habitat

This species is confined to Holbourne Island (Fig. 6.41). It lives in hollow trees, and under logs and coral rubble.

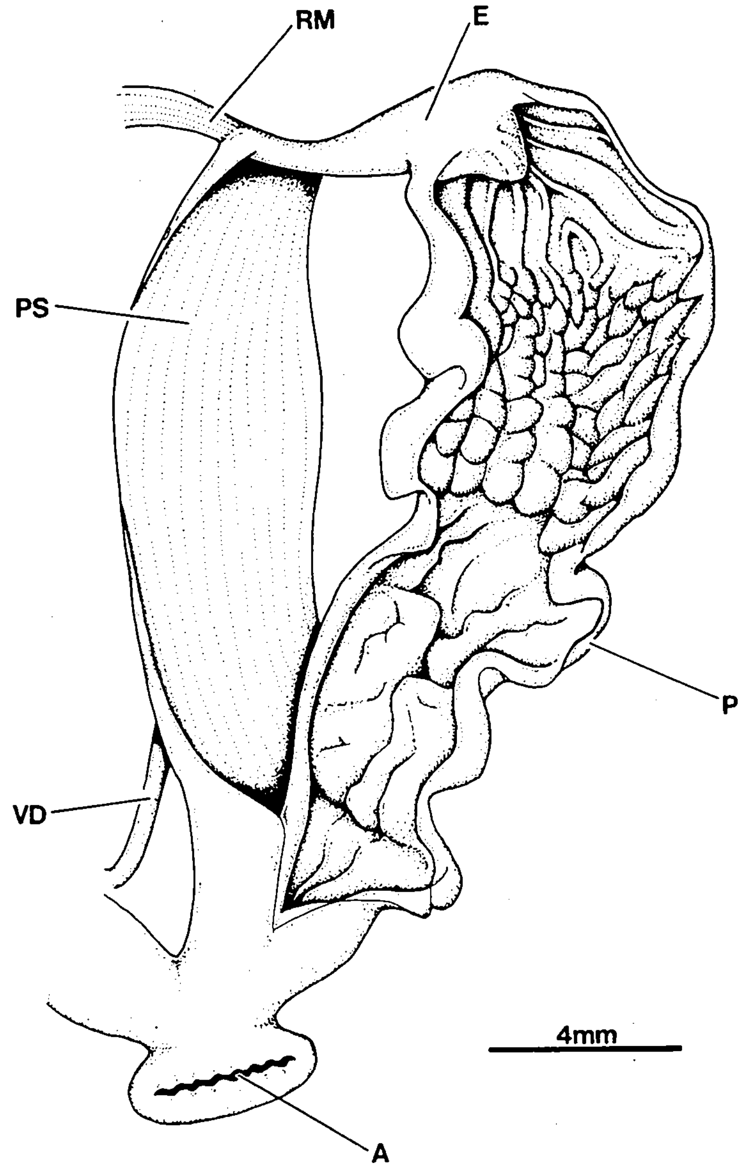


Fig. 6.40: Lining of penis of *Temporena whartoni* (Cox) (Holbourne Island) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens).

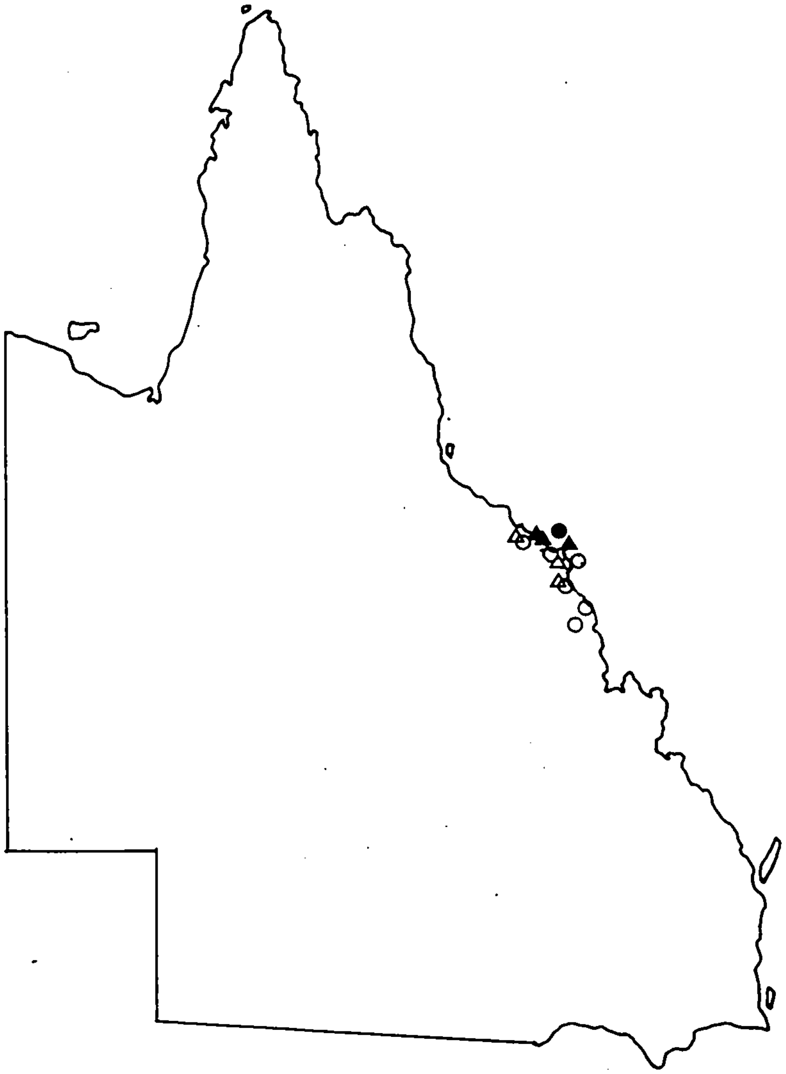


Fig. 6.41: Distribution of *Temporena whartoni* (Cox) (●), *T. coxi* (Crosse) (○), *T. etheridgei* (Brazier) (Δ), and *T. macneilli* (Iredale) (▲).

***Temporena coxi* (Crosse)**

Helix forbesii Cox, 1864a: 490, textfigs - Port Denison, Qld. Not *Helix forbesii* Pfeiffer, 1845.

Helix cerea Cox, 1864b: 36 - new name for *H. forbesii* Cox. Not *Helix cerea* Gould, 1850.

Helix coxi Crosse, 1866: 195 - new name for *H. cerea* Cox.

Helix cerata Cox, 1868: 58, pl. viii, fig. 4 - new name for *H. cerea* Cox.

Helix (Helicostyla) croftoni Cox, 1872: 18, pl. iv, fig. 1 - Hydrometer River, Mackay, Queensland.

Varohadra volgiola fortasse Iredale, 1933: 46

Varohadra probleema Iredale, 1933: 46; Iredale, 1937b: 35, pl. iii, fig. 16 - Hamilton Island, Whitsunday Group, Queensland; Richardson, 1985: 309.

Bentosites coxi (Crosse) Iredale, 1937b: 29; Richardson, 1985: 66.

Bentosites croftoni (Cox) Iredale, 1937b: 29; Richardson, 1985: 67.

Varohadra fortasse Iredale, 1937b: 34, pl. iii, fig. 10 - Lindeman Island, Whitsunday Group, Queensland; Richardson, 1985: 307.

Sphaerospira coxi (Crosse) Smith, 1992: 156.

Diagnosis

Shell medium to large, globose with high spire, pale with few thin dark bands, often dark band around umbilicus, pale lip. Vas deferens with long flagellum. Penial papilla pointed, covered in tiny papillae. Penial sculpture of tiny regular papillae and fine longitudinal ridges.

Description

Shell medium to large, 29.7 to 46.2mm (mean 35.65mm) in diameter, and 20.2 to 37.3mm (mean 31.11mm) in height, with 6.5 to 6.125 (mean 5.31) whorls, H/D ratio 0.671 to 1.078 (mean 0.882). Apical sculpture worn smooth in all material examined, postapical sculpture of fine wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip expanded and moderately flared, reflected over umbilicus wholly occluding it, lip with columellar twist. Shell light with dark bands, dark subsutural band, often dark band around umbilicus. Lip white, glossy. Shell solid. Based on 25 measured adults.

Free oviduct broad, slightly swollen at base, approximately 25% length of vagina. Vagina narrow, equal in length to penis sheath. Spermathecal shaft long and broad. Proximal epiphallus indistinguishable from vas deferens. Epiphallic flagellum medium to long. Penial retractor muscle inserts proximally on bend of epiphallus. Epiphallus simple, with thick pilaster which terminates in shallow penial papilla at junction with penis. Penial papilla with subterminal ejaculatory opening. Penial papilla covered in tiny papillae extending onto proximal penis in subparallel rows, eventually coalescing to form irregular longitudinal ridges separated by small papillae towards genital atrium. Penis folded in penis sheath. Penis sheath thin proximally, thickening abruptly distally, with reciprocal change in thickness of penis wall (Fig. 6.42).

Discussion

Cox (1864a) found this species active on the trunks of fig trees at Port Denison. He initially thought it was a local variety of *Helix lessoni*, but eventually decided it was a new species. He named it after Edward Forbes, but *Helix forbesii* was a preoccupied name. Later (1864b) he realised the error and renamed it *Helix cerea.* Unfortunately, this name was also preoccupied. In 1868, he gave it a third name, *Helix cerata*, but Crosse had already renamed it *Helix coxi* in his honour in 1866.

This species also includes *Helix croftoni*, which differs from *coxi* in the width of the dark shell bands. Intermediates between the two forms are common. The sculpture of the penis lining is identical in both forms.

Shells from the Whitsunday Islands are often thin. Iredale gave the name *Varohadra fortasse* to a medium-sized thin shell from Lindeman Island. A specimen from Dent (West Hamilton) Island which resembled the holotype proved to have the same anatomical characteristics as those of larger, more solid specimens from the mainland. Other names have been informally associated with this species, including *Varohadra volgiola* Iredale (= *Helix andersoni* Cox). I have examined the holotype and topotypic wet material, and have decided that *V. volgiola* does not belong with this genus. It is allied to *Pallidelix.*

Range and habitat

Temporena coxi is found in mid-eastern Queensland, from Mt Inkerman, north of Bowen, to Mirani, west of Mackay (Fig. 6.41). It inhabits rainforest.

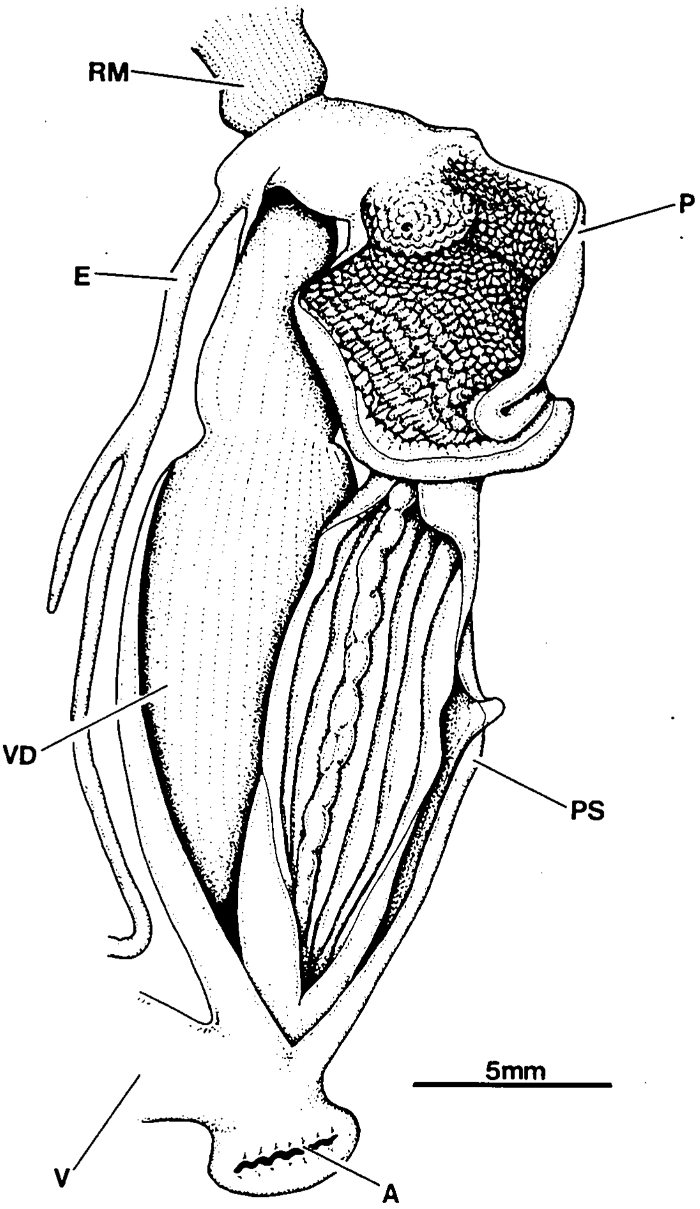


Fig. 6.42: Lining of penis of T*emporena coxi* (Crosse) (Hook Island) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle, V = vagina, VD = vas deferens).

Temporena etheridgei **(Brazier), comb. nov.**

Helix (Calliocochlias) etheridgei Brazier, 1877: 25 - Andromache River, near Bowen; Fulton, 1904: 9, pl.i, fig. 2; Iredale, 1937b: 29 - corrected type locality to Hydrometer River, near Mackay.

Bentosites etheridgei (Brazier) Richardson, 1985: 67

Sphaerospira etheridgei (Brazier) Smith, 1992: 155

Diagnosis

Shell medium, globose with high spire, dark with few to many light bands, dark band around umbilicus, white lip. Vas deferens with tiny flagellum. Penial papilla pointed. Penial sculpture of tiny papillae extending onto proximal penis in subparallel rows, merging into elongate papillae, eventually coalescing to form thick irregular longitudinal ridges towards genital atrium.

Description

Shell medium, 27.0 to 36.7mm (mean 30.66mm) in diameter, and 26.0 to 37.1mm (mean 31.32mm) in height, with 6.825 to 6.0 (mean 5.365) whorls, H/D ratio 0.962 to 1.133 (mean 1.019). Apical sculpture worn smooth in all specimens examined, postapical sculpture of fine wrinkles and radial growth ridges. Shell periphery rounded to very slightly angular, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, wholly occluding it. Shell dark with thin white subsutural band, and one or more lighter bands, sometimes very wide and often running together to give an entirely light shell. Lip white, never dark or showing body whorl banding. Shell relatively solid. Based on 5 measured adults.

Free oviduct narrow, swollen at base, approximately 25% length of vagina. Vagina broad, equal in length to penis sheath. Spermathecal shaft long and broad, swollen at base. Vas deferens with tiny flagellum, no more than a bump, at junction with epiphallus. Proximal epiphallus indistinguishable from vas. Penial retractor muscle inserts midway on bend of epiphallus. Epiphallus simple, with thick pilaster which terminates in shallow penial papilla at junction with penis. Penial papilla with subterminal ejaculatory opening. Penial papilla covered in tiny papillae extending onto proximal penis in subparallel rows, merging into elongate papillae, eventually coalescing to form thick irregular longitudinal ridges towards genital atrium (Fig. 6.43). Penis folded in penis sheath. Penis sheath thin proximally, thickening abruptly distally, with reciprocal change in thickness of penis wall.

Discussion

This species is rarely collected. Unlike most other large camaenids it is markedly arboreal. At the Andromache River, specimens were found on the underside of vines in forest trees (J. Stanisic & D. Potter, pers. comm.).

The shell of this species is very similar to that of *Bentosites gavisa* (e.g. Smith, 1992), but the two species can be differentiated by the colour of the lip. In *T. etheridgei* the lip is always white, while in *B. gavisa* it is dark or shows body whorl banding.

Range and habitat

Temporena etheridgei is found in mid-eastern Queensland, from Mt Inkerman, north of Bowen, to the Andromache River, near Mackay (Fig. 6.41). It inhabits vine forest.

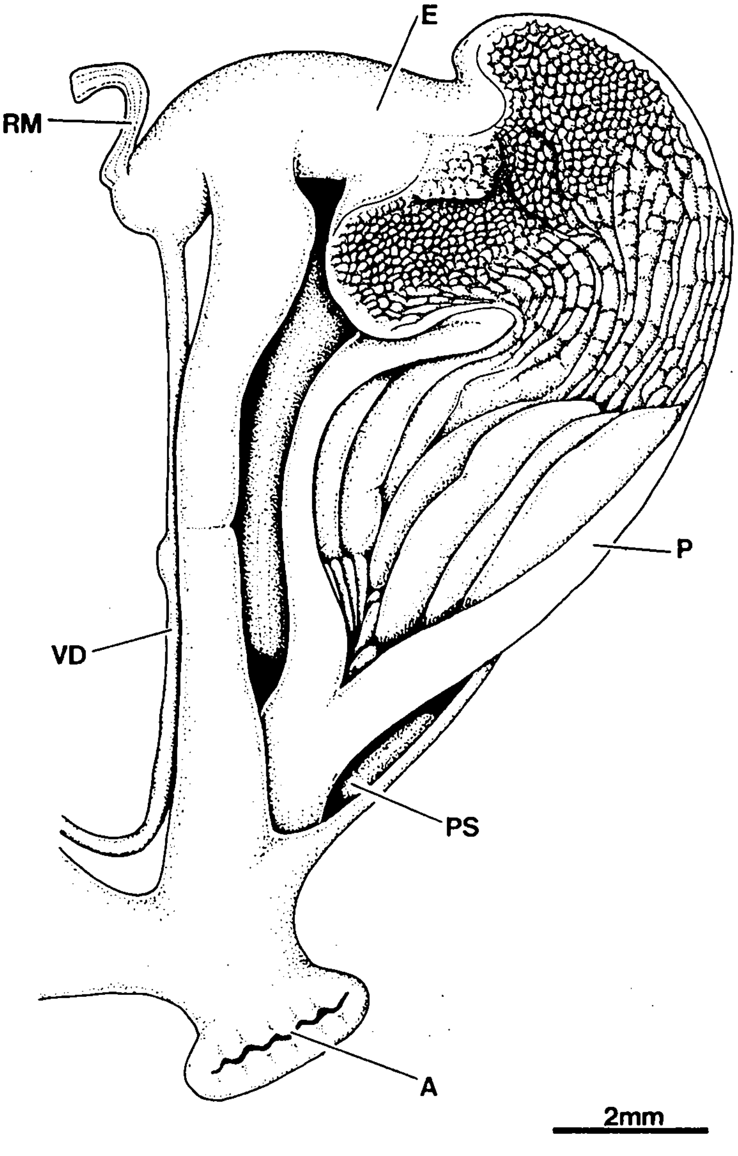


Fig. 6.43: Lining of penis of T*emporena etheridgei* (Brazier) (Mt Jukes) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens).

Temporena macneilli (Iredale), comb. nov.

Varohadra macneilli Iredale, 1937b: 31 - Double Cone Island, Queensland; Richardson, 1985: 308.

Varohadra saxicola Iredale, 1937b: 34, pl. iii, fig. 12 - Stone Island, Port Denison; Richardson, 1985: 310.

Diagnosis

Shell small to medium, globose with moderately elevated spire, light with few to many dark bands, dark band around umbilicus, banding visible on lip. Vas deferens with short flagellum. Penial papilla pointed. Penial sculpture of coarse papillae proximally, eventually coalescing to form anastomosing longitudinal ridges towards genital atrium.

Description

Shell small to medium, 27.2 to 35.0mm (mean 29.61mm) in diameter, and 19.5 to 30.3mm (mean 25.38mm) in height, with 6.5 to 5.625 (mean 5.452) whorls, H/D ratio 0.679 to 1.013 (mean 0.935). Apical sculpture worn smooth in all specimens examined, postapical sculpture of fine wrinkles and radial growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, partially to wholly occluding it. Shell light with few to many darker bands, dark band around umbilicus. Lip showing banding on body whorl. Shell thin. Based on 37 measured adults.

Free oviduct broad, diverging from vagina at right angle, approximately 25% length of vagina. Vagina narrow, equal in length to penis sheath. Spermathecal shaft long and broad, base of shaft swollen at junction with vagina. Vas deferens broad, with short flagellum at junction with epiphallus. Proximal epiphallus slightly wider than vas deferens. Penial retractor muscle inserts proximally on bend of epiphallus. Epiphallus simple, with thick pilaster which terminates in shallow penial papilla at junction with penis. Penial papilla with subterminal ejaculatory opening. Penial papilla covered in coarse papillae extending onto proximal penis, eventually coalescing to form anastomosing ridges towards genital atrium (Fig. 6.44). Penis unfolded in penis sheath. Penis sheath thin proximally, thickening abruptly distally, with reciprocal change in thickness of penis wall.

Discussion

The type specimens of *macneilli* and *saxicola* are very similar, and the type localities (Double Cone Island and Stone Island respectively) are close to each other. Topotypic material was unavailable, so the synonymy is based on shell material only.

This species has a restricted distribution in the Bowen region, but can be very common at times. A single specimen of cf *macneilli* was collected on Holbourne Island, type locality of *T. whartoni.* Unfortunately, the specimen was beginning to decay, so the identification is based on shell alone. It is not included in this study, but is reported here to alert workers in the field to the possibility of two relatively large camaenids occurring sympatrically on Holbourne Island.

Smith (1992) includes *Varohadra macneilli* in the synonymy of *Sphaerospira yulei*, and *Varohadra saxicola* in that of *Sphaerospira mourilyani* (Brazier, 1875). For a discussion of *Helix (Hadra) mourilyani*, see *Species of indeterminate status* below.

Range and habitat

Temporena macneilli is found in the Bowen region, and also on islands of the Whitsunday Group (Fig. 6.41). It occurs in vine thicket and occasionally on foreshore vegetation.

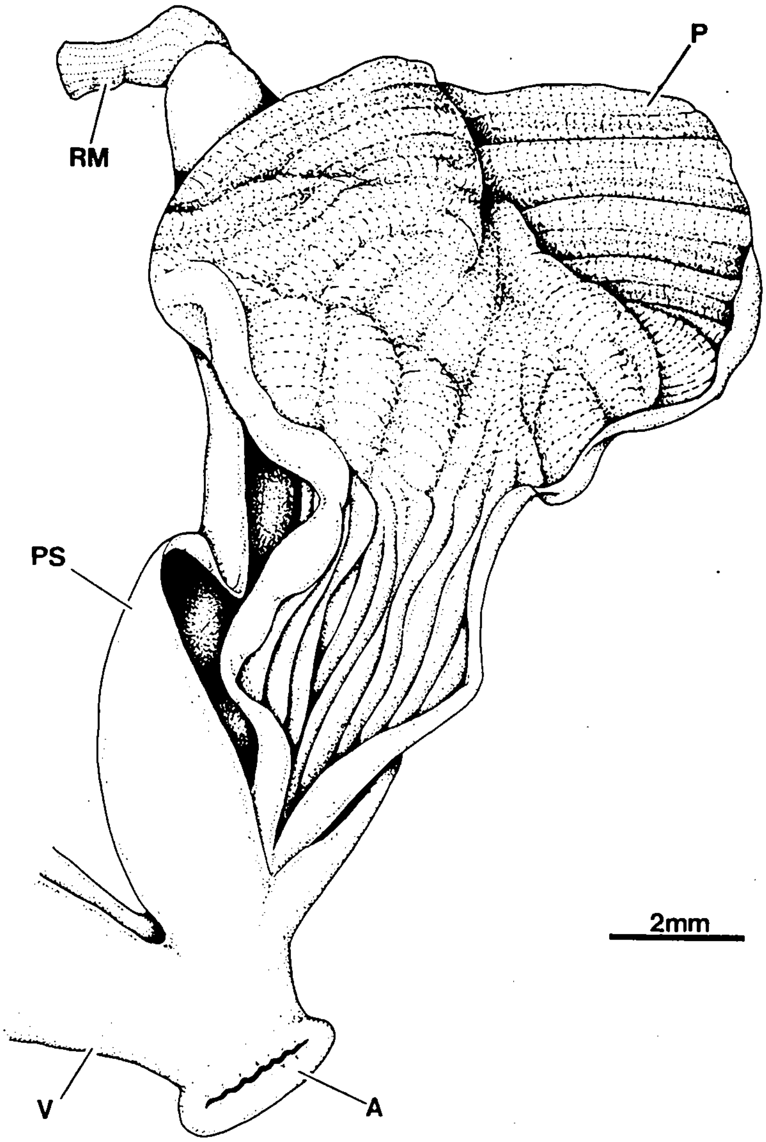


Fig. 6.44: Lining of penis of *Temporena macneilli* (Iredale) (Euri Creek) (A = atrium, P = penis, PS = penial sheath, RM = penial retractor muscle, V = vagina).

Gen. nov. B

Type species

Helix rockhamptonensis Cox, 1873.

Diagnosis

This genus can be distinguished from related genera by the massive muscular penis sheath and the degenerate penis.

Description

Shell medium (*rockhamptonensis*) to large (sp. nov.). Postapical sculpture of very fine subparallel wrinkles and radial growth ridges. Shell periphery angular, base of shell flattened, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, partially occluding it. Umbilicus deep. Shell pale with dark peripheral band, and one or more darker bands, dark subsutural band, dark radial band behind lip, and dark circum-umbilical patch (*rockhamptonensis*) or pale brown with faint banding (sp. nov.). Lip dark brown (*rockhamptonensis*) to mid brown (sp. nov.), glossy. Shell relatively solid.

Foot colour grey.

Free oviduct much less than 25% of vagina, slightly swollen at base. Vagina broad proximally, narrowing towards atrium, very long, equivalent in length to extended penis. Spermathecal shaft long, very swollen at junction with vagina. Spermathecal head lies near base of albumen gland. Vas deferens of uniform width (*rockhamptonensis*) or much broader on male side than on female side (sp. nov.). Epiphallus slightly wider than penis and coiled within sheath (*rockhamptonensis*) or greatly enlarged and straight (sp. nov.). Penial retractor muscle thin, long, inserts on bend of epiphallus approximately halfway. Junction of epiphallus and penis marked externally by thickening of penis sheath (*rockhamptonensis*) or by narrowing of penis sheath (sp. nov.). Penis degenerate, very long, straight (*rockhamptonensis*) or folded within muscular penis sheath (sp. nov.).

Species of Gen. nov. B

There are two species of *Miniwilli*, both confined to Queensland.

- Gen. nov. B *rockhamptonensis* (Cox, 1873)
- Gen. nov. B sp. nov.

Discussion

The type species of this genus, Gen. nov. B. *rockhamptonensis* (Cox), was assigned to *Varohadra* by Iredale (1937b), because of its superficial similarity to *Varohadra oconnellensis*. A study of the anatomy shows that it is quite different to *Varohadra* and belongs in a separate genus.

Key to the species of Gen. nov. B

Shells

Not enough specimens were available to catalogue variation and provide a reliable diagnosis based on shells.

Genitalia

1. Proximal epiphallus much narrower than penis sheath .... *rockhamptonensis*

Epiphallus indistinguishable from penis sheath...................................... sp. nov.

Gen. nov. B *rockhamptonensis* (Cox) comb. nov.

Helix rockhamptonensis Cox, 1873a: 151 - Rockhampton, Queensland.

Helix moresbyi Angas, 1876: 267, pl. xx, figs. 8-9 - Port Denison.

Helix planibasis Brazier, 1881a: 445.

Hadra rockhamptonensis var. *pallida* Hedley & Musson, 1892: 556 - Rockhampton, Queensland.

Varohadra rockhamptonensis (Cox) Iredale, 1933: 45; Richardson, 1985: 309.

Varohadra rockhamptonensis decreta Iredale, 1937b: 31, pl. iii, fig. 5 - Mt Etna Caves district, Queensland.

Sphaerospira rockhamptonensis (Cox) Smith, 1992: 158

Diagnosis

Shell medium, base flat. Vas deferens without flagellum. Distal epiphallus coiled. Penis degenerate, enclosed within highly muscular penis sheath.

Description

Shell medium, 31.4 to 35.6mm (mean 36.18mm) in diameter, and 28.6 to 35.0mm (mean 30.45mm) in height, with 6.75 to 6.0 (mean 5.147) whorls, H/D ratio 0.834 to 0.942 (mean 0.89). Apical sculpture worn smooth in all specimens examined, postapical sculpture of very fine subparallel wrinkles and growth ridges. Shell periphery angular, base of shell flattened, body whorl descending rapidly behind lip.

Lip is expanded and moderately flared, reflected over umbilical opening, partially occluding it. Umbilicus deep. Shell pale with dark peripheral band, and one or more darker bands, dark subsutural band, dark radial band behind lip, and dark circum-umbilical patch. Lip dark brown, glossy. Shell relatively solid. Based on 17 measured adults.

Free oviduct much less than 25% length of vagina, slightly swollen at base. Spermathecal shaft very swollen at junction with vagina. Vagina broad proximally, narrowing towards atrium, very long, equivalent in length to extended penis. Vas deferens of uniform thickness. Epiphallus indistinguishable from vas deferens, but markedly thicker than penis (Fig. 6.45). Penial retractor muscle thin, long, inserts proximally on bend of epiphallus. Distal epiphallus coiled within penis sheath. Junction of epiphallus and penis marked externally by rapid thickening of penis sheath, which is extremely muscular. Penis degenerate, no more than a thin thread, very long, unfolded within muscular penis sheath (Fig. 6.46). Penial sculpture unknown.

Discussion

The degenerate penis and massively muscular penial sheath are peculiar to this genus. It is difficult to envisage how the penis sheath could retract sufficiently to allow the penis to be everted. Even if that were possible, the penis is so thin (thinner than the vas deferens) it is unlikely to function effectively as an intromittent organ. Gen. nov. B *rockhamptonensis* and Gen. nov. B sp. nov. may be self-fertilising or parthenogenetic.

Gen. nov. B *rockhamptonensis* has a very limited distribution. It is confined to vine thickets on limestone in the Mt Etna Caves region north of Rockhampton. Solem (1988) highlighted the short range endemism among camaenids associated with limestone outcrops in the Kimberleys, but Gen. nov. B *rockhamptonensis* is unique among rainforest camaenids on the east coast.

Although several species of camaenids are abundant on limestone at Fanning River and Chillagoe, no other strictly calcicolous species have been identified in north-eastern Australia, but calcicolous non-camaenids probably do occur. *Gyliotrachela* *australis* (Odhner 1917) (Vertiginidae) is found as a subfossil on limestone at Chillagoe. Solem (1981c) examined other *Gyliotrachela* from the Northern Territory and Western Australia, and noted that they were also found on limestone.

Range and habitat

Gen. nov. B *rockhamptonensis* is restricted to vine thicket in the Mt Etna region, near Rockhampton (Fig. 6.47).

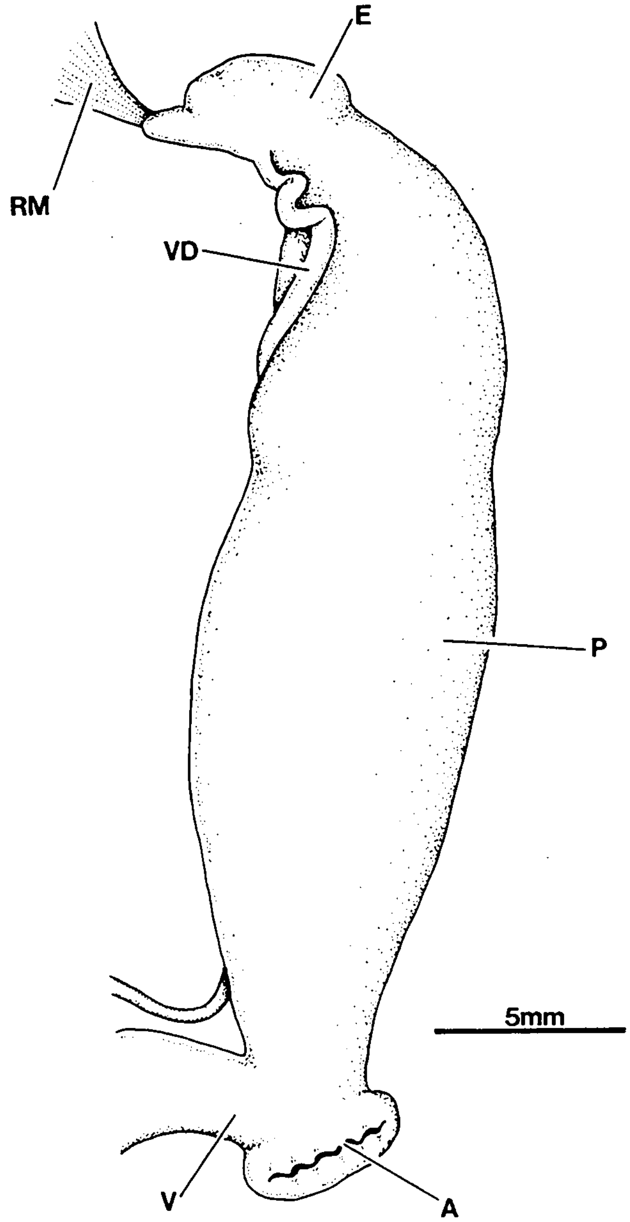


Fig. 6.45: Terminal male genitalia of Gen. nov. B *rockhamptonensis* (Cox) (Rockhampton) (A = atrium, E = epiphallus, P = penis, RM = penial retractor muscle, V = vagina, VD = vas deferens).

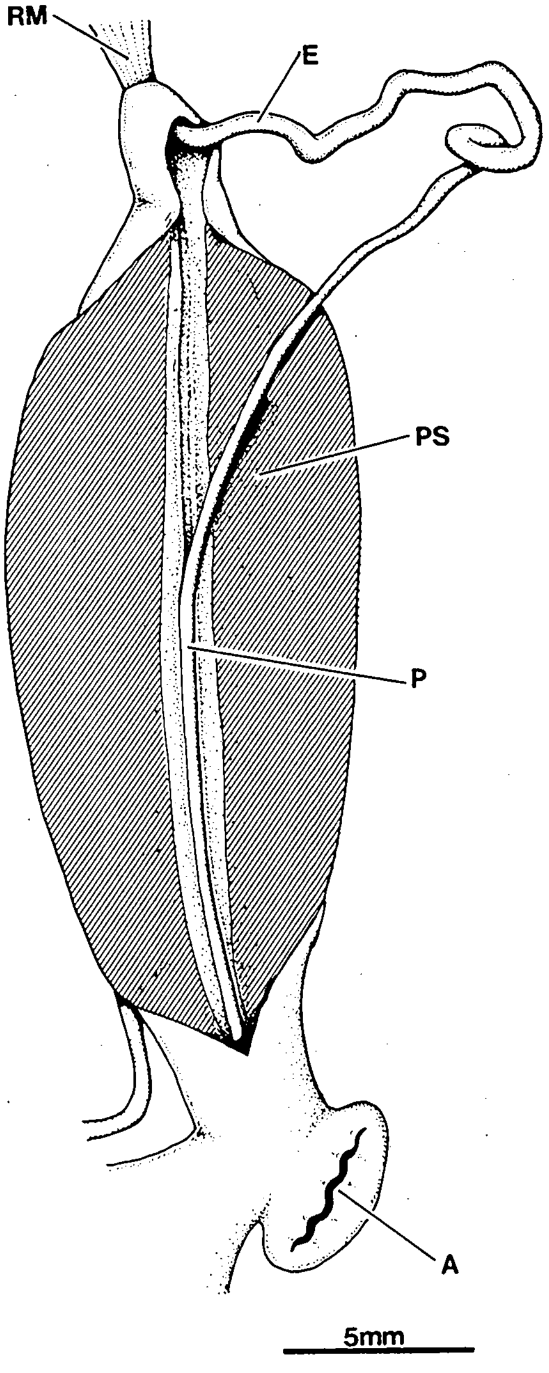


Fig. 6.46: Penis of Gen. nov. B *rockhamptonensis* (Cox) (Rockhampton) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle).

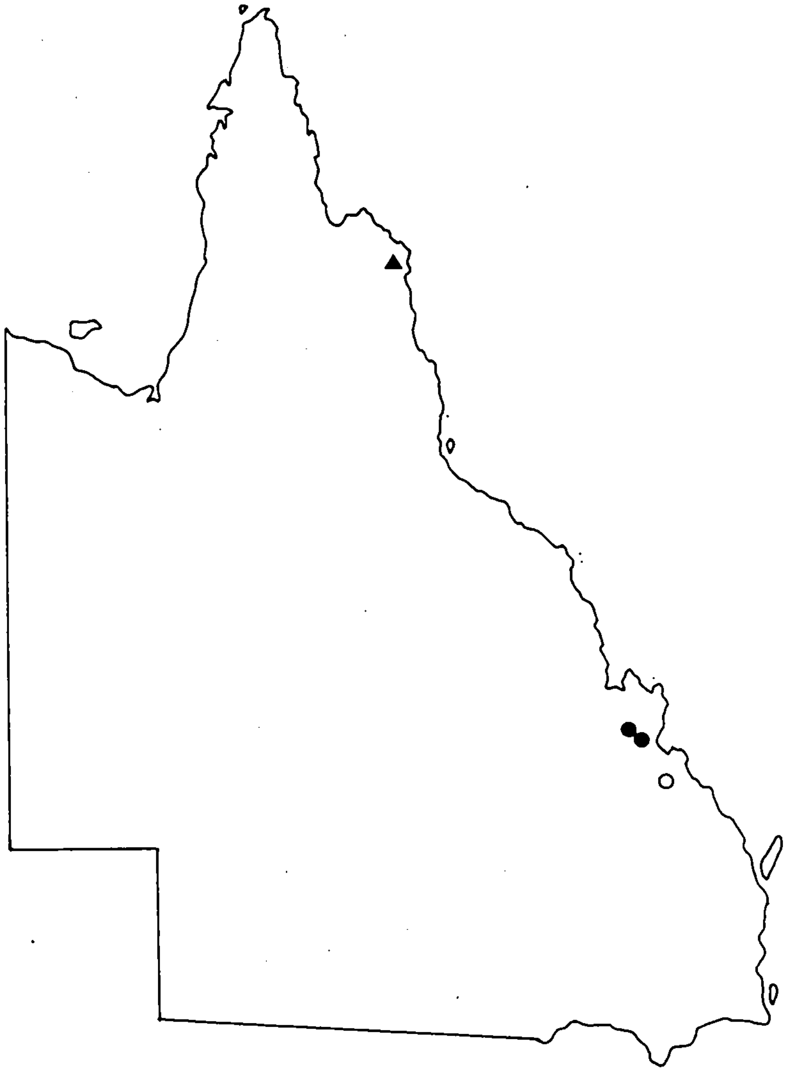


Fig. 6.47: Distribution of Gen. nov. B *rockhamptonensis* (Cox) (●), Gen. nov. B sp. nov. (○) and *Zyghelix forsteriana* (Reeve) (▲).

Gen. nov. B sp. nov.

Diagnosis

Vas deferens without flagellum. Epiphallus greatly expanded. Penis degenerate, folded within muscular penis sheath.

Description

Shell medium, 46.2 to 45.6mm (mean 46.93mm) in diameter, and 42.5 to 46.7mm (mean 43.73mm) in height, with 5.75 to 6.0 (mean 5.916) whorls, H/D ratio 0.944 to 1.011 (mean 0.973) (Fig. 6.48). Apical sculpture worn smooth in all specimens examined, postapical sculpture of fine wrinkles and growth ridges. Shell periphery rounded, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilical opening, almost wholly occluding it. Shell pale brown with faint banding. Lip light to mid-brown, porcellaneous. Based on 3 adults.

Free oviduct much less than 25% of vagina, slightly swollen at base. Spermathecal shaft very swollen at base. Vagina broad proximally, narrowing towards atrium, very long, equivalent in length to extended penis. Vas deferens much broader on male side than on female side, lacking flagellum. Epiphallus greatly enlarged. Penial retractor muscle thin, long, inserts on bend of epiphallus approximately halfway. Junction of epiphallus and penis marked externally by narrowing of penis sheath (Fig. 6.49). Epiphallus very muscular. Penis degenerate, very long, folded within muscular penis sheath (Fig. 6.50). Penial sculpture unknown.

Discussion

This species is known only from the type series, but the differences between it and its congener Gen. nov. B *rockhamptonensis* are distinct. The habitat of this species was not included on the data labels, but the area in which specimens have been collected is simple and complex notophyll vine forest. Much of the Bulburin State Forest has been selectively logged for *Araucaria* and partly cleared for *Araucaria* plantations.

Range and habitat

Gen. nov. B sp. nov. is known only from Bulburin and the Granite Creek area, south west of Miriam Vale, Queensland (Fig. 6.47). It inhabits vine forest.

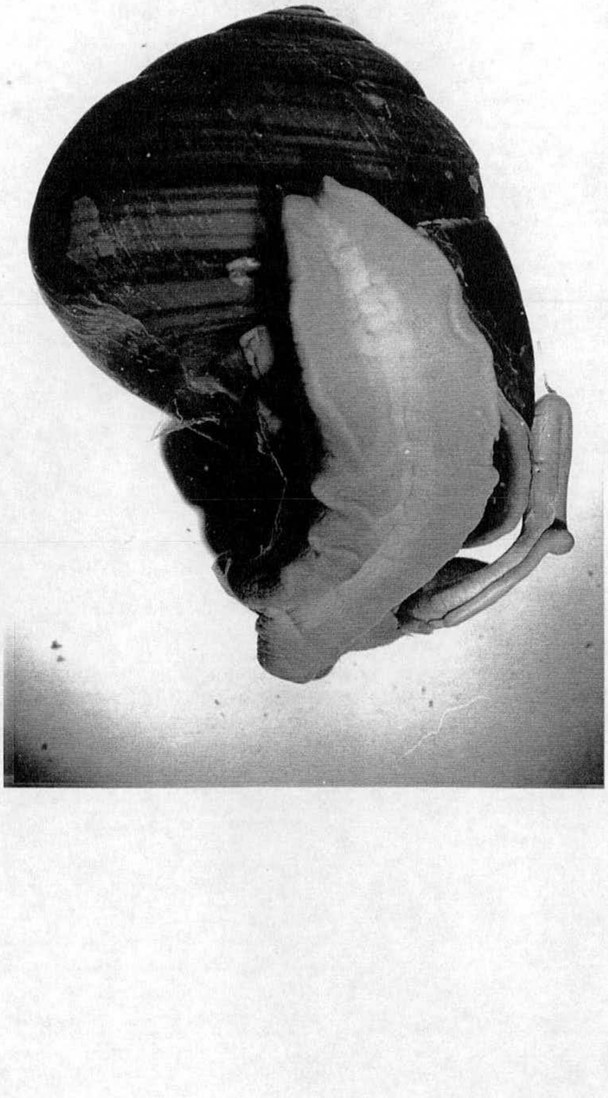


Fig. 6.48: *Gen. nov*. B. *sp. nov*. (Bulburin).

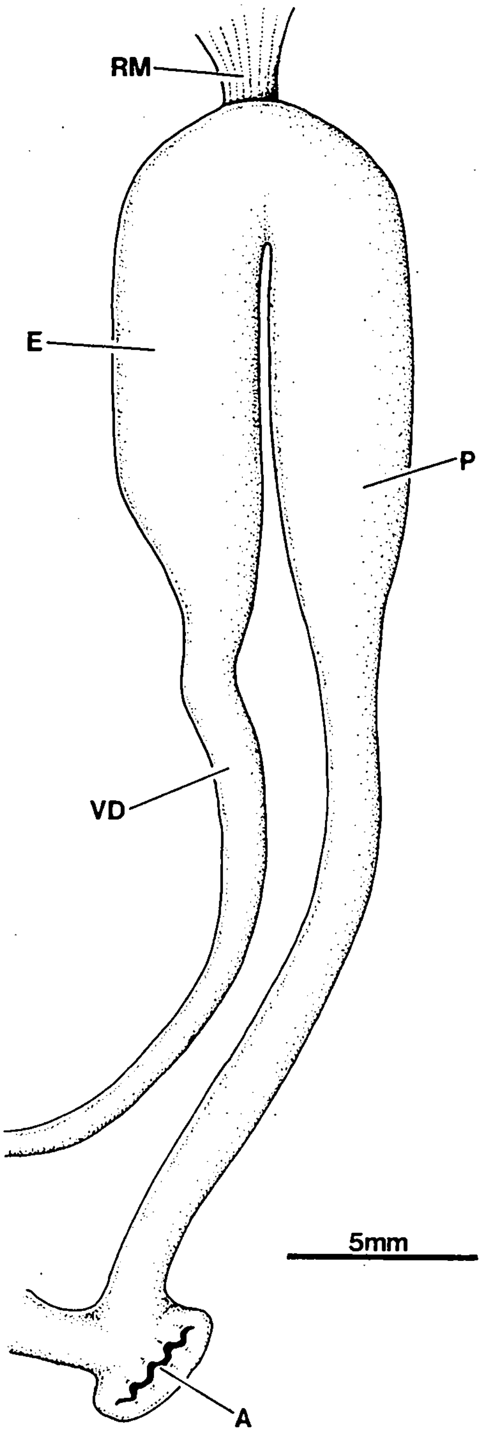


Fig. 6.49: Terminal male genitalia of Gen. nov. B sp. nov. (Bulburin) (A = atrium, E = epiphallus, P = penis, RM = penial retractor muscle, VD = vas deferens).

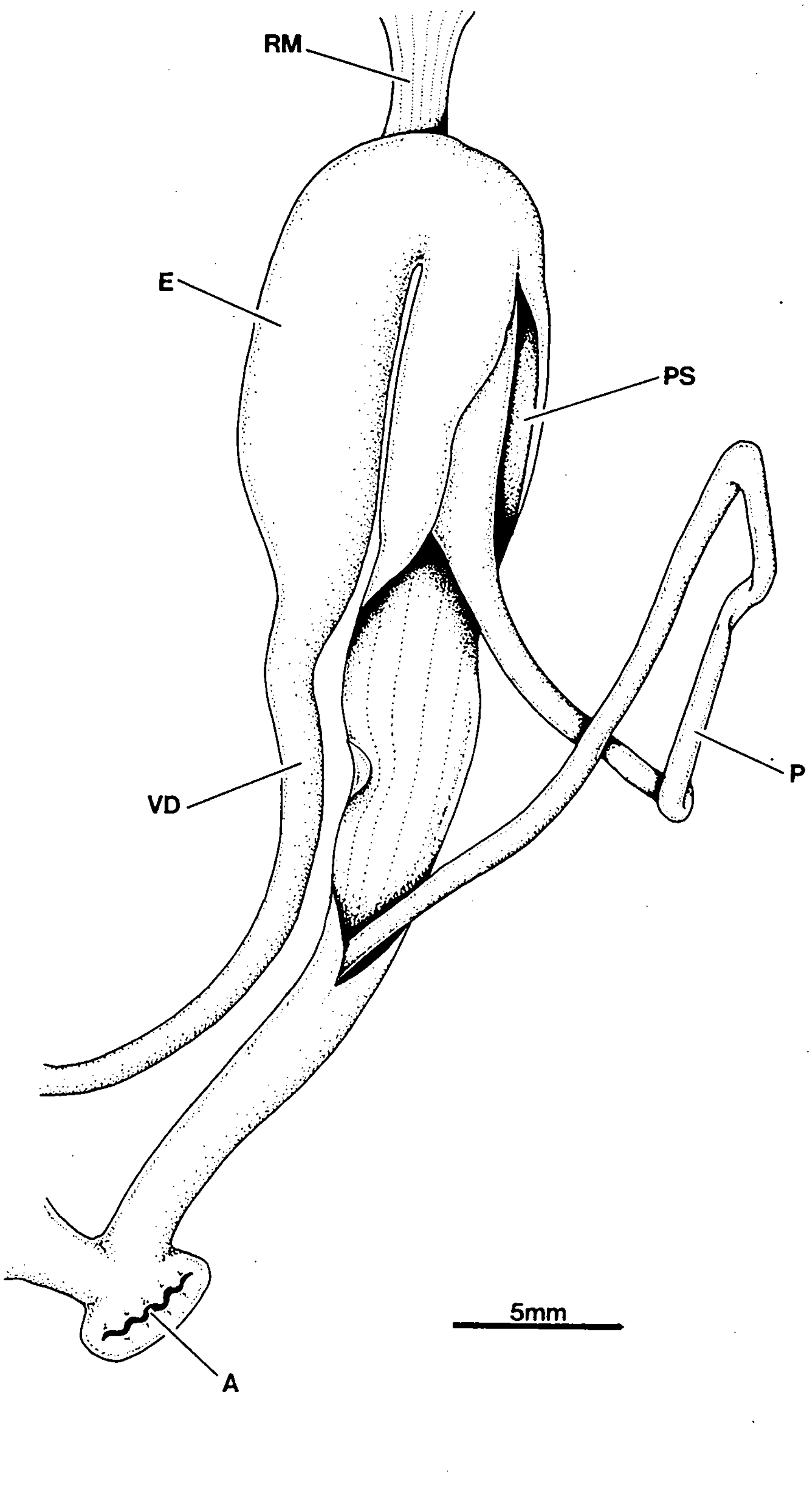


Fig. 6.50: Penis of Gen. nov. B sp. nov. (Bulburin) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, RM = penial retractor muscle, VD = vas deferens).

Zyghelix Iredale

Zyghelix Iredale, 1937b: 23; Richardson, 1985: 322; Smith, 1992: 160. Type species, *Helix forsteriana* Reeve, 1852, by original designation

Diagnosis

See Iredale (1937b: 23).

Description

As for species.

Species of *Zyghelix*

One species of *Zyghelix* is found in Queensland rainforests:

- *Zyghelix forsteriana* (Reeve, 1852)

Discussion

Zyghelix is one of Iredale's better diagnosed genera. Iredale (1937b: 23) referred to the genus as "one of the most perplexing of all the Queensland series", noting its occurrence from around Cooktown south to Cairns. Apart from *Zyghelix forsteriana*, Iredale (1937b) referred to *Z. praehadra* (Odhner, 1917) from Chillagoe and *Z. darwini* (Brazier, 1872b), the type locality of which is simply "north coast of Australia".

Smith (1992) synonymised *Zyghelix* with *Spurlingia*. Although there are a number of anatomical similarities between the two genera, I consider *Spurlingia* to be a junior synonym of *Hadra*, leaving *Zyghelix* as a valid genus.

Zyghelix forsteriana (Reeve)

Helix forsteriana Reeve, 1852: pl. 182, sp. 439 - North Australia

Thersites (Hadra) forsteriana forsteriana (Reeve) Marshall, 1927: 14, pl.ii, fig.6 - Lizard Island

Thersites (Hadra) forsteriana major Marshall, 1927: 15, pl.iii, fig.6 - North East Australia

Thersites (Hadra) forsteriana ada Marshall, 1927: 15, pl.iii, fig.4 - Lizard Island

Zyghelix forsteriana (Reeve) Iredale, 1937b: 23; Richardson, 1985: 322

Spurlingia forsteriana (Reeve) Smith, 1992: 161.

Diagnosis

Shell medium, keeled, sculpture of regular pustules, light brown bands above periphery, umbilicus open. Epiphallus with two caeca, but no sphincter in penis.

Description

Shell medium, 18.4 to 26.4mm (mean 22.73mm) in diameter, and 10.3 to 15.7mm (mean 13.13mm) in height, with 5.0 to 5.875 (mean 5.418) whorls, H/D ratio 0.517 to 0.640 (mean 0.591). Apical sculpture worn smooth in all specimens examined, postapical sculpture of small regular pustules coalescing to form thick wrinkles, overlain with growth ridges. Shell keeled just above periphery, body whorl descending rapidly behind lip. Lip is expanded and moderately flared, reflected over umbilicus, which is wide and open. Shell pale horn with light brown banding above periphery. Lip clear showing shell banding. Based on 39 measured adults.

Foot colour grey.

Free oviduct short, less than 25% length of vagina, which is equal in length to penis. Free oviduct diverges from vagina at right angle and reflexes at right angle before entering uterus. Spermathecal shaft long, swollen at junction with vagina. Penial retractor muscle inserts on proximal epiphallus. Epiphallus long and folded within penis sheath. Epiphallus has two caeca, one proximally at junction with vas deferens, the second at junction with penis (Fig. 6.51). Penis sculpture proximally of high irregular papillae loosely arranged in longitudinal rows gradually becoming regular longitudinal ridges towards genital atrium (Fig. 6.52). Penis sheath thin near insertion of penial retractor, becoming thicker as it approaches atrium.

Discussion

Iredale (1937b) synonymised *Helix hetaera* Pfeiffer, 1860, collected by Macgillivray on Rocky Island, with *Zyghelix forsteriana*. I have been unable to locate the type material and Smith (1992) records it as presumed lost. I cannot confirm Iredale's synonymy, but the occurrence of *H. hetaera* on Rocky Island, between the Howick group, near Cape Melville, and Two Isles, near Cape Flattery is within the range of the species.

Range and habitat

This species is found from north of Cairns to the base of Cape York Peninsula (Fig. 6.47), including islands. It inhabits rainforest.

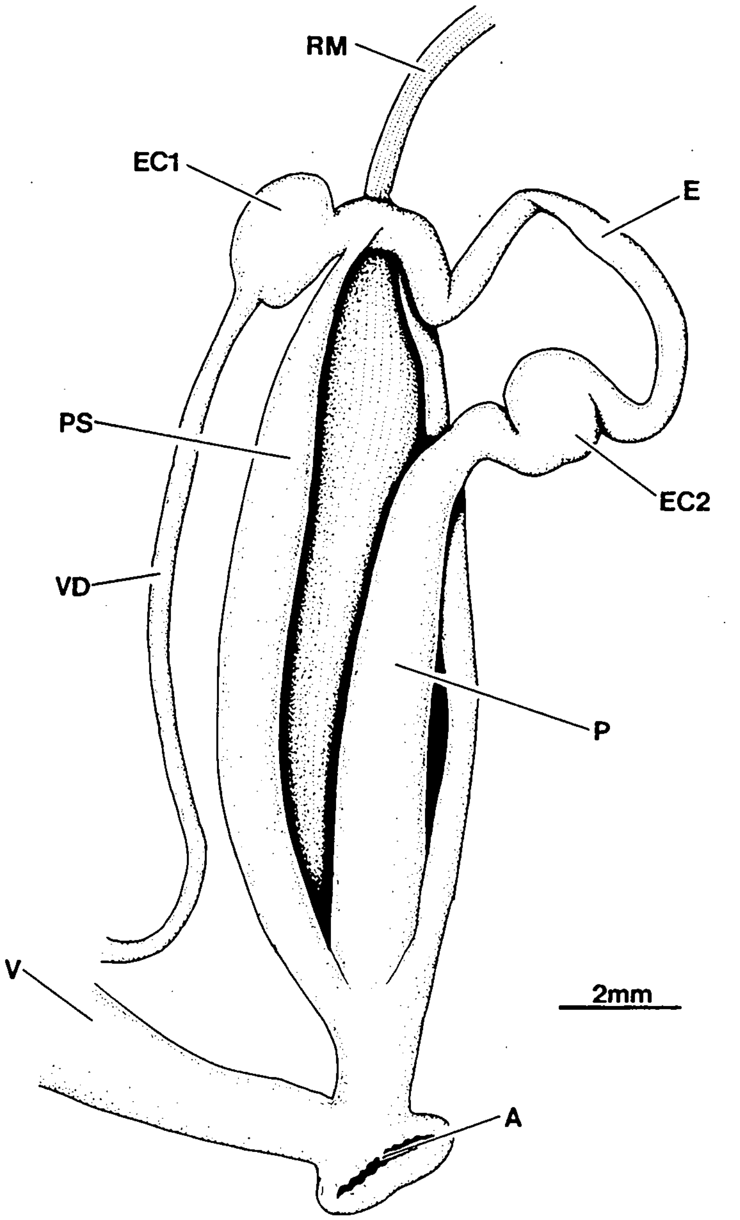


Fig. 6.51: Terminal male genitalia of *Zyghelix forsteriana* (Reeve) (Starcke) (A = atrium, E = epiphallus, EC1, EC2 = epiphallic caeca, P = penis, PS = penial sheath, RM = penial retractor muscle, V = vagina, VD = vas deferens).

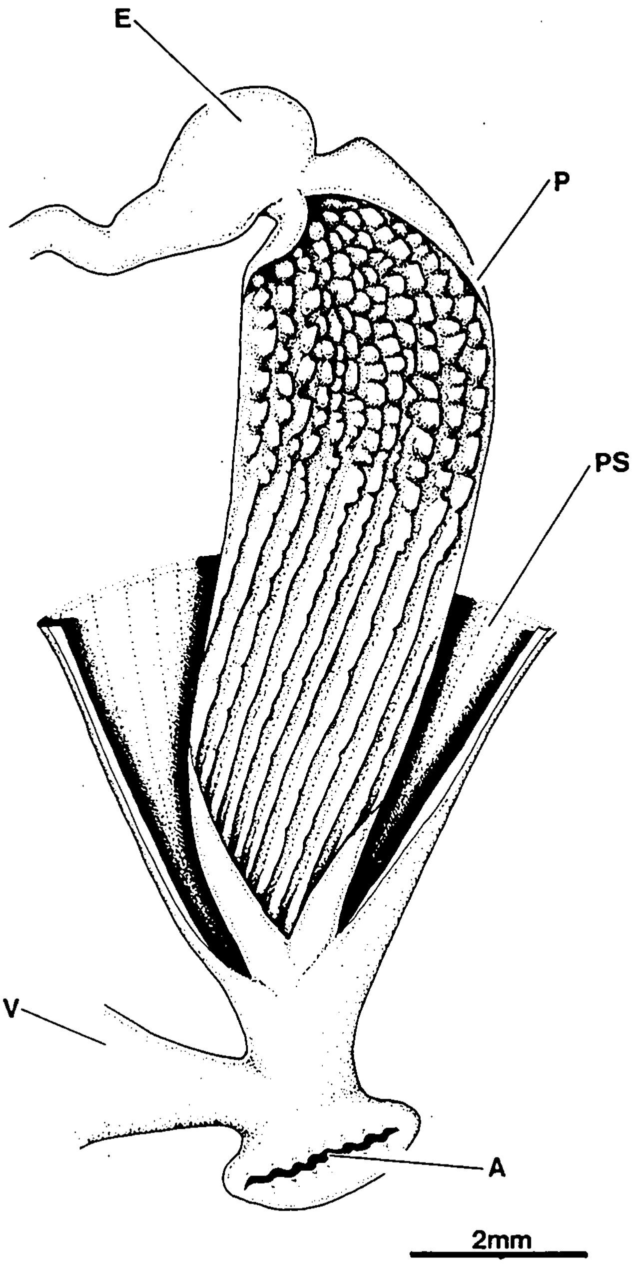


Fig. 6.52: Lining of penis of *Zyghelix forsteriana* (Reeve) (Starcke) (A = atrium, E = epiphallus, P = penis, PS = penial sheath, V = vagina).

***Meridolum* Iredale**

Meridolum Iredale, 1933: 47 - *nom. nud.*

Meridolum Iredale, 1944: 39; Richardson, 1985: 56; Smith, 1992: 133. Type species, *Helix jervisensis* Quoy and Gaimard, 1832, by original designation.

Diagnosis

No attempt is made to diagnose this genus as it is currently the subject of study by other authors (J. Stanisic., pers. comm.)

Discussion

Iredale (1933) named the genus *Meridolum* to cover an unlisted series of shells previously placed in *Badistes* Gould, 1862. Although *Helix jervisensis* Quoy and Gaimard 1832 was selected as the type species, Iredale (1933) failed to diagnose the genus. *Meridolum* did not become a valid name until 1942, when Iredale provided an adequate diagnosis (Iredale, 1942).

Iredale (1938) listed eleven species of *Meridolum*, covering a geographical range from southern Queensland to the New South Wales - Victorian border. Smith (1992) revised Iredale's (1938) classification. Eight species were maintained, while three described after Iredale's revision (McLauchlan, 1954) were added. *Meridolum expeditionis* (Cox, 1868) was assigned to *Galadistes*, and *M. ascensum* Iredale, 1938, and *M. morosa* (Morelet, 1853) were synonymised with *M. gilberti* (Pfeiffer, 1846). *Helix (Hadra) bennetti* Brazier, 1872 was considered to belong to *Meridolum.*

Solem (1992) dissected and figured a specimen of *Badistes gulosum* from Minimurra Falls, SW of Sydney. The gross morphology of the male terminal genitalia in that species differs from that of *Meridolum expeditionis* which was examined in this study. The two species are unequivocally from different genera. Which one (if either) represents *Meridolum* is unknown, as neither Solem (1992) nor I dissected the type species of *Meridolum*, *M. jervisensis*. No attempt is made to diagnose *Meridolum*, as this would pre-empt conclusions made by authors working with this genus.

Species of indeterminate status

Helix sardalabiata Cox, 1871 - Mt Dryander, Port Denison, Queensland.

The type of this species is an albino shell. There is some doubt about the type locality (J. Stanisic, pers. comm.). Iredale (1937b) placed it in *Pallidelix*, with the following species as a junior synonym. There is insufficient evidence to support this placement (see discussion of *Bentosites rawnesleyi*).

Helix (Hadra) stephensoniana Brazier, 1872b - Port Denison, Queensland.

The type of this species is an albino shell, which could belong to either *Bentosites* or *Temporena* (see discussion of *Bentosites rawnesleyi*).

Helix arthuriana Cox, 1873b: 564, pl. xlviii, fig. 1a - L. Island, Torres Strait.

Iredale (1937b) placed this species in *Varohadra* and corrected the type locality to L. Island, Broad Sound. The five probable syntypes reasonably large (29.2 - 32.1mm diameter, 22.5 - 23.3mm height), chocolate brown shells each with a pale subsutural band. They most closely resemble *Varohadra oconnellensis*, and *arthuriana* was synonymised with *V. oconnellensis* by Smith (1992), but the locality is well outside the confirmed range for that species.

Helix (Hadra) mourilyani Brazier, 1875a: 31, pl. iv, fig. 1 - Bowen, Port Denison, Queensland.

The type of this species is presumed lost and the type locality is in doubt. Iredale (1937b) placed this species in *Gnarosophia*, while Smith (1992) treated it as a species of *Sphaerospira*.

Helix (Hadra) johnstonei Brazier, 1875a: 32, pl. iv, fig. 2 - Bowen, Queensland.

The type of this species is presumed lost and the type locality is in doubt. It was placed in *Varohadra* by Iredale (1937b), but Smith (1992) synonymised it with *Sphaerospira coxi*.

Helix (Hadra) hilli Brazier, 1875a: 32 - Mt Elliott, Townsville, Queensland.

The type of this species is presumed lost and the type locality is in doubt. Iredale (1937b) regarded it as a species of *Varohadra*; Smith (1992) included it in the synonymy of *Sphaerospira sardalabiata* (see above).

Helix (Hydra) hanni Brazier, 1876b: 97 - Bowen, Port Denison, Queensland.

The type of this species is presumed lost and the type locality is in doubt. It was considered to be a species of *Varohadra* by Iredale (1937b) and synonymous with *Sphaerospira mourilyani* (see above) by Smith (1992).

Helix (Hydra) tomsoni Brazier, 1876b: 97 - Mt Elliott, Townsville, Queensland.

The type of this species is presumed lost and the type locality is in doubt. Iredale's plate (1937b: pl. iii, fig. 13) suggests that if the locality is correct, this species might be synonymous with *Bentosites rawnesleyi*, which supports Smith's (1992) decision in part to synonymise this species with *Sphaerospira sardalabiata* (see above).

Thersites concors Fulton, 1904: 8, pl. i, fig. 3 - Gayndah, Queensland.

Fulton (1904) noted the resemblance of this species to *Sphaerospira blomfieldi*. The differences were in the elevation of the spire, the occlusion of the umbilicus, and the expansion of the lip. The type locality, Gayndah, is within the range of *S. blomfieldi*. The dimensions given by Fulton are small (diameter = 35mm, height = 28mm) but are close to the minimum sizes recorded for confirmed *S. blomfieldi* (diameter = 31.7mm, height = 29.3mm). There is a major discrepancy in the H/D ratio. The range for confirmed *S. blomfieldi* is 0.918 to 1.087 (mean 0.991), while Fulton's specimen has an H/D ratio of 0.8. Iredale (1937b) treated *concors* as a species of *Varohadra* and Smith (1992) synonymised it with *Sphaerospira sardalabiata* (see above).

Gnarosophia mitifica Iredale, 1933 (= *Helix incei* var. multifasciata Cox, 1864) - "Cape York".

The type of this species is labelled "Wide Bay", although Iredale (1937b) was confused about the locality. It resembles a large *Temporena whartoni* (Cox) (Smith, 1992), but the lack of unequivocal locality data and wet material makes the placement of this species into a genus impossible at this time.

Varohadra halleyae Iredale, 1937b: 36, pl. iii, fig. 21 - Lindeman Island, Queensland.

The holotype of this species is indeed "a very curious form" (Iredale, 1937b: 36). It is uniformly brown with a closed umbilicus, and lacks any obvious wrinkle sculpture. Smith (1992) regarded it as probably a synonym of *Sphaerospira coxi* (Temporena coxi in this study), but until topotypic wet material becomes available for study, the identity of this species will remain uncertain.

Hadra wilsoni Solem, 1979: 139, figs. 33d-f - valley slope on north side of Youwanjela Creek near main campsite, Upper Prince Regent River, Prince Regent River Reserve, Western Australia.

Solem (1979) described this species from damaged shells collected in the Kimberley. He believed that it might belong to an undescribed genus, but unable to examine the anatomy, he assigned the shell to an existing genus rather than erect a new one. The holotype resembles *Hadra barneyi*, but the characteristic wrinkle pattern of *Hadra* is missing.

Chapter 7

PHYLOGENETIC AND BIOGEOGRAPHIC ANALYSES OF THE HADROID CAMAENIDS

Phylogeny of the hadroid camaenids

The data are summarised in Table 7.1.

Outgroup

Bradybaena (Bradybaenidae).

Shell

0 Post-apical shell sculpture: wrinkled (0); smooth (1); pustulose (2). The most common sculpture is the wrinkle pattern which occurs in almost all hadroid camaenids. In many it is obvious, visible to the unaided eye (e.g. *Hadra*), while in others the sculpture is subtle (e.g. *Varohadra*). *Bradybaena* and Gen. nov. A are essentially free of sculpture other than growth lines. Only *Zyghelix* has a pustulose sculpture.

1 Shell size: medium (0); large (1). Almost all hadroid camaenids have large shells.

2 Umbilicus: open (0); closed (1). A closed umbilicus is entirely occluded by the peristome, while an open umbilicus may vary from narrowly to widely open. In a small number of genera, the umbilicus may be open or closed. In these cases, the umbilicus is listed as closed.

3 Keel: absent (0); present (1). Keeling is widespread in the hadroid camaenids, and only species in which no adult specimen has been observed to bear a keel are marked as keel absent.

Male reproductive tract

4 Penis sheath: absent (0); well-formed sheath (1). Most genera of hadroid camaenids possess a penis sheath, although it is greatly reduced in *Thersites*. It is absent in *Meridolum*.

5 Penial papilla: absent (0); rounded (1); tubular (2). In most eastern hadroid camaenids, the penial papilla is either absent or is rounded with a subterminal ejaculatory opening. Only *Meridolum* has a tubular penial papilla.

6 Epiphallic papilla: absent (0); present (1). The epiphallic papilla which projects into the epiphallus at the junction with the vas deferens occurs in *Thersites*, *Sphaerospira* and *Varohadra*.

7 Epiphallic caecum: absent (0); present (1). An epiphallic caecum is a swelling or pocket in the caecum distal to the junction of the epiphallus and vas deferens (see below). This state is present in *Hadra* and *Zyghelix*.

8 Epiphallic flagellum: absent (0); present (1). The epiphallic flagellum occurs at the junction of the epiphallus and vas deferens. It appears to be a diverticulum of the epiphallus and lies along the vas deferens, often bound to it by connective tissue. It occurs in most genera of hadroid camaenids, but is absent in *Varohadra*, gen. nov. A and *Meridolum*.

Female reproductive tract

9 Length of vagina: shorter than penis (0); equal to penis (1). Vaginal length is measured as a function of the penis.

10 Length of free oviduct: long (0); short (1). The free oviduct varies in length, but is short (25% or less of vaginal length) in all hadroid camaenids except *Thersites*.

Foot colour

11 Foot colour: grey (0); orange (1).

character	*Bradybaena*	*Meridolum*	*Varohadra*	*Gen. nov.* B	*Zyghelix*	*Hadra*	*Thersites*	*Sphaerospira*	*Bentosites*	*Gen. nov.* A	*Temporena*	character state	consistency index
SHELL													
0. Post-apical shell sculpture	1	0	0	0	2	0	0	0	0	1	0	A	0.66
1. Shell size	0	0	1	1	0	1	1	1	1	1	1	SR	0.50
2. Umbilicus	0	0	0	0	0	1	1	1	1	0	0	SR	0.50
3. Keel	0	0	1	1	1	1	1	1	0	0	0	SR	0.50
MALE REPRODUCTIVE TRACT													
4. Penis sheath	0	0	1	1	1	1	1	1	1	1	1	S	1.00
5. Penial papilla	0	2	0	0	0	0	1	1	1	1	1	S	0.66
6. Epiphallic papilla	0	0	1	0	0	0	1	1	0	0	0	H	0.50
7. Epiphallic caecum	0	0	0	0	1	1	0	0	0	0	0	H	0.50
8. Epiphallic flagellum	0	0	0	0	1	1	1	1	1	1	1	S	0.50
FEMALE REPRODUCTIVE TRACT													
9. Length of vagina	1	0	0	0	0	1	1	0	1	1	1	S	0.33
10. Length of free oviduct	1	0	0	0	0	0	0	1	0	0	0	H	0.50
FOOT													
11. Foot colour	0	0	0	0	0	0	0	0	1	1	1	S	1.00

Table 7.1: Hadroid camaenid data matrix. 0, plesiomorphy; 1,2, apomorphy; ?, not known; A, autapomorphy; S, synapomorphy; H, homoplasy; R, reversal

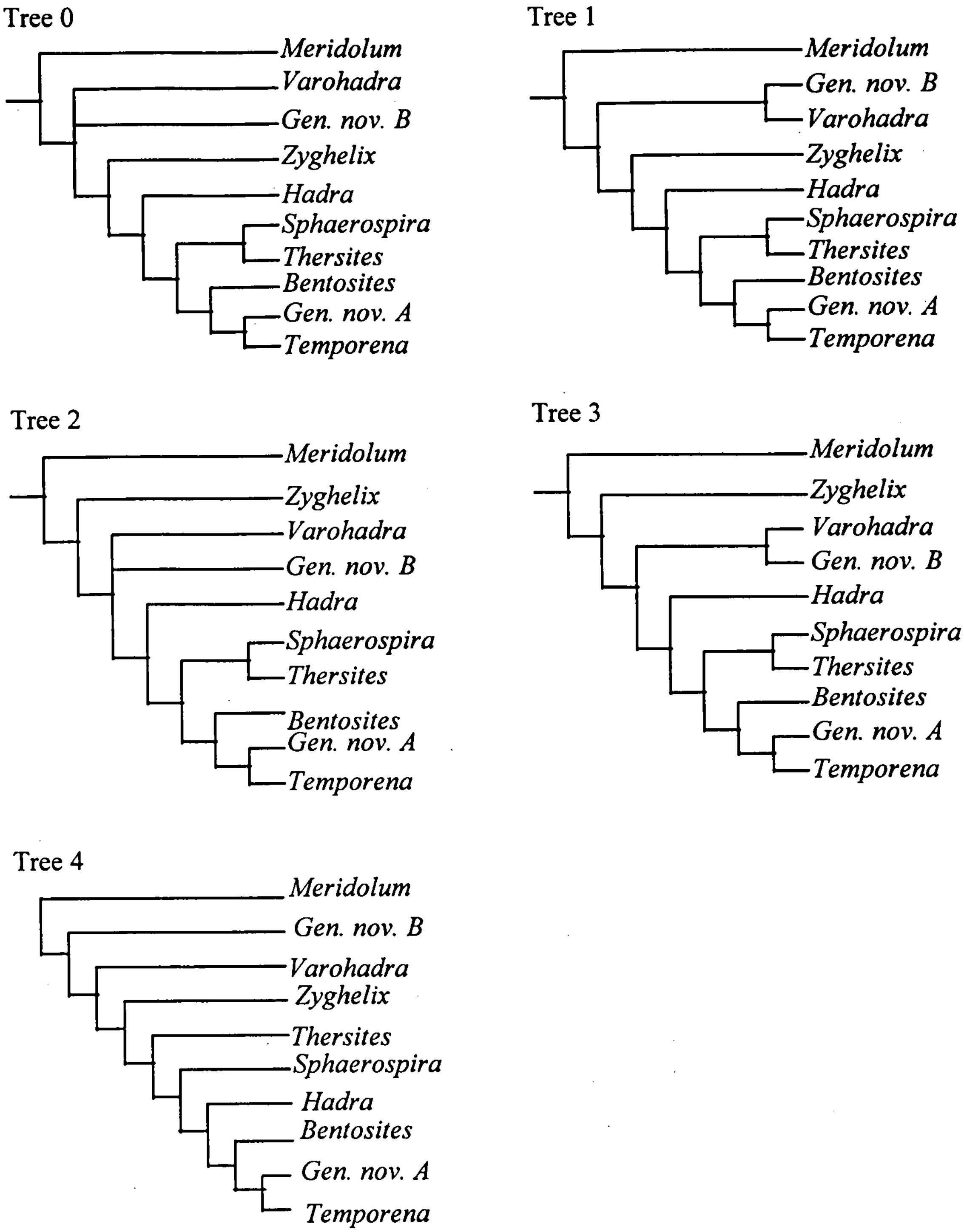


Fig. 7.1: Five most parsimonious cladograms of hadroid camaenids (length = 23; c.i. = 0.60; r.i. = 0.67).

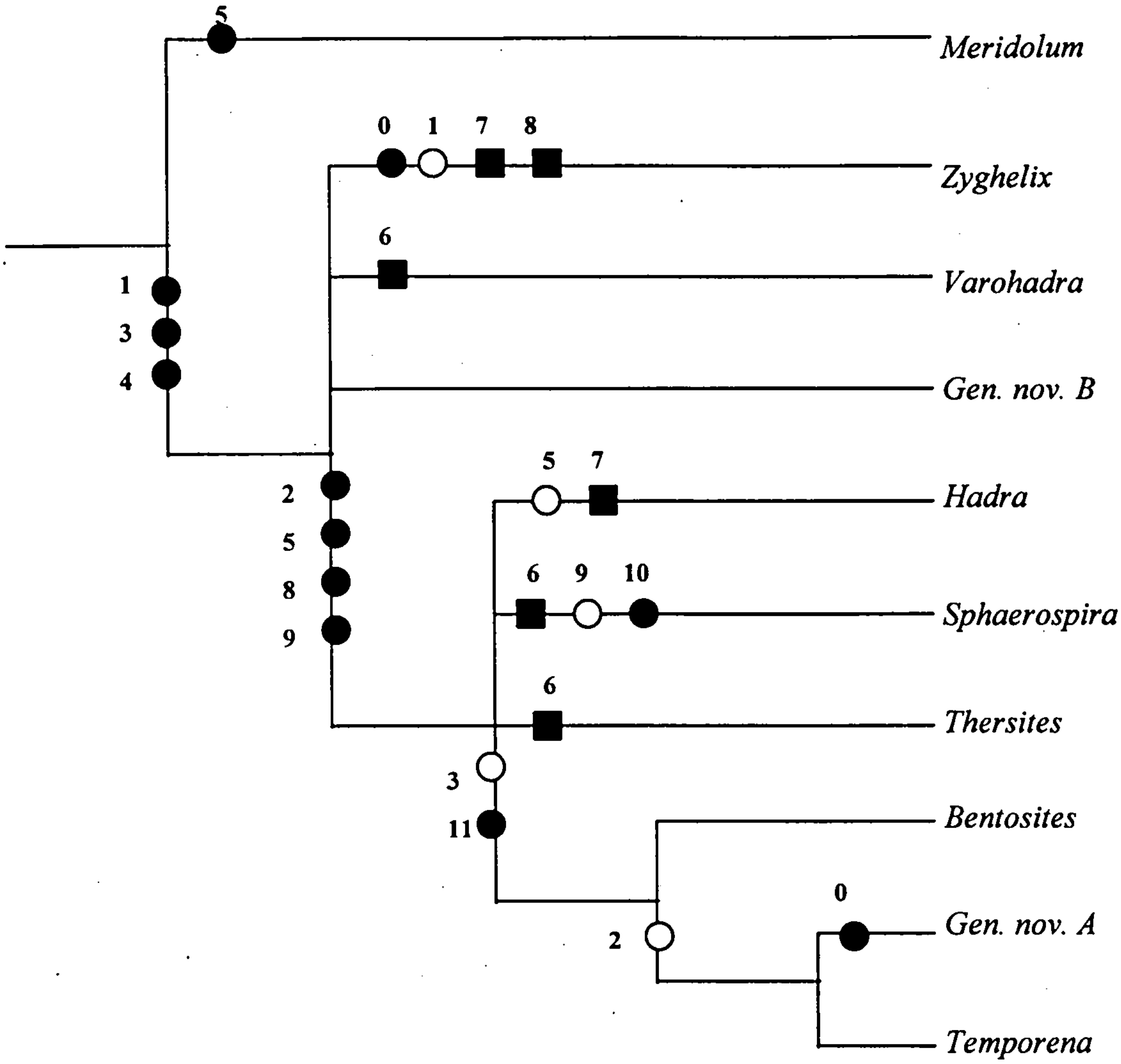


Fig. 7.2: Nelson tree generated from five most parsimonious cladograms of hadroid camaenids (length = 23; c.i. = 0.60; r.i. = 0.67): ● = apomorphy; ○ = reversal; ■ = homoplasy; □ = reversal.

Results

Five most parsimonious cladograms were found on the first pass through the data. These cladograms were 23 steps in length with consistency indices of 0.60 and retention indices of 0.67 (Fig. 7.1). These trees differed in the placement of *Gen. nov.* B, *Varohadra* and *Zyghelix*, which arose from near-basal nodes, and of *Hadra, Sphaerospira* and *Thersites*. The relationships of *Meridolum*, *Bentosites*, Gen. nov. A and *Temporena* did not vary between trees. Only one tree was not fully-resolved.

All nodes were supported by one or more transformations (Fig. 7.2). Sister genera *Sphaerospira* and *Thersites* were supported by the presence of an epiphallic papilla (character 6), a homoplasious character shared with *Varohadra*. *Gen. nov.* A and *Temporena* were defined as sister taxa by a reversal in the condition of the shell umbilicus character 2).

Homoplasies were restricted to characters of the epiphallus: the presence of the epiphallic papilla (character 6; trees 0-3) and the epiphallic caecum (character 7; trees 2-4) were homoplasious, each with a consistency index of 0.50.

The node which gave rise to *Hadra* and the higher camaenids was supported by a forward change in character 2 (umbilicus) in all trees, and in changes in characters 8 (epiphallic flagellum) and 9 (length of vagina). The penial papilla (character 5) appeared at the node from which the *Sphaerospira/Thersites* pair and the orange-bodied snails arose.

The development of an orange pigment was a synapomorphy for the *Bentosites/Gen. nov.* A/*Temporena* trio, supported by a reversal in the shell keeling.

Although the relatively high levels of homoplasy identified in this analysis (c.i. = 0.60) may reflect accurately the plasticity of form suggested by Woodruff and Solem (1990), it may be necessary to test this phylogenetic hypothesis with analyses based on molecular characters.

Biogeography of the hadroid camaenids

Data

The polytomies of *Varohadra*, *Gen. nov.* B, and *Zyghelix*, and of *Sphaerospira*, *Hadra* and *Thersites* (Fig. 7.2) were treated as fully resolved in construction of the data matrix. All combinations of these taxa were tested, but they generated no incongruences in the resolved area cladograms. The data matrix presented below represents a fully resolved phylogenetic cladogram.

Areas

Areas are shown in Fig. 7.3.

A	Cape York Peninsula
B	Starcke area
C	Far North Queensland (Cooktown - Innisfail)
D	Hinchinbrook (Tully - Ingham)
E	North-east Queensland (Seaview Range to Giru)
F	Bowen area
G	Mid-east Queensland
H	South-east Queensland
I	Caves - Bulburin
J	Queensland border
K	central to southern New South Wales (not shown in Fig. 7.2)

Data matrix

The data matrix is shown in Table 7.2.

Results

A Nelson tree (length = 22, c.i. = 0.86, r.i. = 0.89) was constructed from six cladograms found on the first pass through the data (Fig. 7.4).

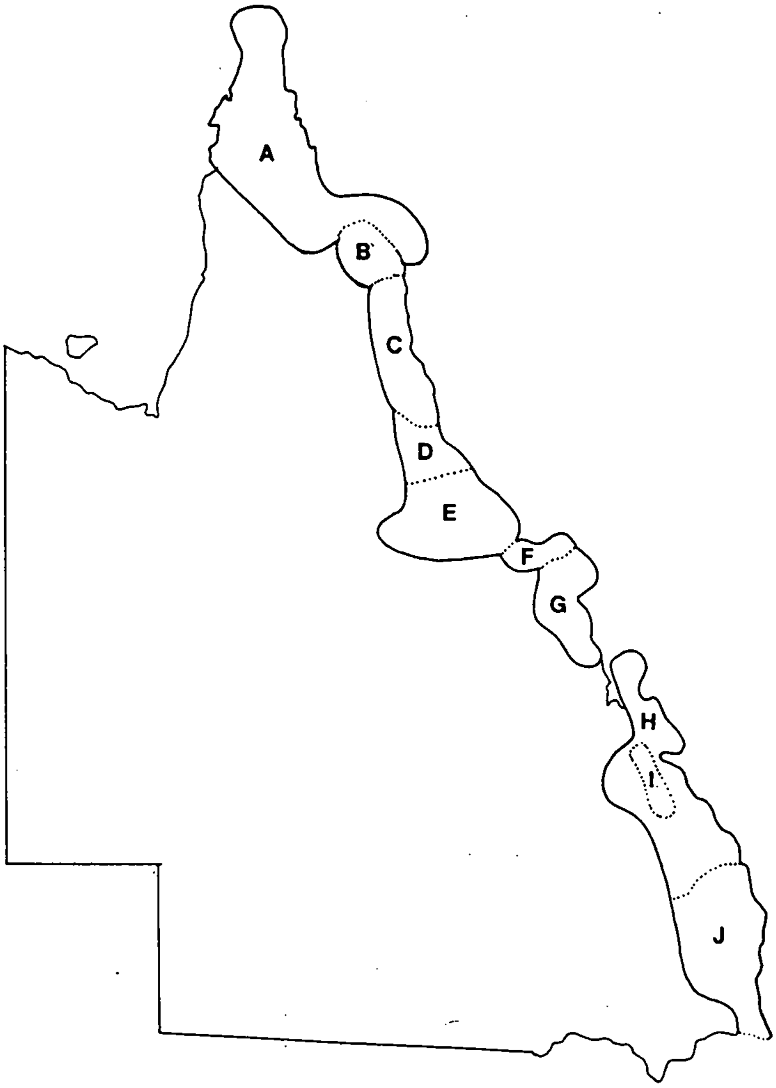


Fig. 7.3: Areas used in biogeographic analysis of hadroid camaenids

	Area										
	A	B	C	D	E	F	G	H	I	J	K
Component											
1	0	0	0	0	0	0	0	0	0	0	1
2	0	0	0	0	0	0	1	0	0	0	0
3	0	0	0	0	0	0	0	0	1	0	0
4	0	1	1	0	0	0	0	0	0	0	0
5	1	1	1	1	0	0	0	0	0	0	0
6	0	0	0	0	0	0	1	1	1	1	0
7	0	0	0	0	0	0	0	0	0	1	0
8	0	0	0	0	0	0	1	1	1	1	0
9	0	0	0	1	1	1	0	0	0	0	0
10	0	0	0	0	0	0	0	1	1	1	0
11	0	0	0	0	0	1	1	0	0	0	0
12	0	0	0	0	0	1	1	1	1	1	0
13	0	0	0	1	1	1	1	1	1	1	0
14	0	0	0	1	1	1	1	1	1	1	0
15	1	1	1	1	1	1	1	1	1	1	0
16	1	1	1	1	1	1	1	1	1	1	0
17	1	1	1	1	1	1	1	1	1	1	1
18	1	1	1	1	1	1	1	1	1	1	1
19	1	1	1	1	1	1	1	1	1	1	1

Table 7.2: Data matrix derived from unresolved area cladogram of hadroid camaenids.

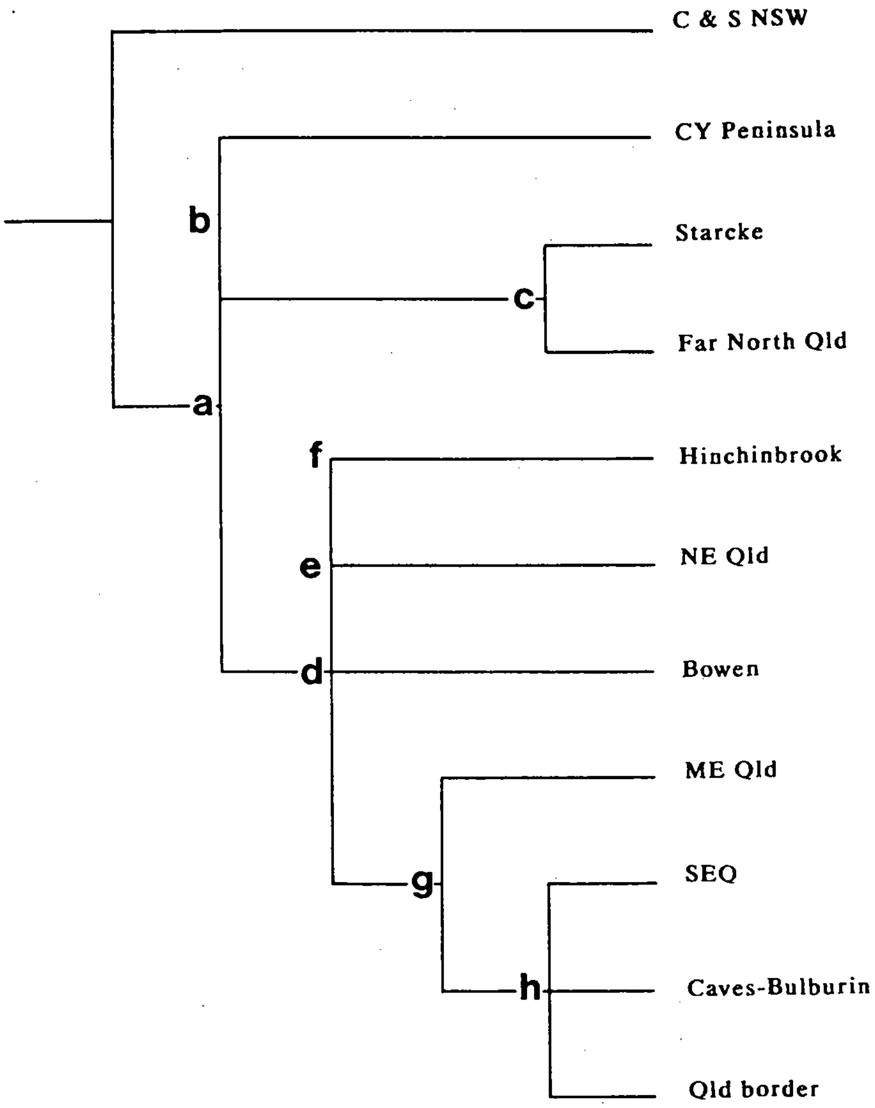


Fig. 7.4: Nelson cladogram generated from six resolved area cladograms of hadroid camaenids analysed under Assumption 0 (length = 22, c.i. = 0.86, r.i. = 0.89) (a - h indicate events discussed in this study).

Phylogeny of *Hadra*

Data

The data are summarised in Table 7.3.

Outgroup

Zyghelix forsteriana.

Shells

0 Shell sculpture: coarse (0); fine (1). Species of *Hadra* have a similar basic pattern, but the coarseness of the sculpture varies between species.

1 Shell shape: round (0); flattened (1).

2 Lip colour: dark (0); white (1).

3 Occlusion of umbilicus: always open (0); variable (1).

4 Shell colour: banded (0); striped (1).

Male reproductive tract

5 Separation of epiphallic caeca: caeca not connected (0); caeca adjacent (1). The presence of two epiphallic caeca is a diagnostic character of *Hadra.*

6 Insertion of retractor muscle: proximal (0); distal (1). The retractor muscle inserts on the bend of the epiphallus, which is reflexed either approximately halfway along its length (proximally) or close to its junction with the penis (distally).

7 Number of penial sphincters: one (0); one plus flap of tissue (1); two (2).

8 Penial sculpture: longitudinal ridges (0); pustules (1).

Female reproductive tract

9 Shape of free oviduct: straight (0); angled (1).

10 Junction of free oviduct/vagina: swollen (0); not swollen (1).

11 Junction of spermatheca/vagina: swollen (0); not swollen (1).

	character	*Z.* forsteriana	*H. bipartita*	*H. dunkiensis*	*H. barneyi*	*H. bellendenkerenis*	*H. rudis*	character state	consistency index
	SHELL								
0.	Shell sculpture	1	0	0	1	0	1	H	0.50
1.	Shell shape	1	0	0	0	0	1	A	0.50
2.	Lip colour	1	0	0	1	1	0	S	1.00
3.	Occlusion of umbilicus	0	1	0	1	1	0	?	0.33
4.	Shell colour	1	0	0	0	1	0	S	1.00
	MALE REPRODUCTIVE TRACT								
5.	Separation of epiphallic caeca	0	0	0	1	0	0	S	1.00
6.	Insertion of retractor muscle	0	1	0	1	0	1	R	0.50
7.	Number of penial sphincters	0	2	0	1	0	0	S	1.00
8.	Penial sculpture	1	0	0	0	1	0	S	1.00
	FEMALE REPRODUCTIVE TRACT								
9.	Shape of free oviduct	1	1	1	0	0	1	?	0.50
10.	Junction of vagina and free oviduct	0	0	0	1	1	1	S	0.50
11.	Junction of vagina and spermatheca	1	0	0	1	1	0	S	1.00

Table 7.3: *Hadra* data matrix. 0, plesiomorphy; 1,2, apomorphy; A, autapomorphy; S, synapomorphy; H, homoplasy; R, reversal.

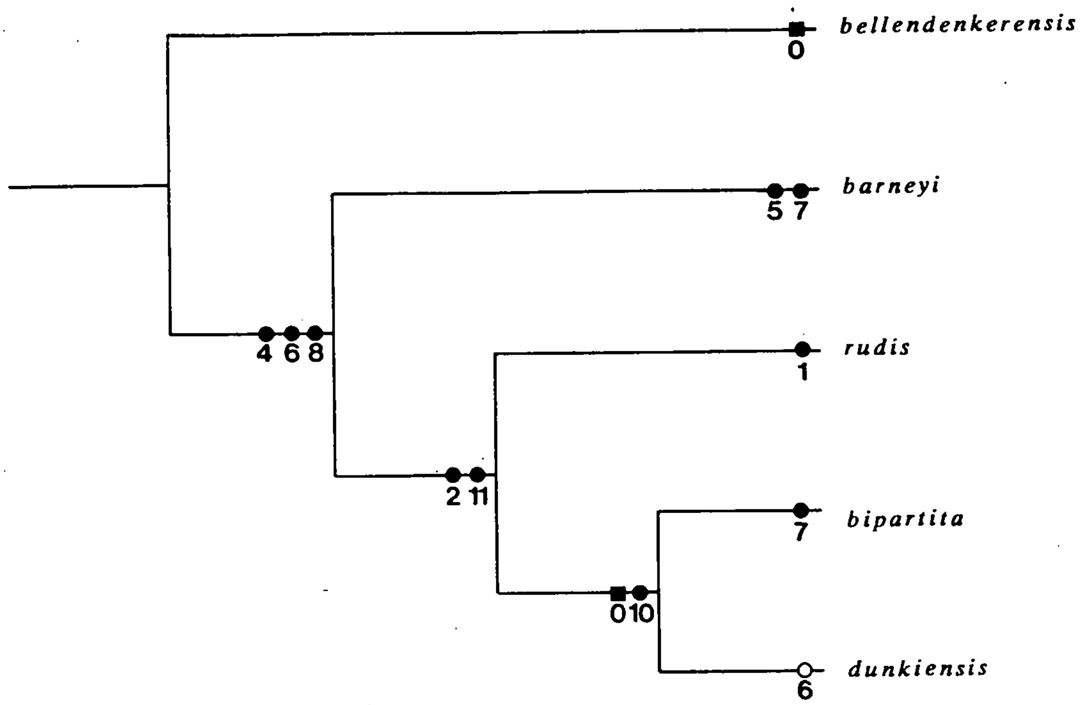


Fig. 7.5: Single most parsimonious tree of *Hadra* (length = 20; c.i. = 0.65; r.i. = 0.56): ● = apomorphy; ○ = reversal; ■ = homoplasy; □ = reversal.

Results

This analysis may not include all species of *Hadra*, as a single species similar to *H. dunkiensis* did not occur in rainforest and was not examined during the course of this study. It is assumed on the basis of conchological characters that this species from in north-eastern Queensland represents a clade with *H. dunkiensis*. As this species occurs only at the type locality and is not sympatric with any other species of *Hadra*, its omission can have no effect on the biogeographic analysis of rainforest patches.

A single most parsimonious cladogram was found on the first pass through the data, which was both unweighted and unordered. It was 20 steps in length with a consistency index of 0.65 and a retention index of 0.56 (Fig. 7.5).

All nodes were supported by one to three synapomorphies. The earliest characters to undergo transformation were shell colour (character 4), insertion of the penial retractor muscle (character 6), and sculpture of the penis (character 8). Character 6 underwent a single reversal in *H. dunkiensis* (c.i. = 0.50).

The *Hadra rudis/bipartita/dunkiensis* clade was supported by synapomorphies of characters 2 (lip colour) and 11 (junction of vagina and spermatheca). *Hadra bipartita* and *H. dunkiensis* were placed as sister species by character 0 (shell sculpture), which was homoplasious (c.i. = 0.50), and character 10 (junction of vagina and free oviduct), which was synapomorphic. Characters 3 (occlusion of umbilicus) and 9 (shape of free oviduct) were equivocal at two or more nodes, so it was impossible to determine character state polarity, and thus the pattern of change between taxa.

Biogeography of *Hadra*

Data

Not all areas inhabited by species of *Hadra* are included in this biogeographic analysis. Taxa allied to *H. dunkiensis* occur in non-rainforest areas and have been omitted from this study. The presence or absence of those areas has no effect on the relationships between rainforest areas.

Areas

Areas are shown in Fig. 7.6.

A	Torres Strait and north-east Cape York Peninsula
B	South-west Cape York Peninsula
C	Lizard and other continental islands
D	Cooktown - Port Douglas
E	Cairns - Innisfail
F	Bellenden Ker Range
G	South Johnstone - Tully
H	Kirrama
I	Hinchinbrook

Area cladogram and data matrix

Two species of *Hadra* (*H. barneyi* and *H. rudis*) were each restricted to single areas, while *Hadra bipartita* occurred in 7 of 9 areas. The unresolved area cladogram and data matrix are shown in Fig. 7.7 and Table 7.4.

Results

A single most parsimonious cladogram (length = 10, c.i. = 0.90, r.i. = 0.85) was generated from the resolved area cladogram of *Hadra* on the first pass through the data (Fig. 7.8).

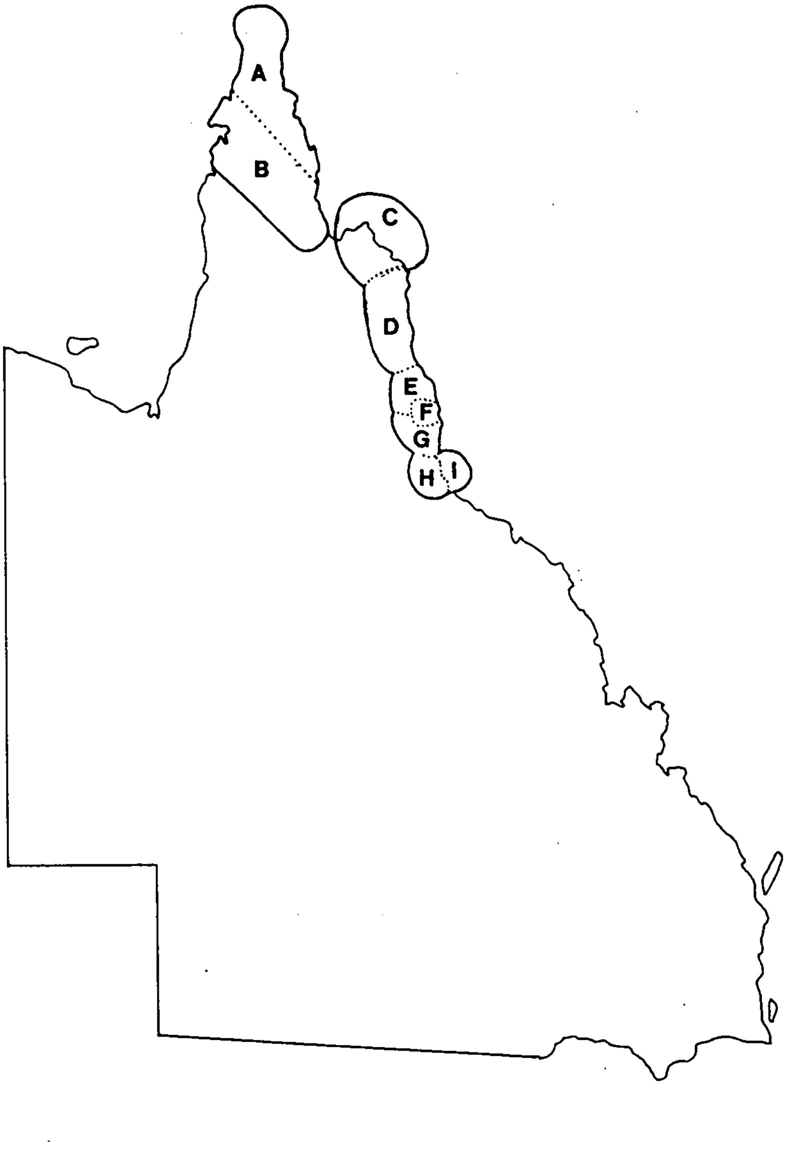


Fig. 7.6: Areas used in biogeographic analysis of *Hadra*

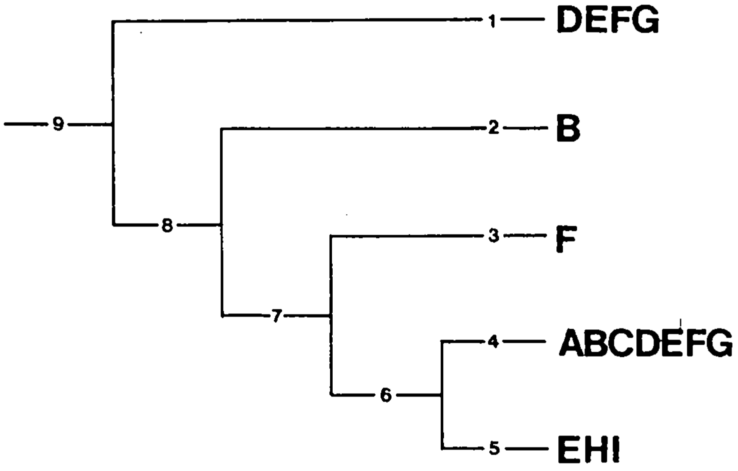


Fig. 7.7: Unresolved area cladogram of *Hadra* (components 1 - 9 are coded after Zandee & Roos, 1987).

	Area								
	A	B	C	D	E	F	G	H	I
Component									
1	0	0	0	1	1	1	1	1	0
2	0	1	0	0	0	0	0	0	0
3	0	0	0	0	0	1	0	0	0
4	1	1	1	1	1	1	1	0	0
5	0	0	0	0	0	0	0	1	1
6	1	1	1	1	1	1	1	1	1
7	1	1	1	1	1	1	1	1	1
8	1	1	1	1	1	1	1	1	1
9	1	1	1	1	1	1	1	1	1

Table 7.4: Data matrix derived from unresolved area cladogram of *Hadra*.

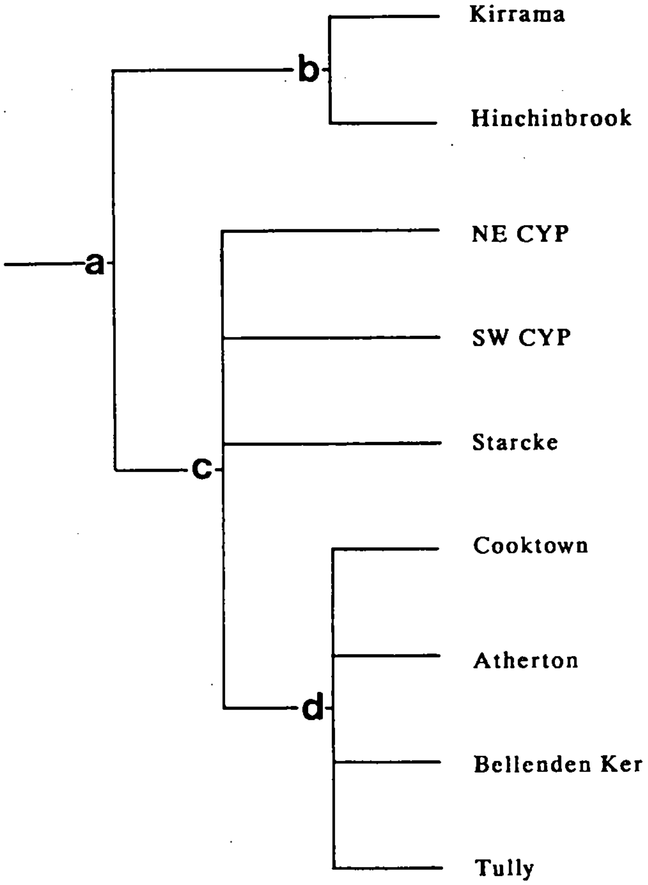


Fig. 7.8: Single most parsimonious cladogram generated from resolved area cladogram of *Hadra* analysed under Assumption 0 (length = 10, c.i. = 0.90, r.i. = 0.85) (a - d indicate events discussed in this study).

Phylogeny of *Sphaerospira*

Data

The data are summarised in Table 7.5.

Outgroup

Thersites richmondiana.

Shells

0 Shell shape: round (0); keeled (1). Keeling occurs when the periphery of the body whorl is angled, giving the shell a sub-triangular profile.

1 Occlusion of umbilicus: complete (0); open or partially open (1).

Male reproductive tract

2 Insertion of penial retractor muscle: distal (0); proximal (1).

3 Penial sculpture: papillae and longitudinal ridges (0); longitudinal ridges only (1); papillae only (2). The sculpture on the penis lining is used as a diagnostic character at species level. In many genera, interspecific variation in pattern is limited.

Female reproductive tract

4 Shape of free oviduct: angled (0); straight (1).

6 Junction of spermatheca and vagina: swollen (0); not swollen (1).

	character	*Thersites richmondiana*	*Sphaerospira fraseri*	*S. blomfieldi*	*S. informis*	*S. sp. nov.*	character state (tree 0)	consistency index (tree 0)	character state (tree 1)	consistency index (tree 1)
				SHELL						
0.	Shell shape	0	0	1	0	1	H	0.50	S	1.00
1.	Occlusion of umbilicus	0	0	1	0	0	S	1.00	A	0.50
				MALE REPRODUCTIVE TRACT						
2.	Insertion of penial retractor muscle	1	0	1	1	0	S	1.00	H	0.50
3.	Penial sculpture	0	0	1	0	0	A	1.00	A	1.00
				FEMALE REPRODUCTIVE TRACT						
4.	Shape of free oviduct	1	0	1	1	1	A	0.50	S	1.00
5.	Junction spermatheca and vagina	0	0	0	1	0	S	1.00	S	1.00

Table 7.5: *Sphaerospira* data matrix. 0, plesiomorphy; 1, 2, apomorphy; A, autapomorphy; S, synapomorphy; H, homoplasy.

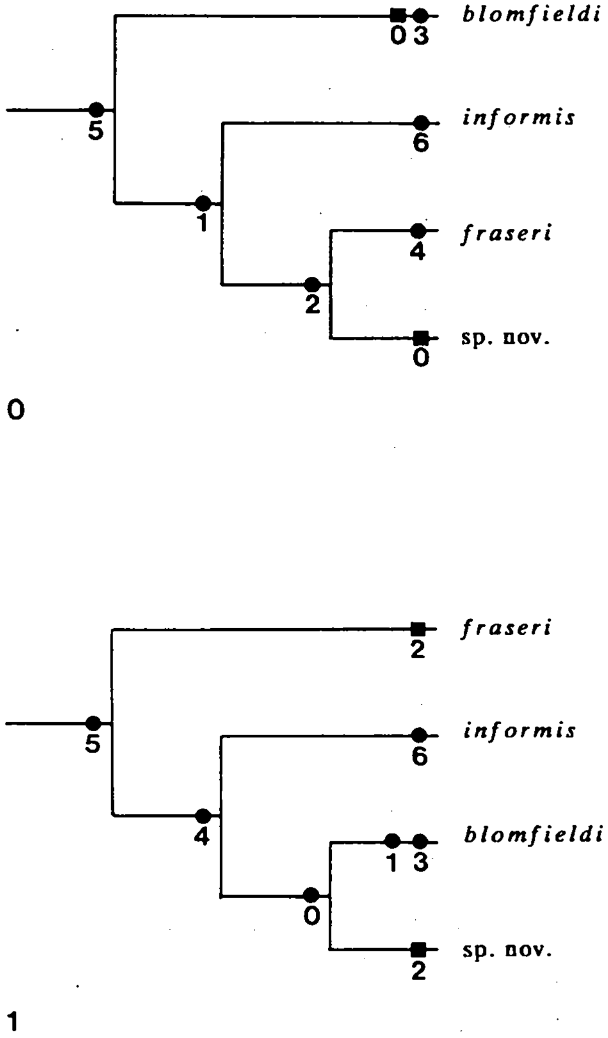


Fig. 7.9: Most parsimonious cladograms for *Sphaerospira* (length = 9, c.i. = 0.77, r.i. = 0.50): ● = apomorphy; ○ = reversal; ■ = homoplasy; □ = reversal.

Results

Two most parsimonious cladograms were found on the first pass through the data, each were nine steps in length with consistency indices of 0.77 and retention indices of 0.50 (Fig. 7.9).

Each node was supported by a single synapomorphy. Trees 0 and 1 differed in the placement of *Sphaerospira fraseri* and *S. blomfieldi*, and thus in the interpretation of synapomorphic and homoplasious character states.

Sphaerospira blomfieldi was identified as the most primitive species in Tree 0. The *S. informis*/*fraseri*/sp. nov. clade was supported by a forward change in the degree of umbilical occlusion (character 1). Sister species *S. fraseri* and *S.* sp. nov. were paired by the apomorphic state of the insertion of penial retractor muscle (character 2). Character 0 (shell shape) was homoplasious in both *S. blomfieldi* and *S.* sp. nov.

Sphaerospira fraseri was placed at the base of Tree 1. The apomorphic state of character 4 (shape of free oviduct) supported the *S. informis*/*blomfieldi*/sp. nov. clade. *Sphaerospira blomfieldi* and *S.* sp. nov. were identified as sister species by a change in shell shape (character 0). Character 2 (insertion of penial retractor muscle) was homoplasious in *S. fraseri* and *S.* sp. nov.

Biogeography of *Sphaerospira*

Data

Areas

Areas are shown in Fig. 7.10

A	Mideastern Queensland: between Bowen and Koumala.
B	Bulburin: west of Gladstone
C	Rockhampton/Mary River: from Shoalwater Bay to the Sunshine Coast.
D	Southeastern Queensland: including northern New South Wales.

Area cladogram and data matrix

Three of four species of *Sphaerospira* were each restricted to a single area, while *S. blomfieldi* occurred in two areas. Data matrices for phylogenetic trees 0 and 1 were constructed from unresolved area cladograms (Fig. 7.11, Table 7.6).

Results

Phylogenetic hypotheses generated alternative area cladograms, which differed in the placement of two areas: Rockhampton/Gladstone (area C) and southeastern Queensland (area D) (Fig. 7.12.). Tree 0 was rejected because it hypothesised the devlopment of a barrier between two non-adjacent areas.

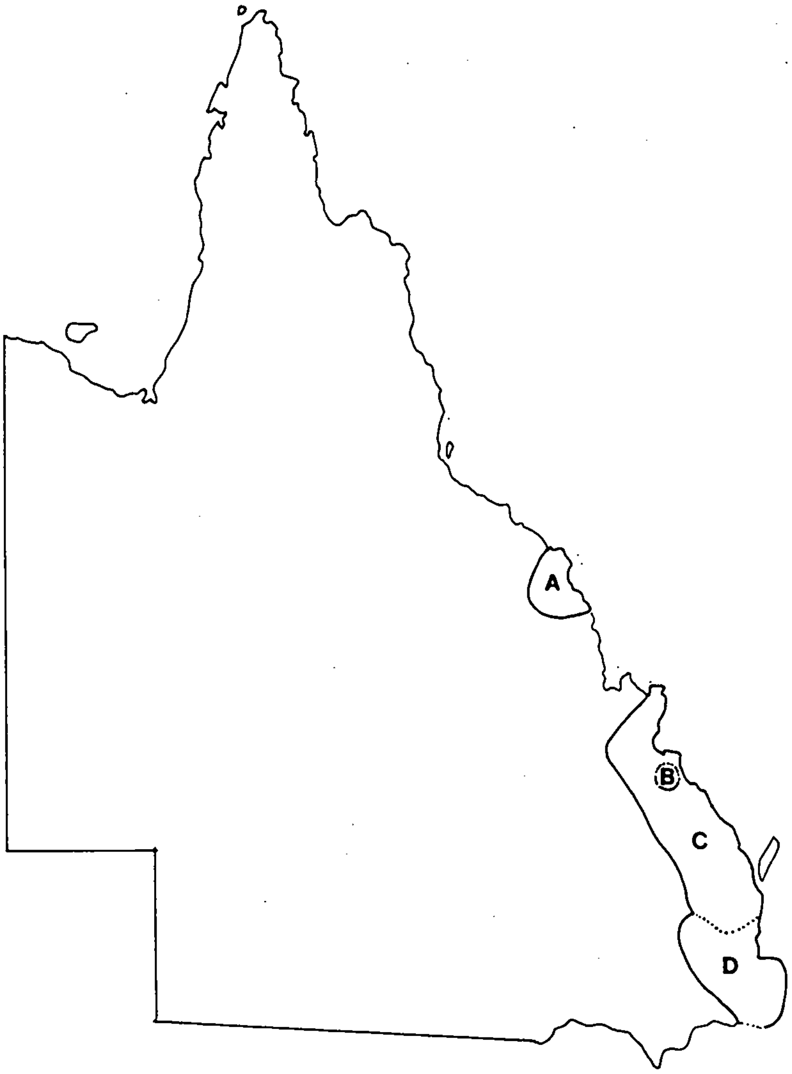


Fig. 7.10: Areas used in biogeographic analysis of *Sphaerospira*.

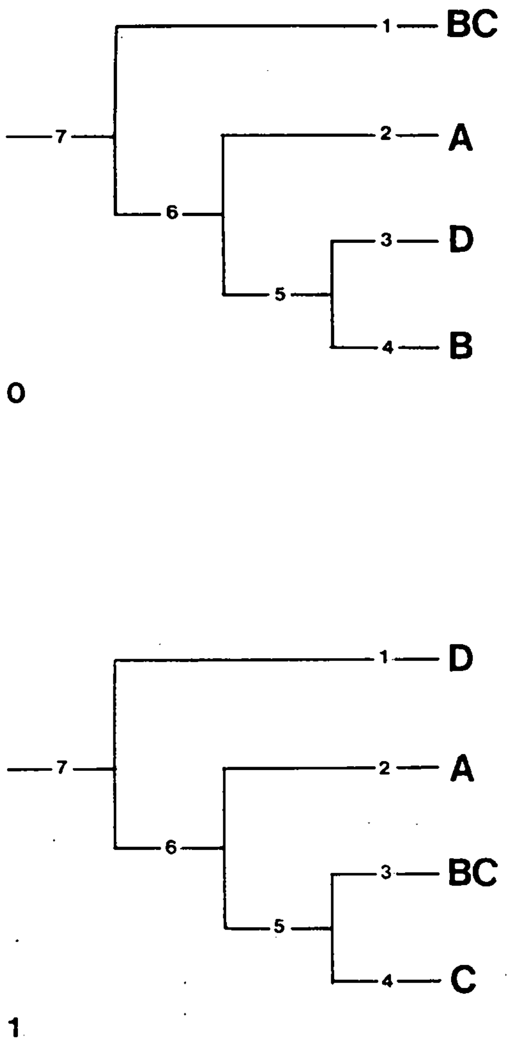


Fig. 7.11: Unresolved area cladograms of *Sphaerospira*.

	AREA			
	A	B	C	D
Component				
Tree 0				
1	0	1	1	0
2	1	0	0	0
3	0	0	0	1
4	0	1	0	0
5	0	1	0	1
6	1	1	0	1
7	1	1	1	1
Tree 1				
1	0	0	0	1
2	1	0	0	0
3	0	1	1	0
4	0	1	0	0
5	0	1	1	0
6	1	1	1	0
7	1	1	1	1

Table 7.6: Data matrix derived from unresolved area cladograms of *Sphaerospira*.

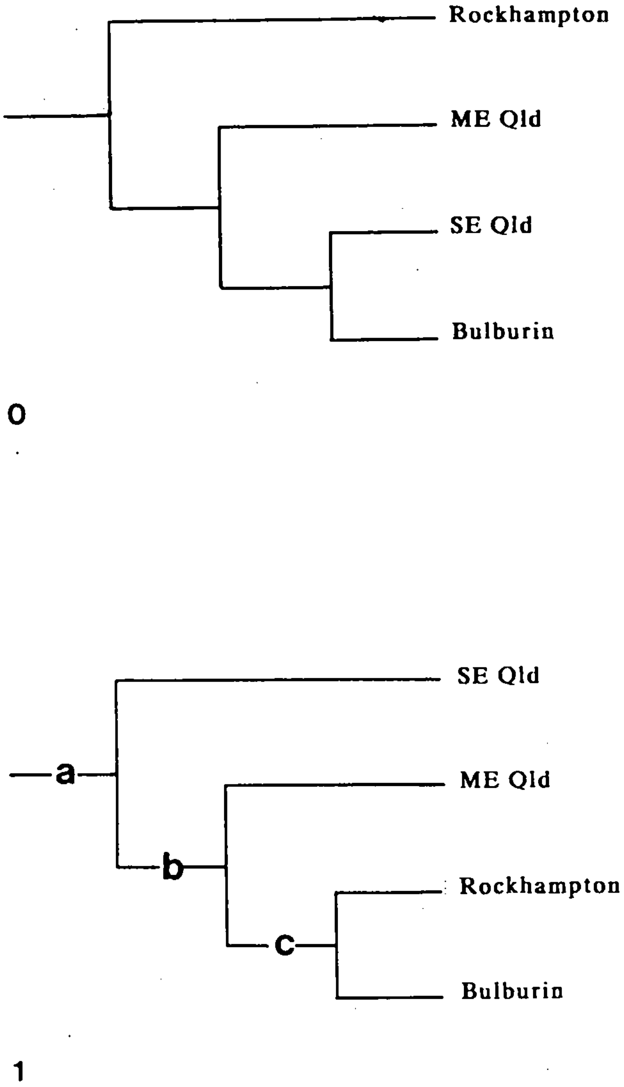


Fig. 7.12: Most parsimonious cladograms generated from unresolved area cladograms of *Sphaerospira* analysed under Assumption 0: **0**, length = 8, c.i. = 0.87, r.i. = 0.66; **1**, length = 7, c.i. = 1.00, r.i. = 1.00 (a - c indicate events discussed in this study).

Phylogeny of *Bentosites*

Data

The data are summarised in Table 7.7.

Outgroup

Sphaerospira fraseri.

Shell

0 Occlusion of umbilicus: open or partial (0); closed (1).

1 Lip colour: dark (0); translucent (1). Markings on the outer surface of the shell are visible from the interior in species where the shell lip is classed as translucent.

Male reproductive tract

2 Insertion of penial retractor muscle: distal (0); proximal (1).

3 Penial pouch: present (0); absent (1). A penial pouch is a an outpocketting or fold in the wall of the penis close to its junction with the epiphallus.

4 Penial papilla: rounded (0); pointed (1). *Bentosites* is characterised by the presence of a penial papilla with basal ejaculatory duct.

5 Folding of penis: unfolded (0); folded (1). The penis is fully enclosed by the penis sheath, and is classed as folded only if it is folded within that sheath.

Female reproductive tract

6 Shape of free oviduct: straight (0); angled (1).

7 Junction of free oviduct and vagina: free oviduct diverges evenly from vagina (0); free oviduct diverges at angle (1).

8 Shape of spermathecal shaft: straight (0); angled (1).

9 Junction of spermatheca and vagina: spermatheca diverges evenly from vagina (0); spermatheca diverges at angle (1).

	character	*Sphaerospira fraseri*	*Bentosites macleayi*	*B. yulei*	*B. rawnesleyi*	*B. mulgravensis*	*B. zebina*	*B. mazee*	*B. gavisa*	*B. sp. nov.*	character state	consistency index
	SHELL											
0.	Occlusion of umbilicus	0	1	0	0	0	0	1	0	1	H	0.33
1.	Lip colour	1	1	1	1	1	0	1	0	1	H	0.50
	MALE REPRODUCTIVE TRACT											
2.	Insertion of penial retractor muscle	0	0	0	1	1	1	0	0	1	H	0.33
3.	Penial pouch	1	1	0	1	1	0	1	0	0	S	0.50
4.	Penial papilla	0	0	1	0	0	1	0	0	1	SR	0.50
5.	Folding of penis	0	0	0	1	1	0	1	1	0	S	1.00
	FEMALE REPRODUCTIVE TRACT											
6.	Shape of free oviduct	0	0	1	0	1	0	1	1	1	SR	0.50
7.	Junction of free oviduct and vagina	0	0	1	1	1	0	1	1	1	S	1.00
8.	Shape of spermathecal shaft	0	0	1	1	1	0	1	0	0	H	0.50
9.	Junction of spermatheca and vagina	0	0	0	1	0	0	1	1	1	H	0.33

Table 7.7: *Bentosites* data matrix. 0, plesiomorphy; 1, apomorphy; A, autapomorphy; S, synapomorphy; H, homoplasy; R, reversal; ?, equivocal

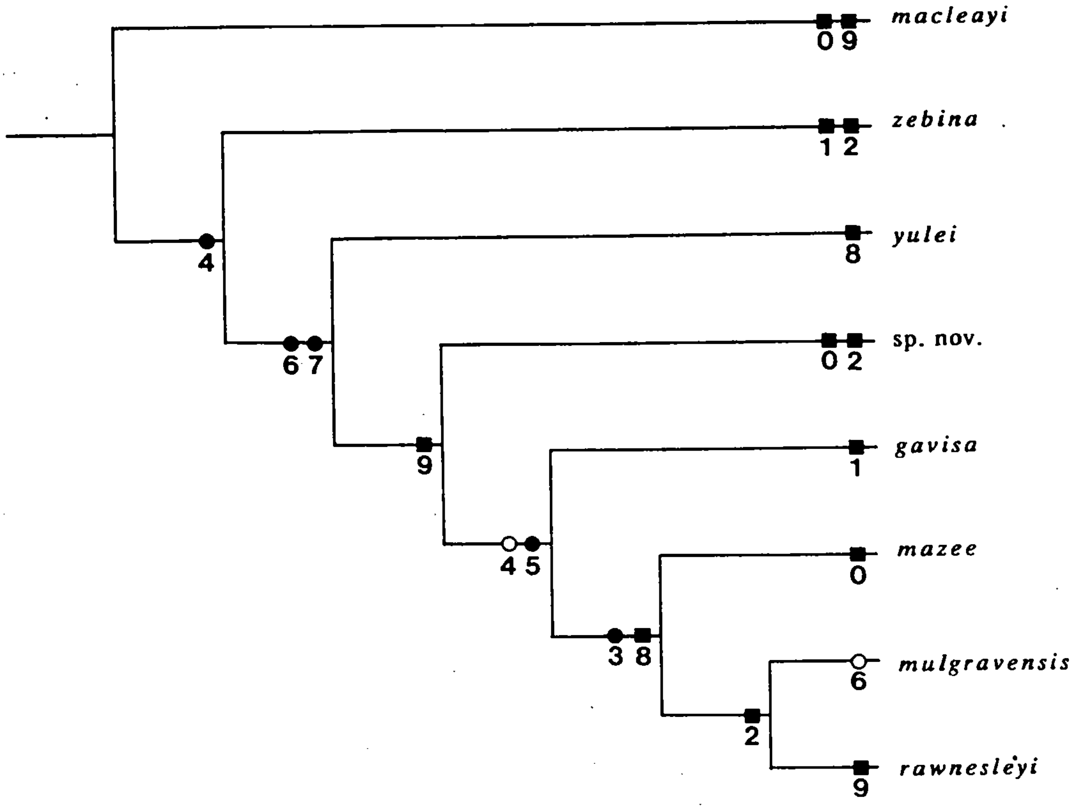


Fig. 7.13: Single most parsimonious cladogram for *Bentosites* (length = 21, c.i. = 0.47, r.i. = 0.56): ● = apomorphy; ○ = reversal; ■ = homoplasy; □ = reversal.

Results

A single most parsimonious cladogram was found on the first pass through the data. It was 21 steps in length with a consistency index of 0.47 and a retention index of 0.56 (Fig. 7.13).

All nodes were supported by at least one character state transformation. *Bentosites macleayi* was the most primitive species, possessing plesiomorphic states for 9 of 11 characters. The two remaining characters (0: occlusion of umbilicus; 9: junction of spermatheca and vagina) were homoplasious.

The node giving rise to all other species was supported by the transformation of the penial papilla from rounded to pointed (character 4). Three of the five subsequent nodes were supported by 1-2 synapomorphies, three by single homoplasies, and one by a reversal. Characters 3 (penial pouch), 5 (folding of penis), 6 (shape of free oviduct) and 7 (junction of free oviduct and vagina) were all synapomorphic.

Five characters (0, 1, 2, 8, 9) were homoplasious (c.i. = 0.33-0.55). Homoplasy was so widespread that convergences occurred in 50% of the nodes, and in all terminal taxa except *B. mulgravensis*. Homoplasious characters which each supported a node were 2 (insertion of penial retractor muscle), 8 (shape of spermathecal shaft) and 9 (junction of spermatheca and vagina).

A reversal in character 4 (penial papilla) occurred in conjunction with a forward change in character 5 (folding of penis).

No characters were equivocal.

Biogeography of *Bentosites*

Data

Areas

Areas are shown in Fig. 7.14. The distribution of *Bentosites* was interrupted in the Bowen region, with groups of species to the north and south of this region.

A	Hinchinbrook: Innisfail south to the Cardwell and Kirrama Ranges.
B	Seaview: Seaview, Paluma and Coane Ranges.
C	Townsville.
D	Palm Group: continental islands to the north of Townsville (including Orpheus Island).
E	Western Ranges: drier hills and mountain ranges W and SW of Townsville.
F	Burdekin: mouth of Burdekin River, also including magnetic Island, Many Peaks Range near Townsville, and Cape Cleveland.
G	Whitsunday Islands.
H	Proserpine: area around town to Conway Range.
I	Seaforth: south of Proserpine to the Sarina-Koumala region.
J	Connors Range: inland of Sarina.

Area cladogram and data matrix

The unresolved area cladogram and the data matrix derived from it are shown in Fig. 7.15 and Table 7.8 respectively. Species occupied 1-3 areas each, with half restricted to single areas.

Results

A single fully-resolved cladogram was found on the first pass through the data. It was 17 steps in length, with a consistency index of 0.88, and a retention index of 0.90 (Fig. 7.16).

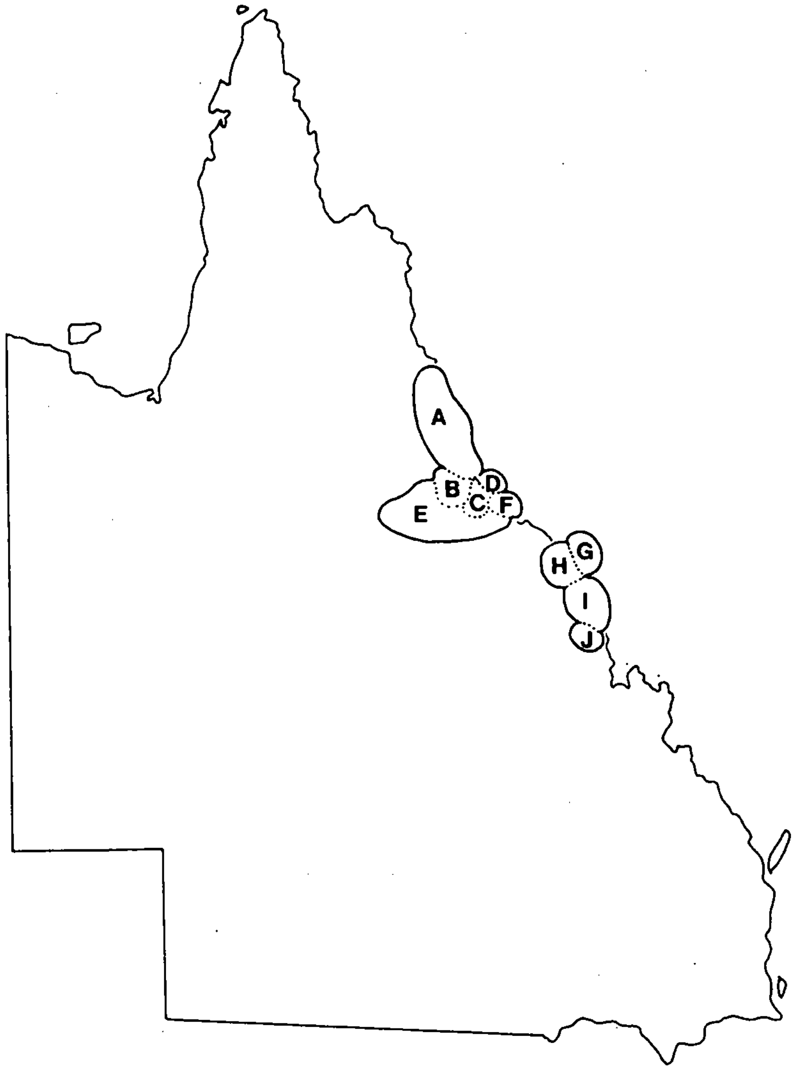


Fig. 7.14: Areas used in biogeographic analysis of *Bentosites*.

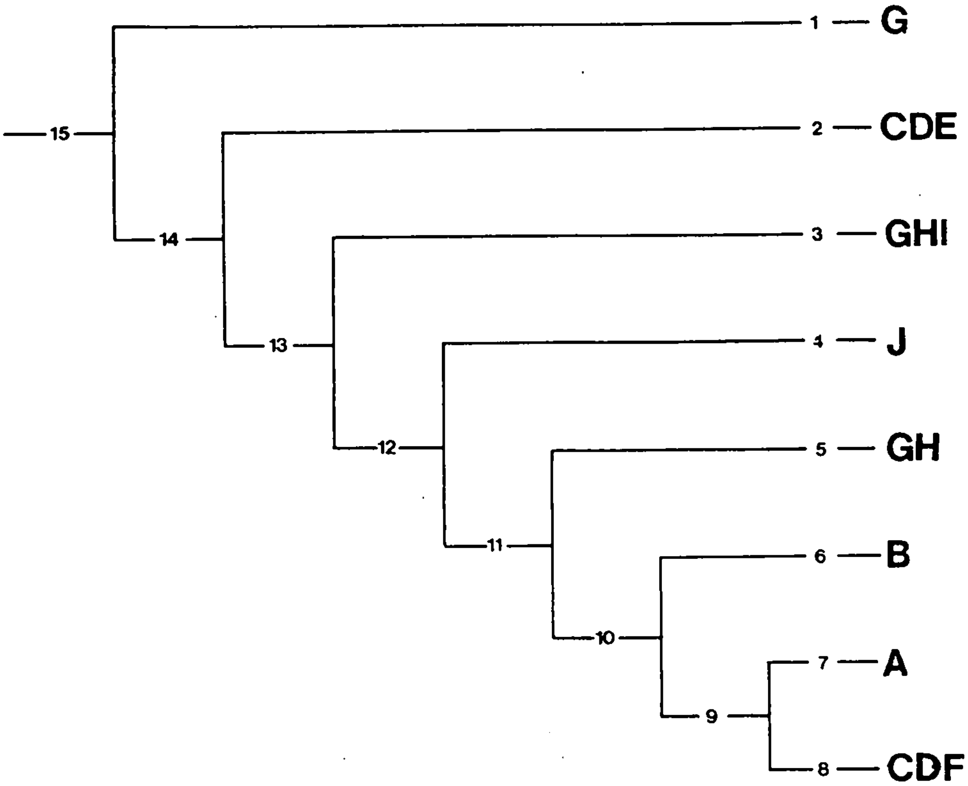


Fig. 7.15: Unresolved area cladogram of *Bentosites* (components 1-15 are coded after Zandee & Roos, 1987).

	Area									
	A	B	C	D	E	F	G	H	I	J
Component										
1	0	0	0	0	0	0	1	0	0	0
2	0	0	1	1	1	0	0	0	0	0
3	0	0	0	0	0	0	1	1	1	0
4	0	0	0	0	0	0	0	0	0	1
5	0	0	0	0	0	0	1	1	0	0
6	0	1	0	0	0	0	0	0	0	0
7	1	0	0	0	0	0	0	0	0	0
8	0	0	1	1	0	1	0	0	0	0
9	1	0	1	1	0	1	0	0	0	0
10	1	1	1	1	0	1	0	0	0	0
11	1	1	1	1	0	1	1	1	0	0
12	1	1	1	1	0	1	1	1	0	1
13	1	1	1	1	0	1	1	1	1	1
14	1	1	1	1	1	1	1	1	1	1
15	1	1	1	1	1	1	1	1	1	1

Table 7.8: Data matrix derived from unresolved area cladogram of *Bentosites*.

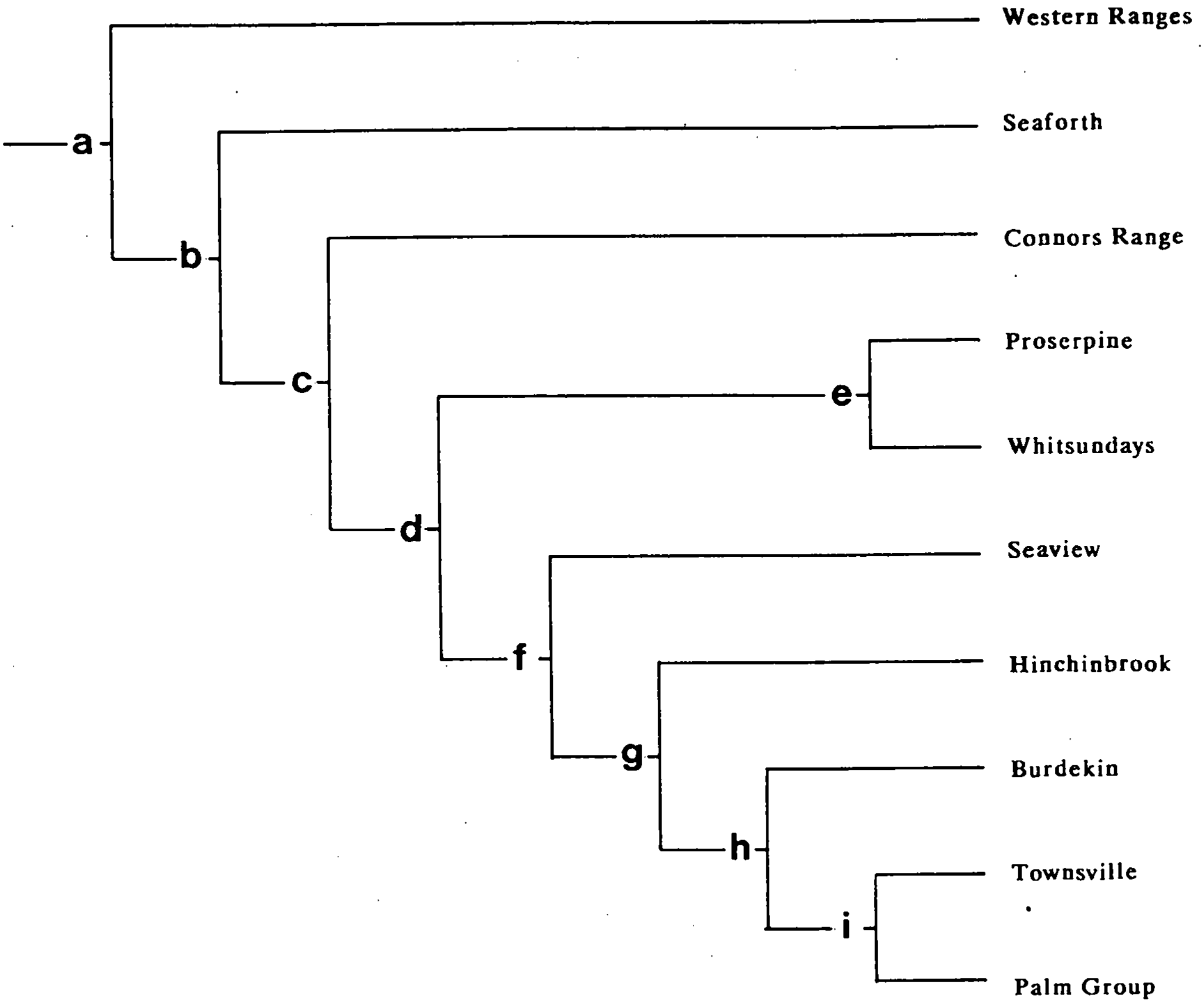


Fig. 7.16: Resolved area cladogram of *Bentosites* analysed under Assumption 0 (length = 17, c.i. = 0.88, r.i. = 0.90) (a-h indicates events discussed in this study) .

Phylogeny of *Temporena*

Data

Data are summarised in Table 7.9.

Outgroup

Gen. nov. A *incei*.

Shell

0 Shell structure: solid (0); thin (1).

1 Occlusion of umbilicus: partial (0); complete (1).

2 Lip colour: white (0); transparent (1).

Male reproductive tract

3 Insertion of penial retractor muscle: proximal (0); distal (1).

4 Penial sculpture: pustules (0); longitudinal ridges (1)

Female reproductive tract

5 Shape of free oviduct: angled (0); straight (1)

6 Junction of spermatheca and vagina: swollen (0); not swollen (1).

	character	*Gen. nov. A incei*	*Temporena whartoni*	*T. macneilli*	*T. coxi*	*T. etheridgei*	character state (tree 0)	consistency index (tree 0)	character state (tree 1)	consistency index (tree 1)
	SHELL									
0.	Shell structure	1	0	0	1	1	H	0.50	S	1.00
1.	Occlusion of umbilicus	0	0	1	1	1	S	1.00	?	0.50
2.	Lip colour	1	0	0	1	1	H	0.50	S	1.00
	MALE REPRODUCTIVE TRACT									
3.	Insertion of penial retractor muscle	0	0	0	1	1	?	0.50	S	1.00
4.	Penial sculpture	0	1	0	1	1	A	0.50	?	0.50
	FEMALE REPRODUCTIVE TRACT									
5.	Shape of free oviduct	1	1	0	1	0	S	1.00	H	0.50
6.	Junction of spermatheca and vagina	1	1	0	1	0	S	1.00	H	0.50

Table 7.9: *Temporena* data matrix. 0, plesiomorphy; 1, apomorphy; A, autapomorphy; S, synapomorphy; H, homoplasy; R, reversal; ?, equivocal

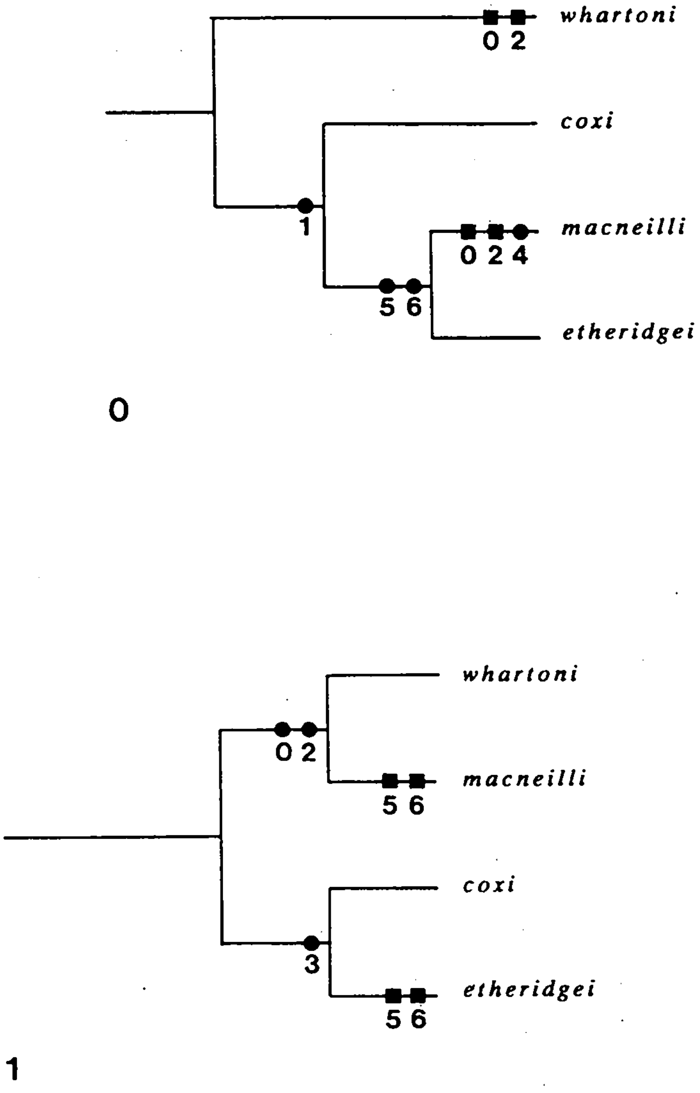


Fig. 7.17: Two most parsimonious cladograms for *Temporena* (length = 11, c.i. = 0.63, r.i. = 0.42): ● = apomorphy; ○ = reversal; ■ = homoplasy; □ = reversal.

Results

Two most parsimonious trees were found on the first pass through the data. They were 11 steps in length with consistency indices of 0.63 and retention indices of 0.42 (Fig. 7.17). The trees were markedly different and did include common components.

Nodes in both trees were supported by 1-2 synapomorphies. Homoplasious characters occurred in two terminal taxa in each tree.

Tree 0 was nested, with *T. whartoni* as the most primitive species. The *T. coxi/macneilli/etheridgei* clade was supported by characters 5 (shape of the free oviduct) and 6 (junction of spermatheca and vagina). Two shell characters were homoplasious (0, structure; 2, lip colour; c.i. = 0.50) in *T. whartoni* and *T. macneilli*. Character 3 (insertion of penial retractor muscle) was equivocal.

Taxa in Tree 1 were grouped into two pairs of sister species. *Temporena whartoni* and *T. macneilli* were supported by synapomorphies of characters 0 and 2, while *T. coxi* and *T. etheridgei* were supported by character 3. Characters 5 and 6 were homoplasious (c.i. = 0.50)., while characters 1 and 4 were equivocal.

Biogeography of *Temporena*

Data

Areas

Areas are shown in Fig. 7.18.

A	Inkerman
B	Bowen
C	Holbourne Island
D	Northern Whitsunday Group
E	Southern Whitsunday Group
F	Proserpine
G	Seaforth

Area cladograms and data matrix

Unresolved area cladograms and data matrices were produced from the two phylogenetic cladograms (Fig. 7.19, Table 7.10).

Results

Tree 0 generated four resolved area cladograms which were used to produce a partially-resolved Nelson tree (length = 8, c.i. = 0.87, r.i. = 0.88). Tree 1 generated a single partially-resolved tree, which was shorter (length = 7, c.i. = 1.00, r.i. = 1.00) (Fig. 7.20).

Gen. nov. A

No attempt was made to analyse Gen. nov. A, as the range of characters and states available was insufficient to distinguish between the three species.

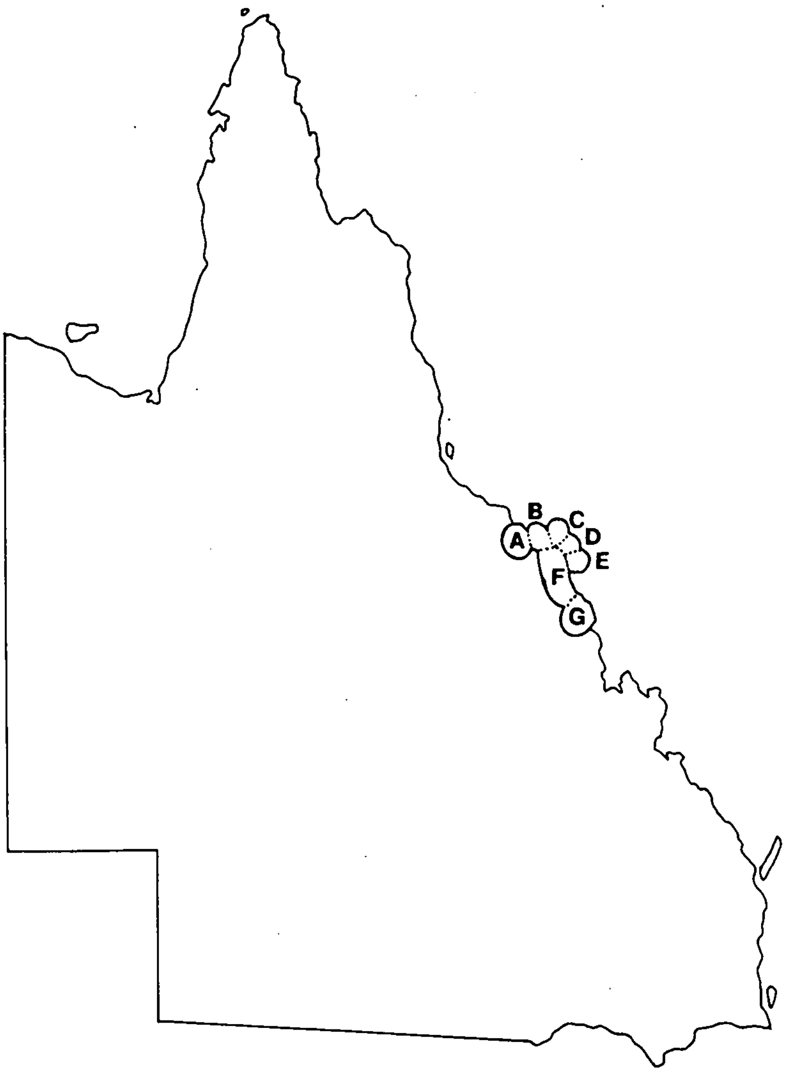


Fig. 7.18: Areas used in biogeographic analysis of *Temporena*.

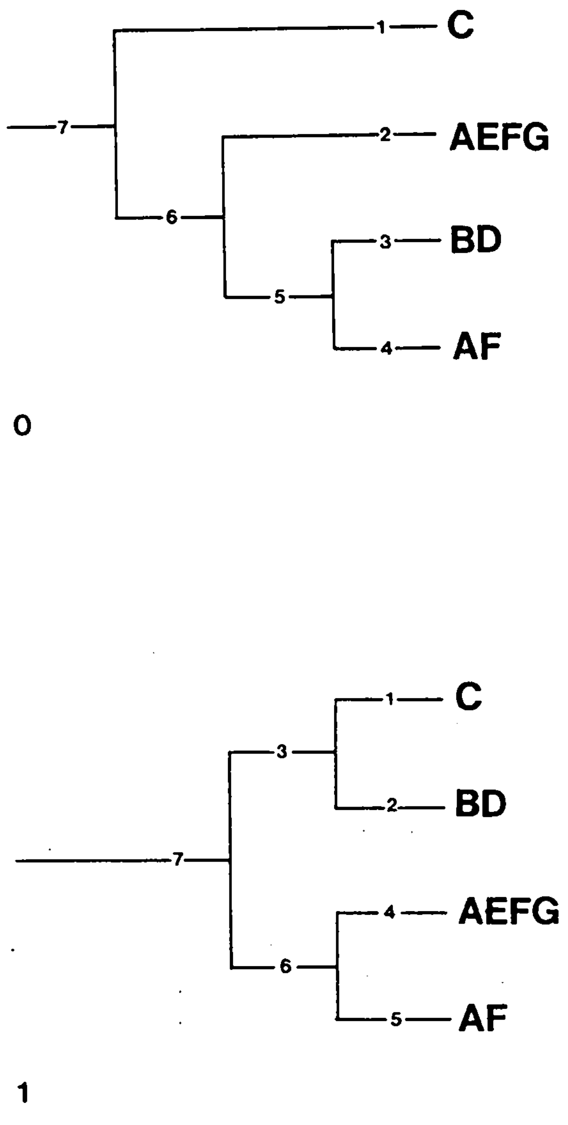


Fig. 7.19: Unresolved area cladograms of *Temporena* (components 1-7 are coded after Zandee & Roos, 1987).

	AREA						
	A	B	C	D	E	F	G
Component							
Tree 0							
1	0	0	1	0	0	0	0
2	1	0	0	0	1	1	1
3	0	1	0	1	0	0	0
4	1	0	0	0	0	1	0
5	1	1	0	1	0	1	0
6	1	1	0	1	1	1	1
7	1	1	1	1	1	1	1
Tree 1							
1	0	0	1	0	0	0	0
2	0	1	0	1	0	0	0
3	0	1	1	1	0	0	0
4	1	0	0	0	1	1	1
5	1	0	0	0	0	0	0
6	1	0	0	0	1	1	1
7	1	1	1	1	1	1	1

Table 7.10: Data matrices derived from unresolved area cladograms of *Temporena*.

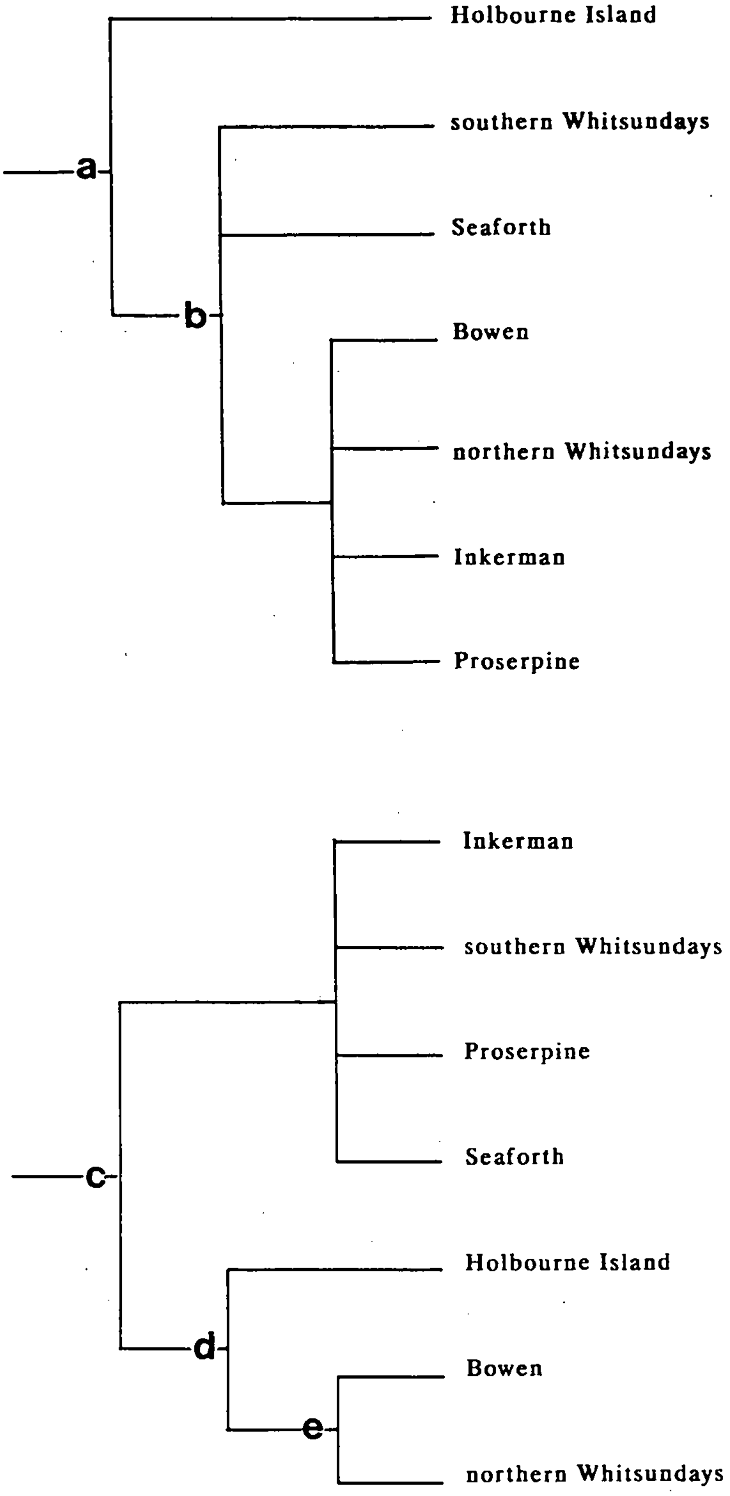


Fig. 7.20: Resolved area cladograms of *Temporena* analysed under Assumption 0: **0**, length = 8, c.i. = 0.87, r.i. = 0.88; **1**, length = 7, c.i. = 1.00, r.i. = 1.00 (a-c indicate events discussed in this study).

Chapter 8

DISCUSSION

Camaenidae: monophyletic, paraphyletic or polyphyletic?

The superfamily cladogram supported the dissolution of the Camaenidae into at least two groups congruent with geographical distribution. The Australasian Camaenidae and Asian Bradybaenidae occurred as sister groups, while the American Camaenidae was sister group to the Helicidae and Helminthoglyptidae (Fig. 8.1a). Previous analyses have placed the Camaenidae (as a monophyletic family) with the Sagdidae (Emberton, 1991) (Fig. 8.1b) and, tentatively, as a sister group to the Helicarionidae, Haplotrematidae and Vitrinidae (Tillier, 1989) (Fig. 8.1c).

The Australasian and American Camenidae had only seven out of 12 (58.3%) character states in common, of which three were apomorphic (25%), while the Australasian Camaenidae and Bradybaenidae had 9 out of 12 (75%) character states in common, of which five were apomorphic (41.7%) (Table 8.1). The sister groups Helicidae and Helminthoglyptidae also shared 41.7% of their apomorphic character states.

The sister-group relationship between the Australasian Camaenidae and Bradybaenidae is supported by the derived state of character 2, which also occurs as a unrelated transformation in the Helicarionidae. A shortened intestine may be a product of overall reduction in size, adoption of carnivory, or development of limacisation (Tillier, 1989). The Australasian camaenids and the bradybaenids are medium to very large snails, neither group has developed predatory or unusual dietary habits, and all are fully-shelled. The Helicarionidae are also medium to very large snails, but they exhibit varying degrees of limacisation. Many species are semi-slugs, possessing a fragile, uncalcified shell, into which they are unable to withdraw. The occurrence of this character state in the Australasian Camaenidae-Bradybaenidae sister taxa may be a synapomorphy, while the development of the same character in the Helicarionidae may be a parallelism.

Pairing of the Australasian Camaenidae and Bradybaenidae may suggest they are confamilial, and that the Australasian Camaenidae are simply aberrant bradybaenids. The absence of any apomorphies supporting the Australasian Camaenidae strengthens this argument for inclusion. The tropical Western Australian genus *Rhagada* lacks a dart sac and associated glands, and the absence of these structures identifies it as a camaenid (Pilsbry, 1939), but it also possesses a permanently everted headwart (Solem, 1985), which is a characteristic shared by some Camaenidae and Bradybaenidae (Taki, 1935). Loss of the dart sac and accessory glands is possible: among Helicidae, a family characterised by the presence of a well-developed dart sac, some snails, including *Ashfordia (=Monacha) granulata* (Alder, 1830), lack both dart sac and dart gland (Watson, 1923). Bradybaenids, such as *Nesiohelix* Kuroda & Emura, 1943, and *Cathaica* Möllendorff, 1884, may have reduced dart sacs and glands (Schileyko, 1973). Further investigations are required to elucidate the evolutionary relationships between Australasian Camaenidae and Bradybaenidae.

The synapomorphy which supported the American Camaenidae, Helicidae and Helminthoglyptidae clade was a reversal in the advanced state of the kidney. Lamellae in the kidney increase the surface area for the production of filtrate and the secretion of uric acid (reabsorption does not take place in the pulmonate kidney) (Vorwohl, 1961). It might be expected that transformations of kidney structure would be correlated with ecological, behavioural, physiological or anatomical changes, which accommodate the different patterns of urine production. Factor analysis of pallial characters suggests that undifferentiated kidneys are associated with an open or absent ureteric tube, which in turn is associated with an elongate body shape (Tillier, 1989). This is not an invariable association, as the Helminthoglyptidae, Bradybaenidae and Zonitidae, for example, have undifferentiated kidneys and closed ureters (Tillier, 1989).

The relationship between the Sagdidae and American Camaenidae is interesting. In this study, the two groups share eight character states, of which only one is derived (presence of a calcified shell). In Emberton's study, which uses different characters, the two groups have identical states for 17 of 18 characters, and nine of these states are apomorphic.

A complete revision of the Camaenidae in Australia, Asia and the Americas is necessary to test the hypothesis of polyphyly. Anatomical investigations may be insufficient to resolve completely the phylogenetic relationships between the Australasian and American Camaenidae and the Bradybaenidae, but will provide a basis for subsequent molecular or ultrastructural studies.

Should further studies show that the Australasian and American Camaenidae do belong to separate taxa, nomenclatural changes would be minimal. Australasian taxa would retain the name Camaenidae (*Camaena* Albers 1860, is an Asian genus), and Pleurodontidae would be reinstated as the family name for the American taxa. Should Camaenidae and Bradybaenidae be shown to be confamilial, Camaenidae would take priority over Bradybaenidae as the oldest available name.

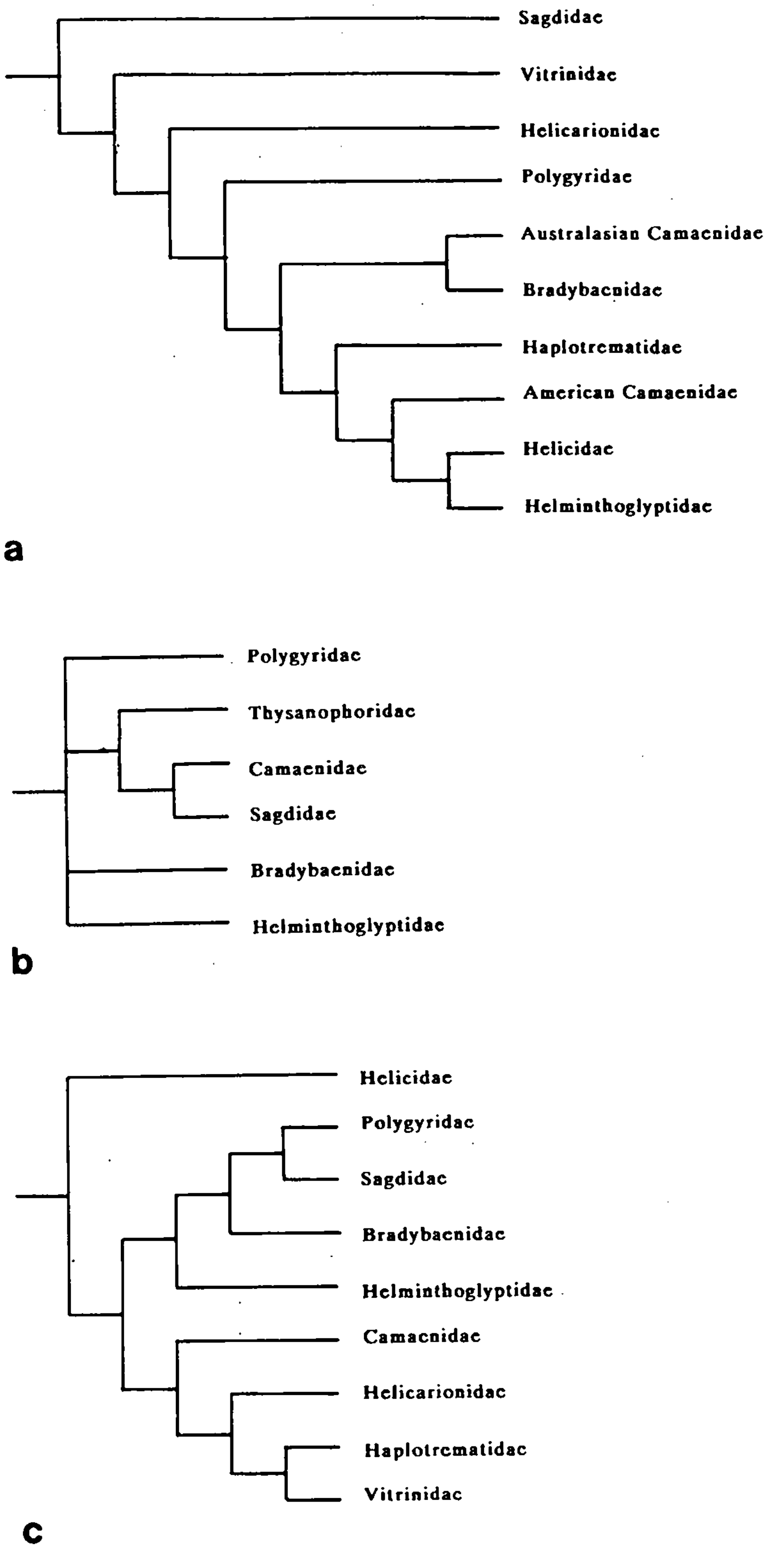


Fig. 8.1: Alternative phylogenetic hypotheses for the superfamily Helicoidea: a, this study; b, Emberton (1991); c, Tillier (1989).

	American Camaenidae	Australasian Camaenidae	Bradybaenidae
Oesophageal crop	advanced (1)	advanced (3)	advanced (3)
Gastric crop	advanced	advanced	advanced
Intestinal length	primitive	advanced	advanced
Kidney length	advanced	primitive	primitive
Kidney morph.	primitive	advanced	advanced
R. cerebral connective	primitive	primitive	primitive
Ratio of lengths of cp connectives	advanced	advanced	primitive
Position of visceral ganglion	primitive	primitive	primitive
Position of left parietal ganglion	primitive	primitive	primitive
Fusion of visceral ganglion	primitive	advanced (1)	advanced (2)
Shell structure	advanced	advanced	advanced
Calcified dart	primitive	primitive	primitive

Table 8.1: Character states for American Camaenidae, Australasian Camaenidae and Bradybaenidae

Biogeography of the Helicoidea

The range of the helicoid ancestral taxon was almost cosmopolitan, including eastern Gondwana, parts of western Gondwana, and much of Laurasia. The nature of vicariance events suggested by the area cladograms is not determined, but all events were large scale and probably included rifting of continental plates, changes in sea-level, mountain-building or widespread volcanic activity. The following geographical scenario is corroborated by the area cladogram (Fig. 8.2):

(a) The biota of eastern Gondwana became isolated from the rest of the ancestral range.

The break up of Gondwana in the late Mesozoic may have provided the impetus for early differentiation. Although the sequence of rifting is not revealed by the cladogram, geological evidence indicates that, of the areas represented, India was the first element to break away, followed by Africa and Madagascar, the result of sea-floor spreading during the early Cretaceous (Norton & Sclater, 1979; Tarling, 1988).

Shortly after the start of the Gondwanan dissolution, Australia began to separate from Antarctica. A rift valley system developed from west to east between the two continental masses, and Australia began to peel away, although it remained in contact with Antarctica along its eastern margin until the late Cretaceous (Veevers, 1991). Major marine transgressions during the early to mid-Cretaceous separated southern Australia from the island formed from central Australia and the Kimberley, and the volcanic arc of north eastern Australia (Audley-Charles, 1987; Veevers, 1991).

Towards the end of the Cretaceous, sea floor spreading split the New Zealand Plateau and Lord Howe Rise from Australia. By the Eocene, rifting between Australia and Antarctica was complete.

(b) Australia and Asia were separated from Europe, North Africa and the Americas. Australia became isolated from Asia, which then split into eastern Asia and south-east Asia

Although the island of Australia is a single mass, much of south east and eastern Asia is composed of microcontinental fragments which have rifted from larger land masses. Indonesia and the Malayan Peninsula, for example, are believed to be formed of a mosaic of elements derived from Gondwana and Indo-China (Burton, 1970; Audley-Charles, Carter & Milson, 1972; Acharyya, 1979; Hamilton, 1979; Norvick, 1979; Buffetaut, 1982; Achache, Courtillot and Besse, 1983; Pigram & Panggabean, 1984; Burrett & Stait, 1985; Helmke, 1985; Charlton, 1986; Gatinsky & Hutchinson, 1986; Metcalfe, 1988; Hutchinson, 1989; Harbury *et al*, 1990; Burrett *et al*, 1991; Michaux, 1991).

The scenario presented in this study indicates that helicoids in Asia were present on terranes associated with northern Australia following partitioning of the continent by marine transgressions in the mid- to late Cretaceous (Audley-Charles, 1987). However, previous studies propose that all fragments, except for those which form the Moluccas, northern New Guinea, and islands of the Banda Sea, had broken away from northern Australia before the Cretaceous (Burton, 1970; Acharyya, 1979; Pigram & Panggabean, 1984; Helmke, 1985; Metcalfe, 1988; Hutchinson, 1989; Harbury *et al*, 1990; Burrett *et al*, 1991).

This study suggests that the terranes of South China/Indo-China and Sibumasu (parts of Burma, Thailand, peninsular Malaya, Sumatra; Audley-Charles, 1983; Metcalfe, 1988) rifted from the northwest coast of Australia during the late Cretaceous and migrated north. Common fossil deposits place Sibumasu and North China adjacent to the west coast of Australia and South China to the north coast in the early Palaeozoic (Burrett & Stait, 1985). Audley-Charles (1987) and Harbury *et al* (1990) suggest that Sibumasu broke away from Australia in the Jurassic, but Burrett, Long and Stait (1990) identify the separation of Sibumasu as a Permian event. Evidence for time of rifting is clearly equivocal.

The rifting of South China/Indo-China from Sibumasu and associated terranes occurred after the separation from Australia. Elements of Borneo, for example, were derived from the South China/Indo-China plate in the mid- to late Cretaceous (Gatinsky & Hutchinson, 1986; Hutchinson, 1989; Metcalfe, 1988). This might indicate different rates of migration for the South China/Indo-China block and the Sibumasu terranes. South China/Indo-China may have travelled more rapidly than Sibumasu, leaving behind microcontinental fragments, such as parts of Borneo and Palawan. Sibumasu docked with South China/Indo-China in the mid- to late Cretaceous, while terranes probably derived from it formed part of Borneo and Sulawesi (Audley-Charles, 1987; Harbury *et al*, 1990).

(c) Eastern North America or Western Palaearctic and/or North Africa became isolated from the rest of Laurasia/western Gondwana

North America, South America and Africa were adjacent in western Pangea until the late Mesozoic (Bullard, Everett & Smith, 1965; LePichon & Fox, 1971; Van der Voo & French, 1974; Van der Voo, Mauk & French, 1976; Pindell & Dewey, 1982; Burke *et al*, 1984; Duncan & Hargraves, 1984). Rifting between the east coast of North America and the north-west coast of Africa opened up the equatorial Atlantic in the early Cretaceous, isolating Africa from neighbouring land masses (Pindell & Dewey, 1982).

Northward expansion of the Atlantic during the early Tertiary severed connections between the Western Palaearctic and North America below the Arctic Circle. Contact was maintained along their northern margins, with broad-leaved forests extending into very high latitudes (Wolfe & Upchurch, 1987). Separation of the two land masses through tectonic movement and subsequent changes in climate would have isolated helicoid taxa in the Western Palaearctic.

Inundation of the Western Interior of North America by a Cretaceous seaway, which extended south from the Canadian Arctic to the Gulf of Mexico, effectively split eastern North America from western and southern areas. Flooding began in the Cretaceous, and did not fully recede until the Miocene (Williams & Stelck, 1975).

(d) Western North America separated from the Caribbean and Central America, followed by a split between the Caribbean and Central America

Western North America was separated from Central America and the Caribbean islands by a fault zone which ran south of Honduras (Sykes McCann & Kafka, 1982). North America moved westward, while the Caribbean islands, which were located between Honduras and Colombia, were displaced to the east. The Caribbean islands (principally the Greater Antilles) were adjacent to each other and to Central America in the Eocene, but changes in sea-level and tectonic movement during the Oligocene and Miocene separated all elements (Pindell & Dewey, 1982; Sykes *et al*, 1982; Duncan and Hargraves, 1984; Buskirk, 1985).

Vicariance events leading to the differentiation of American helicoid taxa terminated with the closure of the seaway between North and South America in the late Oligocene or early Miocene (Holden & Dietz, 1972)

Laurasian origin and dispersal hypothesis

Widespread distributions of Helicarionidae, Bradybaenidae and Camaenidae can be interpreted using a vicariance hypothesis rather than one which invokes dispersal. The presence of Helicarionidae in Madagascar, India, Asia, Australia and islands of the western Pacific appears to be a plesiomorphic distribution. Helicarionids did not disperse to southern and western areas from Asia, but were present in them when they were connected in the land mass of eastern Gondwana. Since taxa in these areas have been separated for considerable time, during which helicoids on other terranes differentiated at the family level, it is possible that the Helicarionidae now represents a suprafamilial taxon.

Similarly, dispersal hypotheses are not required to explain the distributions of Bradybaenidae and Australasian Camaenidae. In fact, dispersal models do not account for the absence from India (Bradybaenidae, Australasian Camaenidae) or parts of southern Australia (Australasian Camaenidae), when the families are present in adjacent areas. It is unlikely that rivers or narrow seaways would have been barriers to a family which is thought to have dispersed from the Northern Hemisphere and then island-hopped through Indonesia to Australia (Solem, 1959, 1981). Similarly, the family's failure to colonise southern Western Australia is difficult to explain. Deserts do not appear to represent barriers to dispersal as arid Australia supports a relatively diverse land snail fauna (Solem, 1988, 1993). The absence of the Bradybaenidae and Australasian Camaenidae in India suggests that the families were fully differentiated before India collided with the Asian plate in the early Eocene. The apparent absence of bradybaenids from Australia is likely to be a taxonomic artefact as it is probable that the Bradybaenidae is confamilial with the Australasian Camaenidae (see above).

Pacifican vicariance hypothesis

Allochthonous terranes along the Pacific coasts of North and South America were believed to have rifted from Pacifica (Nur & Ben-Avraham, 1977, 1981; Kamp, 1980), taking with them helicoid ancestors from that part of Gondwana (Miller & Naranjo-García, 1991). The analysis presented in this study shows that the allochthonous terranes of western and Central America are not closely related biogeographically to those of eastern Asia, as would be predicted by the Pacifican hypothesis. Eastern Asia rifted from the Gondwanan terranes of north western Australia and south east Asia, the pattern of separation independent of activity in the western central Palaearctic and the Americas.

Geological evidence suggests that many of the western American terranes were of oceanic, not continental, origin (Howell, Jones & Schermer, 1985; Hallam, 1986; Megard, 1989), and did not support terrestrial fauna or flora. Continental terranes between southern California and Alaska were probably never united in a single Pacifica land mass: their origins have been calculated as north of the area occupied by eastern Gondwana (Cox, DeBiche & Engebretson, 1989).

Helicoids are known from Pacific islands. Helicarionids are present on Vanuatu and Fiji, which were once part of Gondwana (Burrett *et al*, 1991), but there is no evidence of occupation of Pacific islands by other helicoid land snails. Land snail fossils have been recovered from the islands of Midway, Bikini, Eniwetok and Funafuti, but these fossils all belong to the Endodontidae and date back to the Miocene (Ladd, 1958, 1968; Ladd, Tracey & Gross, 1970; Solem, 1977). No helicoid fossils are known from these areas.

Pangean vicariance hypothesis

The hypothesis proposed in this study attempts to explain the distribution of helicoid families without invoking mass dispersals and extinctions or hypothetical land masses. Most of the helicoid families appear to have originated in the Cretaceous, during the tectonic activity which first broke up Pangea, and subsequently Gondwana and Laurasia. Events in the Americas persisted into the Tertiary, and differentiation at the family level may have continued into the Miocene.

The sequence of vicariance events presented here indicates that Asian terranes maintained contact with northern Australia until the late Cretaceous, which is later than is suggested in current palaeogeographical hypotheses. The presence of taxa in mainland Asia, Indonesia and Australia is frequently explained as the result of dispersal, usually from north to south (e.g. Solem, 1959, 1969, 1993; Smith-White, 1959; Burbridge, 1960; Lange, 1982), but for taxa with low vagility, such as snails, other terrestrial invertebrates, and many plants, it is likely to be the result of a shared ancestral stock. Even taxa with great abilities to disperse, such as birds, may be prevented from doing so by relatively small barriers. Garnett (1991) lists twenty-two species of rainforest birds, populations of which are thought to be isolated in north-eastern Australia because they are unable or unwilling to cross the 140km-wide Torres Strait, despite the many islands providing `stepping stones' between the tip of Cape York and southern New Guinea.

The hypothesis of helicoid biogeography presented here conforms largely with current ideas about the break-up of Pangea. However, tests of this vicariant relationship between mainland Asia, the Indonesian archipelago, and Australia should be sought in biogeographic analyses of other taxa.

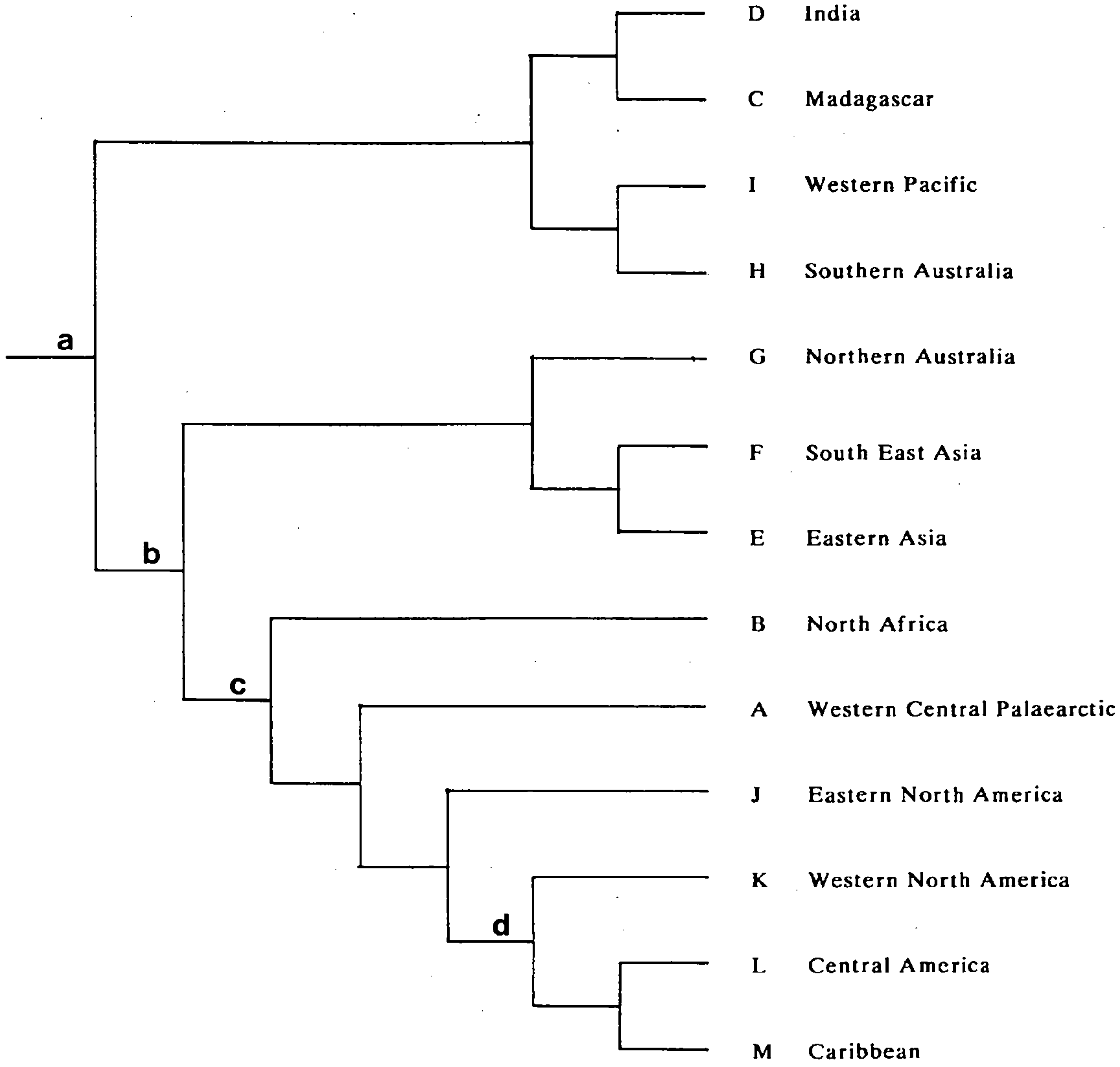


Fig. 8.2: Geographical scenario corroborated by area cladogram and current geological evidence (a-d indicate events discussed in this study).

Structure and function of the camaenid headwart

Histological investigations suggested that the eversible headwart of the camaenids is homologous to the permanently-everted headwart of the bradybaenids (Taki, 1935; Takeda & Tsuruoka, 1979; Takeda, 1980, 1981). However, differences were recorded between the cells of the headwart and those of the surrounding head area of the Camaenidae and Bradybaenidae. These differences can be summarised as changes in the shape of the cells and in the density and composition of secretory cells.

The refractive layer on the surface of the headwart and head epithelium is likely to have been composed of microvilli. Although too fine to be resolved with a light microscope, microvilli can be detected as a thin PAS-positive `cuticle' (Lane, 1963). Their role may be to absorb material from the environment (Newell, 1977), to trap and hold secretions (Lane, 1963) or to distribute secretions (Takeda, 1981). Takeda (1981) observed swellings, possibly filled with secretory material, at the tips of microvilli on the bradybaenid headwart.

Microvilli were not restricted to the headwart in camaenids and appeared to be distributed over the remainder of the head and dorsal surface. The general distribution of microvilli on bradybaenids was not recorded by Takeda (1981).

The epithelial cells of the camaenid headwart were columnar and similar in size to those of the surrounding integument. The epithelium of the bradybaenid headwart is much thicker than that of the surrounding tissue. During development of the bradybaenid headwart, normal epithelial cells (which are approximately 15mm in length) become elongate, resulting in a thickening of the headwart epithelium (Takeda & Tsuruoka, 1979). Full development of the bradybaenid headwart coincides with maturation of the gonads (Takeda, 1980), but nothing is known of headwart development in Camaenidae.

Subepithelial glands in the camaenid headwart were less diverse and less abundant than those in the surrounding integument, suggesting that mucus secretion was not an important function of the headwart. The adjacent head region contained a larger number and variety of secretory cells, secreting all types of mucopolysaccharides as well as protein. Mucus is formed from acid and neutral mucopolysaccharides which may be mixed with proteins (Cook & Shirbhate, 1983). These substances are produced by a variety of secretory cells in the skin of the snail (Campion, 1961). They may be released separately or in combination, depending on the purpose for which the mucus is required (Cook & Shirbhate, 1983). Neutral or weakly acid mucus may be fluid, while strongly acid mucus is viscous (Hunt, 1973). The addition of protein thickens the mucus further (Denny & Gosline, 1981). Mucus from the head region has a mainly hygienic function, assisting in the removal of irritants (Cook & Shirbhate, 1983). The reduction in mucus secretion on the headwart may prevent surface material from being washed away.

No histochemical study was undertaken by Takeda & Tsuruoka (1979) or Takeda (1981), so no information is available about mucosubstances secreted by the tissue of the bradybaenid headwart. Takeda (1981) observed only rough endoplasmic reticulum and an increase in the number of granules near the Golgi apparatus of epithelial cells during the breeding season. This may be linked to the production of a protein-based pheromone (Takeda, 1981).

Reduction in amount of pigment under the headwart may be important; this condition is also found in cephalic dimple of *Achatina achatina* (Chase & Piotte, 1980). This information, together with the siting of the headwart over the cerebral ganglion, may indicate a role in determining photoperiod, as some slugs are known to possess extraocular photoreceptors associated with the CNS which can distinguish between long- and short-day photoperiods (McCrone & Sokolove, 1979; Beiswanger *et al*, 1981).

The function of the camaenid headwart remains unclear. Evidence for the secretion of a protein-based contact pheromone in the bradybaenid headwart (Takeda & Tsuruoka, 1979) is inconclusive. Other mollusc contact pheromones are thought to be lipid-based (Chase & Boulanger, 1978; Bousefield *et al*, 1981), but neither this study nor that of Takeda (1981) searched for the presence of lipids in the tissue. The next steps are to test for pheromone secretion and to test alternative hypotheses explaining its function.

Phylogeny of the hadroid camaenids

Shell and anatomical characters produced a robust and almost fully-resolved phylogeny for genera of hadroid camaenids (c.i = 0.70, r.i. = 0.80). Synapomorphies were widespread, while homoplasy was restricted to two characters of the epiphallus, and reversals to three characters of the shell. Woodruff and Solem (1990) suggested that it may not be possible to construct a phylogeny based on cladistic analysis of anatomical data. Their comments were based on the occurrence of homoplasies and reversals within the `Ningbing radiation', four genera of endemic camaenids from northern Western Australia. Complex patterns of character state transformations are not confined to these taxa, and this study demonstrated that it is possible to generate a phylogeny for an equivalent group by use of this method. It is essential, however, to restrict analysis to a monophyletic group (Hennig, 1966) and to select taxa at the appropriate taxonomic level. Phylogenetic hypotheses derived from anatomical characters are available for testing with molecular data.

The hadroid camaenids represent a clade within the Australasian Camaenidae. The clade includes those taxa referable to the "*Hadra-Sphaerospira-Meridolum* aggregation" (Iredale, 1937b: 19) within the helicoid family Hadridae Iredale, 1937. The grouping of these large rainforest snails of eastern Queensland and northern New South Wales by Iredale (1933, 1937b, 1938), a taxonomic decision based on shell characters alone, was supported by the examination of anatomical characters in this study. There was no evidence, however, to suggest that this clade could be distinguished at the family level from other Australasian camaenids, so the conclusion of Smith (1992) that the Hadridae has no status as a family, is also supported.

The hadroid camaenids belong to the Camaeninae, which includes taxa from southern Australia (Solem, 1992). The phylogenetic coherence of the hadroids suggests that the split between eastern-mesic and southern-xeric faunae was an early occurrence, with both groups developing in isolation. *Meridolum*, which appears at the base of the hadroid clade, retains the largest number of plesiomorphic character states, and thus must resemble the hadroid ancestor more closely than does any other taxon in its clade. *Meridolum* is the most southerly distributed hadroid and may also be the least dependent on rainforest. Some species are restricted to rainforest, but many occur in open forest (Smith, 1992), as do members of the southern fauna (Solem, 1992). The open forest or xeric habitat may represent the ancestral habitat of the Camaeninae, including the hadroid camaenids. The evolutionary trend within the hadroids may involve adaptations towards occupation of a more mesic and stable habitat (rainforest).

Evolutionary patterns in the distal reproductive tract

Patterns of intergeneric variation

Divergence in characters of the intromittent organ is a widespread phenomenon in animals, including many molluscs (Tompa, 1984; Eberhard, 1985). Reproductive structures which demonstrated the greatest morphological variation within the hadroid camaenids were those of the distal male reproductive tract. These changes were restricted to the epiphallus and penis, both of which are directly involved in copulation.

The cladistic analysis identified *Meridolum* as the most primitive genus of hadroid camaenids. This genus possessed the largest number of plesiomorphic character states, with a single synapomorphy: a tubular penial papilla. This state is unique within the hadroid Camaenidae, but is found in other Australian Camaenidae such as *Melostrachia* (Solem, 1979) and *Contramelon* (Solem, 1992).

The development of the penis sheath diagnosed the northern rainforest group of hadroid camaenids. Although the presence of the sheath was unique to this group within the hadroid clade, its presence in other Australian Camaenidae (e.g. *Xanthomelon*, *Trachiopsis*, Solem, 1979; *Tatemelon*, *Dirutrachia* Solem, 1993) indicated that this character was homoplasious within the context of the familial clade (Solem, 1993). This situation - multiple development and perhaps multiple loss of the penis sheath - also occurs in other families (e.g. Bulimulidae, Breure, 1979; Polygyridae, Emberton, 1988). The penis sheath is a variable structure, ranging from a thin sheet of tissue to a thick muscular casing (gen. nov. B).

The epiphallic flagellum was present in all species of the *Hadra* clade, while the epiphallic caecum occurred only in *Hadra* and *Zyghelix*. Prior to or during mating, autosperm is packaged into chitinous spermatophores within the epiphallus. The walls of the epiphallus secrete the outer coating which will protect autosperm during transfer between mating partners. It acts as a mould, so the shape of the spermatophore is determined by the internal morphology of the epiphallus. The role of the flagellum is to secrete the tail portion of the spermatophore (Lind, 1973).

Lengthening of the vagina occurred in all genera in this clade, except *Thersites*, in which the short vagina was considered as a character state reversal.

The penial papilla (called a verge by other authors, e.g. Bishop, 1978a; Stanisic, 1990; or a vergic papilla, e.g. Solem, 1979) was lacking in most of the more primitive genera (*Varohadra*, gen. nov. B, *Zyghelix* and *Hadra*). It appeared as a rounded structure with a narrow basal opening at an early node. This type of papilla is not widespread among the Australasian Camaenidae. A rounded to pointed papilla with a subterminal pore is found in the South Australian genera *Cupedora* and *Cooperoconcha* (Solem, 1992). *Trachiopsis* (Solem, 1979) has a large papilla with a distinct groove along one side, as do the tropical Western Australian genera *Setobaudinia*, *Retroterra*, *Kendrickia* and *Rhagada* (Solem, 1985) and the Central Australian *Semotrachia* (Solem, 1993).

Sphaerospira and *Thersites* were identified as sister groups. No strict synapomorphy defined them, but among the higher hadroids, they alone bore a papilla at the internal junction of the vas deferens and epiphallus. This character state was convergent with that of the more primitive *Varohadra*. The role of the epiphallic papilla is unknown, but as the sole function of the vas deferens is to transport autosperm, the papilla may regulate the entry of sperm into the epiphallus.

Patterns of intrageneric change

Variations in two reproductive tract characters were common to all genera of hadroid camaenids examined. These were the point of insertion of the penial retractor muscle, and the shape of the free oviduct. Variations in other characters were restricted to individual genera.

The point of insertion of the penial retractor muscle showed parallel trends within the three genera. In *Hadra*, *Sphaerospira* and *Bentosites* the advanced condition was a distal insertion (Fig. 8.3a). The mechanics of copulation in snails are unknown, but migration of the insertion point toward the penis may not only allow the penis to be withdrawn quickly and with relatively little effort, but may also allow the penial sphincter (*Hadra*) or papilla (*Sphaerospira*, *Bentosites*) to be moved *in copulo*.

Although it was impossible to determine the polarity of the shape of the free oviduct in *Hadra*, in both *Sphaerospira* and *Bentosites* the free oviduct was apomorphically flexed (Fig. 8.3b). In *Bentosites*, this was associated with the divergence of the free oviduct from the vagina at an angle, not in a straight line as in *Sphaerospira*. This might be expected, as the free oviduct, diverging from the vagina at an angle, would have to flex to return to the uterus, which is positioned along the same axis as the vagina. However, in *B. mulgravensis* (Brazier), the free oviduct is curved, rather than flexed, although its junction with the vagina is angled.

Hadra

Hadra is characterised by the presence of an epiphallic caecum and flagellum, and penial sphincters (Fig. 6.5). Elaborations of the ephiphallus suggest that a large and complex spermatophore must be produced during mating. The degree of fusion between the caecum and flagellum is probably indicative of the length of the spermatophore.

The function of the penial sphincters is unknown, but they vary in number between species, from one (primitive state) to two. In species with a single sphincter, contraction causes the sphincter to resemble a penial papilla or verge (Fig. 6.11). The second sphincter of *H. bipartita* is probably not contractile, but may form a collar behind the first when the penis is everted. This could assist in anchoring the penis during copulation. The penis of *H. barneyi* is also equipped with a flap of tissue, regarded in this study as an incomplete sphincter, which may serve the same purpose.

The penial sculpture in four of five species of *Hadra* consists of longitudinal ridges. The anomalous species, *Hadra bellendenkerensis*, has a penial sculpture of lozenge-shaped papillae. The penis of this species is also greatly lengthened in comparison with all other species.

Bentosites

Lengthening of the penis, and the subsequent requirement for it to be folded within the penis sheath, also occurred in the four most advanced species of *Bentosites*, only one of which is sympatric with other species of *Bentosites*.

The penial papilla, found in all species of *Bentosites*, was either rounded (plesiomorphic state) or pointed. In five species, the papilla was associated with a pouch or outpocketting in the penis wall. The opening of the ejaculatory duct is at the base of the papilla, not at its apex, as is the case in many other Australian camaenids. The role of the papilla in *Bentosites* cannot be for direct delivery of the spermatophore, but may be to stimulate the female genitalia, to dilate either spermatheca or free oviduct, or perhaps to block either duct during copulation (see below).

Causes of change

Differences between the distal genitalia of closely-related species may be explained as mechanisms to prevent fertilisation in non-conspecific mates (reproductive character displacement) or to facilitate fertilisation in conspecific mates (female choice). In both the emphasis is on characters of the male tract which vary more than those of the female tract. These hypotheses were examined with data from *Hadra* and *Bentosites*, for both of which there were fully-resolved trees. The alternative trees for *Sphaerospira* did not permit testing.

Reproductive character displacement

Reproductive character displacement should occur in those species in which the chance of non-conspecific matings is greatest, that is, closely-related sympatric species (Eberhard, 1985). However, this is difficult to test unless sympatric and allopatric sister species can be compared. The cladograms of both *Hadra* and *Bentosites* were fully-resolved, but in neither was more than one sister pair available for testing. Both sister pairs (*H. bipartita*/*H. dunkiensis*; *B. mulgravensis*/*B. rawnesleyi*) demonstrated the smallest number of differences within their genera, although species of the former pair were sympatric and of the latter allopatric (Table 8.2).

Phylogenetically adjacent pairs of species (e.g. *H. bellendenkerensis*/*H. barneyi*; *H. barneyi*/*H. rudis*) whether sympatric or allopatric did not provide evidence of character displacement. Adjacent allopatric species of *Hadra* demonstrated a slightly greater number of genitalic differences than did adjacent sympatric species, but generally, differences were shown to accumulate as phylogenetic distance increased, regardless of distribution (Table 8.2, Fig. 8.4). The results of this study support the conclusion of Emberton (1988, 1991), in his work on triodopsinid polygyrids, that no differences in genitalic structure were directly attributable to character displacement.

Reproductive character displacement is interpreted as a shift in genitalic structure which causes some form of physical incompatibility (Eberhard, 1985). Physical incompatibility, however, is probably less feasible in soft-bodied animals than in those with external skeletons. The body of the snail is capable of great deformation, which means that there are probably few physical constraints on the size or shape of intromittent which can be accommodated. Madec and Guiller (1993, 1994) found evidence of partial mechanical isolation in geographically separated forms of *Helix aspersa*. Enlargement of the genitalia of one form of *H. aspersa* prolonged but did not prevent copulation between different forms.

Lengthening of the penis in one of a pair of sympatric congeners has been suggested as a mechanism for ensuring reproductive isolation (Solem, 1981a, 1992). However, this may not be effective as the function of the penis is to introduce the spermatophore into the spermatheca or free oviduct, which lies at the proximal end of the vagina. This can be achieved with only partial insertion of the penis. Lengthening of the penis in one species will not prevent this, but reduction in penis length or elongation of the vagina of one species of a congeneric sympatric pair might have an isolating effect. This would only be a practical method of isolation if there were no spermatophore transport within the vagina, and sperm delivered to the vagina rather than spermatheca were expelled or incapacitated. Even so, it would only prevent insemination by *one* of a non-conspecific mating pair, unless mating was terminated because the correct stimulus (e.g. distension of vagina, agitation of free oviduct or spermatheca) was absent.

Female choice

Data from hadroid camaenids are consistent with predictions from the female choice hypothesis, but conclusive evidence is lacking. Variation of the genitalia of the hadroid camaenids is most marked in the epiphallus and penis, which are the only structures involved in transmission of sperm. Both will have contact with the female genitalia, either directly (penis) or indirectly (epiphallus).

Structural elaborations on the spermatophore may increase its resistance to displacement from the female tract. Studies of *Helix pomatia* Linnaeus (Helicidae) demonstrate that, following mating, a spermatophore placed in the spermatheca of a mating partner is slowly digested while sperm escape from the spermatophore `tail' and move into the free oviduct (Lind, 1973). When a second spermatophore is deposited during a subsequent mating (Murray, 1964; King, 1975), two things may happen: the first spermatophore may prevent the second from being placed in the spermatheca, or the second spermatophore may push the first further into the spermatheca. Should the former occur, then the second spermatophore may be expelled from the female tract. If this were the case, selection would probably act against multiple mating, as only sperm from the first mating would be used to fertilise eggs. In the latter situation, some sperm from the first spermatophore might escape digestion, but displacement during a subseqent mating would ensure that remaining sperm were digested in the spermatheca. This might explain why the spermatheca of hadroid camaenids is invariably longer than the spermatophore (calculated as the length of the epiphallus + flagellum, where present).

Penial papillae and sphincters may distend the female tract and stimulate ovulation. Alternatively, these terminal structures may also be involved in the displacement of spermatophores from previous matings, or in blocking the free oviduct to ensure that the spermatophore is placed in the spermatheca. The presence of a rounded papilla is associated with the divergence of the spermatheca from the vagina at an angle, a strongly homoplasious character, which may be consistent with the function of the papilla as an occluding structure.

Penial sculpture may be adapted to prevent the penis from slipping out or being pushed out by hydrostatic pressure during mating (Emberton, 1988).

In summary, variation in distal male genitalia is species-specific. This was not attributable to reproductive character displacement, as there were no differences between the degree of divergence of genitalia in allopatric and sympatric pairs. Female choice may be the cause of divergence, but until more is known of the mechanics of copulation in land snails, evidence in support of this theory is inconclusive.

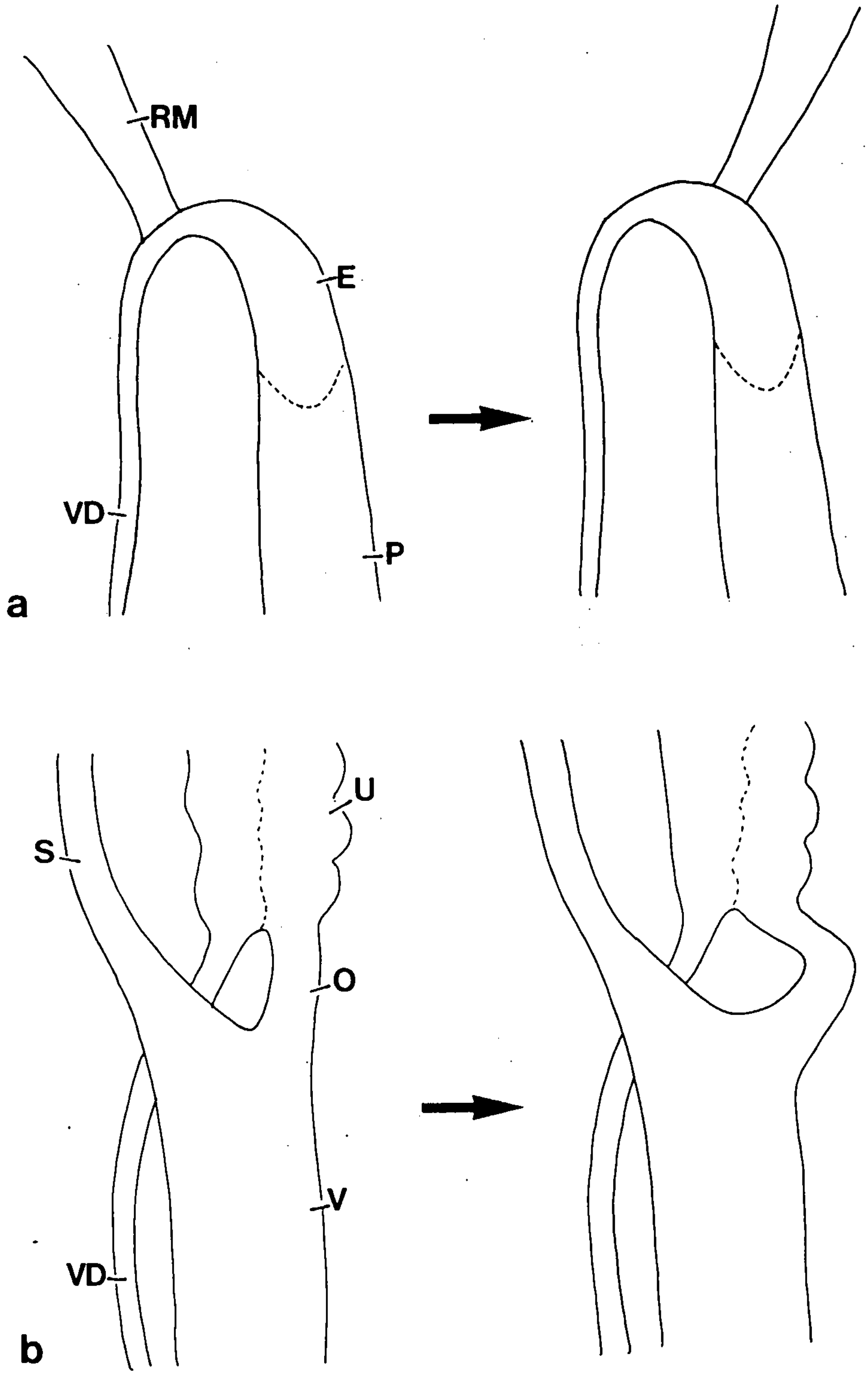


Fig. 8.3: Plesiomorphic and apomorphic states of hadroid camaenid reproductive tract characters: **a**, insertion of penial retractor muscle; **b** shape of free oviduct (E = epiphallus; O = oviduct; P = penis; RM = retractor muscle; S = spermatheca; U = uterus; V = vagina; VD = vas deferens).

Species pairs	Distribution	No. of differences	Phylogenetic distance
HADRA			
bellendenkerensis/barneyi	allopatric	6	2
bellendenkerensis/rudis	sympatric	5	3
bellendenkerensis/bipartita	sympatric	7	4
bellendenkerensis/dunkiensis	sympatric	5	4
barneyi/rudis	allopatric	5	2
barneyi/bipartita	sympatric	4	3
barneyi/dunkiensis	allopatric	5	3
rudis/bipartita	sympatric	6	2
rudis/dunkiensis	sympatric	4	2
bipartita/dunkiensis	sympatric	4	1
SPHAEROSPIRA			
fraseri/informis	allopatric	7	2
fraseri/blomfieldi	parapatric	4	3
*fraseri/*sp. nov.	allopatric	4	3
informis/blomfieldi	allopatric	4	2
*informis/*sp. nov.	allopatric	3	2
*blomfieldi/*sp. nov.	sympatric	4	1
BENTOSITES			
macleayi/zebina	allopatric	4	2
macleayi/yulei	sympatric	5	3
*macleayi/*sp. nov.	allopatric	3	4
macleayi/gavisa	sympatric	4	5
macleayi/mazee	allopatric	3	6
macleayi/mulgravensis	allopatric	2	7
macleayi/rawnesleyi	allopatric	4	7
zebina/yulei	allopatric	3	2
*zebina/*sp. nov.	allopatric	3	3
zebina/gavisa	sympatric	6	4
zebina/mazee	allopatric	7	5
zebina/mulgravensis	allopatric	6	6
zebina/rawnesleyi	sympatric	6	6
*yulei/*sp. nov.	allopatric	2	2
yulei/gavisa	sympatric	5	3
yulei/mazee	allopatric	4	4
yulei/mulgravensis	allopatric	5	5
yulei/rawnesleyi	allopatric	5	5
sp. nov./*gavisa*	allopatric	3	2
sp. nov./*mazee*	allopatric	4	3
sp. nov./*mulgravensis*	allopatric	5	4
sp. nov./*rawnesleyi*	allopatric	5	4
gavisa/mazee	allopatric	3	2
gavisa/mulgravensis	allopatric	4	3
gavisa/rawnesleyi	allopatric	2	3
mazee/mulgravensis	allopatric	1	2
mazee/rawnesleyi	allopatric	1	2
mulgravensis/rawnesleyi	allopatric	2	1

Table 8.2: Differences in genitalia in species pairs of hadroid camaenids.

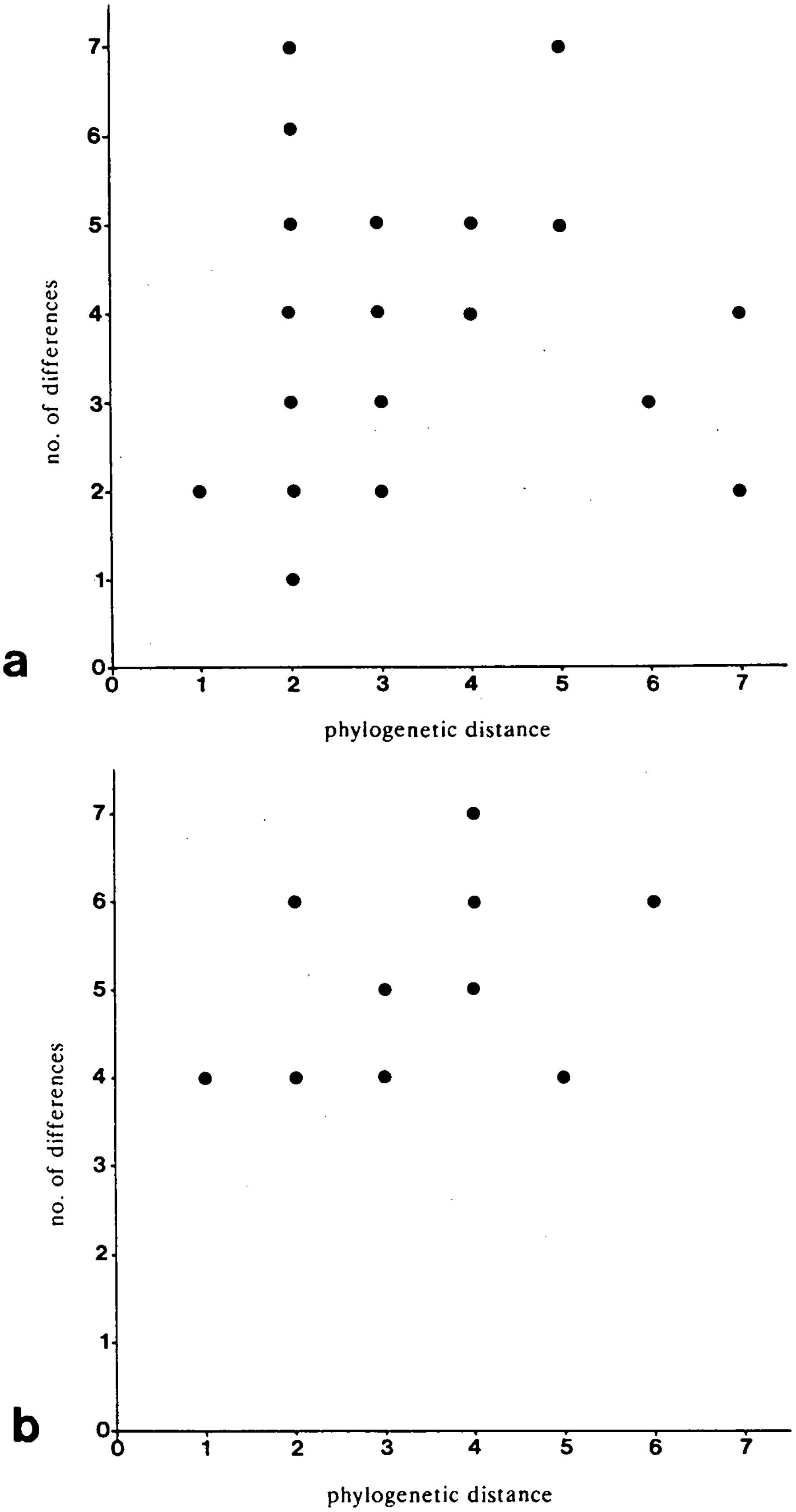


Fig. 8.4: Relationship between number of differences and phylogenetic distance between species pairs of *Hadra*, *Sphaerospira* and *Bentosites*: **a**, allopatric pairs; **b**, sympatric pairs.

Biogeography of the hadroid camaenids

Number of areas

Distributions of species of hadroid camaenids indicate that eastern Queensland may be divided into 41 biogeographical areas (Fig. 8.5). This suggests that continuity in rainforest blocks (e.g. Wet Tropics) is a secondary phenomenon, and treatment of each of these blocks as a single biogeographic unit obscures fine-scale patterns.

Area relationships

The distribution of modern hadroid species indicates that the hadroid ancestor extended along the Australian coast east of the Great Dividing Range. The hadroid clade may have split from the rest of the camaenid lineage as far back as the late Cretaceous or early Tertiary, when the Great Dividing Range was produced by widespread volcanism and tectonic uplift (Jones & Veevers, 1980, 1983). Subsequent disruption of the ancestral range may have resulted from volcanism, block faulting and cycles of marine transgression and regression which continued throughout the Tertiary and Quaternary (Grimes, 1980). The nature, position and timing of each vicariance event is difficult to determine, but analysis of other taxa will provide information to assist in pinpointing events.

Eastern Queensland

The biogeographical hypothesis for eastern Queensland is based on all genera of hadroid camaenids, except *Meridolum*, the most primitive genus, which occurs principally in New South Wales. Central and southern New South Wales was isolated from eastern Queensland and far northern New South Wales before these latter areas were interrupted by vicariance events (Fig. 7.4). Far northern New South Wales is thus part of the Queensland border biogeographical area, and the flora and fauna of this area are more closely related to those of Queensland than to those of central and southern New South Wales (Iredale, 1937a; Keast, 1961; Matthews, 1974; Cracraft, 1982, 1986).

The biogeographic hypothesis suggested by the resolved area cladogram of the hadroid camaenids (Fig. 7.4) supports the results of Joseph, Moritz and Hugall (1993). Far North Queensland and areas to the north were separated from the rest of eastern Queensland by a vicariance event at the southern end of the Atherton Tablelands (Fig. 8.6, a). These areas are defined by the presence of *Hadra* and *Zyghelix*, which are relatively old genera. Many other `old' taxa of plants and animals inhabit the rainforests of North Queensland (e.g. Walker, 1976; Monteith, 1980; Kikkawa Monteith & Ingram, 1981; Johnson & Strahan, 1982; Malipatil & Monteith, 1983; Covacevich & McDonald, 1984). The northern block subsequently differentiated, when barriers developed at the base of Cape York Peninsula (Normanby Barrier, Schodde & Mason, 1980; Schodde, 1982; Ford, 1986, 1987a, 1987b) and north of Cooktown (Fig. 8.6, b,c).

Development of another major barrier separated the Bowen, north-east Queensland and Kirrama-Hinchinbrook areas from mid-east Queensland and areas to the south (Fig. 8.6, d). The Burdekin Gap encompasses areas within this region, and is occupied by species of *Bentosites* and *Temporena*. Differentiation within this region isolated the Bowen area (Fig. 8.6, e), then north-east Queensland and Kirrama-Hinchinbrook (Fig. 8.6, f). The latter areas are inhabited by *Hadra dunkiensis* and endemic species of *Bentosites*.

Mid-east Queensland became isolated from southern areas (Fig. 8.6, g). The mid-east Queensland area has the highest diversity of endemic hadroid camaenids, which include *Sphaerospira informis*, species of *Bentosites* and *Temporena*, and the monotypic genus *Varohadra*. This contrasts with the low diversity of endemic vertebrates, which Winter (1988) suggested was due to the Quaternary contraction of rainforests to fragments too small to support viable populations of rainforest-dependent species of vertebrates. The large number of hadroid species indicates the area was disrupted at some stage, although it is impossible to determine from this data whether the disruption was due to climate-driven rainforest contraction or marine inundation.

Southern Queensland differentiated into three areas by two vicariance events (Fig. 8.6, h). At least three species of narrow range hadroid camaenids occur in vine thicket between mid-east Queensland and South-east Queensland. Their presence supports the model of an interrupted vine thicket connection between the two regions, rather than an unbroken connection (Joseph, Moritz & Hugall, 1993). One species occurs on the limestone outcrops of the Rockhampton Cave region, while the other two species are found in the Bulburin area, close to Kroombit Tops, which has been identified as an area of endemism for frogs (Czechura, 1986) and charopid snails (Stanisic, 1990).

Cape York Peninsula and the Wet Tropics

Cape York Peninsula extends from the Torres Strait south to approximately 14^{0}S (Lavarack & Godwin, 1987). The Wet Tropics is usually interpreted as extending from the Cooktown region south to Bluewater and Mt Halifax near Townsville and is treated as a coherent biogeographical unit (Tracey & Webb, 1975; Tracey, 1982; Williams & Tracey, 1984; Winter *et al*, 1987). However, the partially-overlapping distributions of *Hadra* and *Bentosites* suggest that the Wet Tropics is not a single area, but is composed of several major areas. This is supported by the distributions of other fauna, including scaraboid beetles (Matthews, 1972, 1974; Stebnicka & Howden, 1994), elaterid beetles (Calder, Lawrence & Trueman, 1993), cockroaches (Roth, 1977) and frogs (McDonald, 1992). The Far North Queensland and Kirrama-Hinchinbrook areas and part of the north-east Queensland area as defined in this study are included within the boundaries of the Wet Tropics (Fig. 7.6).

The historical sequence shown in Fig. 7.8 is based on the genus *Hadra*. It suggests that the earliest vicariance event was the separation of northern areas (Cape York and part of the Wet Tropics) and southern areas (remainder of Wet Tropics) (Fig. 8.7, a). The southern areas later differentiated into mainland (Kirrama) and island (Hinchinbrook) areas (Fig. 8.7, b), probably as a result of sea level change in the late Tertiary or Quaternary. Cape York Peninsula including the Starcke area then became isolated (Fig. 8.7, c), with events on the Atherton Tablelands, which form the major structural element of the Wet Tropics, occurring later (Fig. 8.7, d).

North-east and mid-east Queensland

Although parts of north-east Queensland have been identified with the Wet Tropics, many of the other areas are closely associated with the Burdekin gap (see below). The range of *Bentosites* includes both north-east and mid-east Queensland indicating that these regions are closely allied.

The Western Ranges area was the first area to be isolated (Fig. 8.8, a). This area is characterised by the presence of *Bentosites zebina* (Brazier), which extends as far inland as Wando Vale (170km from the coast) where its principal habitat is vine thicket. The next area to be isolated was the Cape Hillsborough-Seaforth area (Fig. 8.8, b), followed by the Connors Range, which represents the most southerly extent of *Bentosites* (Fig. 8.8, c). The wide barrier which developed between northern and southern regions (Fig. 8.8, d) may be interpreted as part of the Burdekin gap (Keast, 1961; Galbraith, 1967; Bishop, 1981; Ford, 1982, 1986, 1987a, 1987b) (see below).

The Whitsunday Group then became isolated from the mainland (Fig. 8.8, e). *Bentosites macleayi*, the most primitive species in the genus, is restricted to these islands, which it shares with the more widespread *Bentosites yulei.* The islands are the mountain peaks of a drowned coastline, which resulted from late Tertiary or Quaternary block faulting (Paine, 1972).

Isolation of the Seaview Range (Fig. 8.8, f) was followed by the flooding of the Hinchinbrook Channel, which separated Hinchinbrook Island and the mainland (Fig. 8.8, g), placing this sequence in temporal context with that presented for the Wet Tropics. Differentiation of the Burdekin area (Fig. 8.8, h) preceded separation of the Townsville/Magnetic Island and Palm Group areas, probably due to a rise in sea-level, rather than tectonic processes such as faulting (Fig. 8.8, i).

Bowen and Whitsunday Group

These areas straddle the Burdekin gap and mid-east Queensland (Keast, 1961; Galbraith, 1967; Ford, 1982, 1986, 1987a, 1987b). Bowen and Inkerman fall within the interpretation of the Burdekin gap, while the remaining areas contain well-developed vine forest and are usually placed within the mid-east Queensland rainforest block (Keast, 1961; Cracraft, 1982, 1986; Ford, 1982, 1986, 1987a, 1987b; Joseph, Moritz & Hugall, 1993). *Temporena* is restricted to this area, and species of this genus are the only hadroid camaenids found in the Bowen, Inkerman and Holbourne Island areas. Elsewhere they are sympatric with species of *Bentosites* and with *Varohadra oconnellensis*.

Two biogeographic hypotheses were presented in chapter 7 (Fig. 7.20), which differed principally in their interpretation of vicariance events in the Whitsunday Group of islands. In both hypotheses, the postulated sequence of events implied that northern and southern islands of the Whitsunday Group were separated at different times. In the first hypothesis Holbourne Island was isolated (Fig. 8.9, a), followed by separation of the southern Whitsunday islands and Seaforth areas from the northern regions (Fig. 8.9, b). In the second hypothesis, southern and western areas were differentiated from northern and eastern areas (Fig. 8.9, c) prior to the separation of Holbourne Island (Fig. 8.9, d). The final vicariance event in this sequence separated the Bowen and northern Whitsunday areas (Fig. 8.9, e).

The two hypotheses differed in the placement of Holbourne Island, which is further from the coast than islands of the Whitsunday Group. If inundation of land were the source of vicariance events, then the first hypothesis is plausible, as in the sequence presented Holbourne Island was isolated before any other area. This might be expected as areas closest to the edge of the continental shelf would be the first to be inundated as sea-levels rose during interglacial periods. The second hypothesis proposed that the Holbourne Island, Bowen and the northern Whitsunday areas maintained connections with each other for longer than they did with the other areas. This suggests the initial vicariance event extended along the present coastline, disrupting contact between most of the mainland and southern islands and the Bowen-northern islands-Holbourne Island axis. Extensive block-faulting and tilting during the late Tertiary or Quaternary submerged the mountain range which is now represented by the islands (Paine, 1972), but this did not allow contact to persist between the northern Whitsunday islands and the Bowen area. Movement of the Whitsunday Block would have disrupted the Bowen-northern islands-Holbourne Island axis.

South-east Queensland

The south-east Queensland region extends from Rockhampton and the Parnassus Range to northern New South Wales. Alternative interpretations exclude areas north of Gladstone (e.g. Matthews, 1972, 1974; Cracraft, 1982; Young & McDonald, 1987), but the presence of *Sphaerospira blomfieldi* in the Byfield district and other hadroid camaenids at the Caves extends the region north to Rockhampton and Shoalwater Bay.

The earliest vicariance event in the postulated sequence separated the Queensland border area from the rest of the region (Fig. 8.10, a). A barrier subsequently developed between mid-east and south-east Queensland (Fig. 8.10, b). This barrier coincides with the St Lawrence Gap (see below). Differentiation of the Bulburin area, which is embedded within the larger area of south-east Queensland, followed (Fig. 8.10, c).

Barriers

Modern species of rainforest animals and plants are thought to have originated in the Quaternary as a result of cycles of climate change. Global cooling and associated aridity caused the contraction and fragmentation of rainforests and the isolation of populations of plants and animals within them (Mengel, 1964; Ridpath & Moreau, 1966; Haffer, 1969, 1981, 1982; Avise, 1992; Bermingham *et al*, 1992). Rainforest is believed to have persisted in moist refugia during the glacial periods, although the nature of these refugia (montane or lowland) is disputed (Bush & Colinvaux, 1990).

Distributions of hadroid camaenids suggest that the continuity of large rainforest blocks is not primary and they have been dissected by the development of barriers during the past. Subsequent spreading of rainforest may have obscured some or all of these barriers (Kemp, 1981; Kershaw, 1974, 1978, 1986). Their persistence, and thus the opportunity to identify them, depends on their nature. Avian hybrid zones have been used to determine the position of major barriers, believed to have been expanses of xeric vegetation which developed on lowlands during Quaternary glaciations (Keast, 1961; Galbraith, 1967; Ford, 1982, 1986, 1987a, 1987b). These zones coincide with modern 'dry' regions (e.g. Normanby, Burdekin, St Lawrence gaps), which are dominated by open eucalypt woodland. The assumption that these regions are devoid of rainforest is erroneous, however, as patches persist along rivers and on higher ground. Whether these patches would have remained during arid phases is unknown, but could be determined from fossil pollen analysis.

Although increasing aridity would have dissected rainforest vegetation, the change in climate during the interglacial periods may have had an equally disruptive effect. Rises in sea-level of as only a few metres above present levels would have inundated low-lying coastal areas (such as river flood plains), transforming mountain ranges into islands. Gillison (1987) noted the floristic resemblance between inland vine thickets and littoral forests and postulated that rainforest vegetation migrated westward with the Tertiary marine transgressions, which occurred in areas now considered to be lowland dry corridors. The effects of marine incursions on different taxa would have depended on the nature of both the taxon and the emergent land. For example, small animals with low vagility, such as snails and frogs, would be unable to cross the saltwater barriers and would thus be restricted to the newly-formed islands. Populations of snails, which are primary consumers and detritivores, might be able to persist in areas where populations of frogs might not. Thus relatively small pockets of rainforest within areas such as the Burdekin gap might contain endemic snails, whereas only the largest areas (such as Mt Elliot) would be inhabited by endemic frogs.

Increased rainfall would also have had a significant effect on coastal river systems. Some barriers identified in this study coincide with rivers, such as the Tully River (between the Atherton and Kirrama areas) and the Herbert River (between the Kirrama and Seaview areas). The Herbert River was once part of the Einasleigh River system, connected to the upper reaches of the Burdekin River along the western edge of the coastal plateau (de Keyser *et al*, 1965). Volcanic activity redirected the river eastward, and it began cutting the Herbert River gorge during episodes of uplift in the late Tertiary or early Quaternary. Changes in sea level and further uplift are recorded in a series of knick points and river terraces along the gorge (de Keyser *et al*, 1965).

The effect of freshwater barriers on taxa would have differed from that of marine barriers. Frogs, for example, which would have been confined by saltwater, would have been unaffected by river systems, but snails might still have been restricted.

Two of the three major barriers, which are regarded as significant avian hybridisation zones, are associated with extensive river systems and all are sites of potential marine inundation. The semi-arid Normanby or Torresian barrier runs from Princess Charlotte Bay across the base of eastern Cape York Peninsula (Schodde & Mason, 1980; Schodde, 1982; Ford, 1986, 1987a, 1987b). This barrier coincides with the extensive flood plains of the Normanby, Moorehead, Hann and Kennedy Rivers (Lucas & de Keyser, 1965), and seasonal rains cause these rivers to flood, inundating the surrounding savannah. Quaternary estuarine, alluvial and lacustrine deposits in that area overlie Pliocene sediments (Grimes, 1980; Coventry *et al*, 1980), so the presence of an aquatic barrier at this locality is not an exclusively Holocene phenomenon.

The Burdekin gap, a broad band of xeric vegetation between Townsville and Bowen (Keast, 1961; Galbraith, 1967; Bishop, 1981; Ford, 1982a, 1982b, 1986, 1987a, 1987b; Cracraft, 1986, 1991), constitutes a significant barrier to fauna (Galbraith, 1969; Ford, 1986, 1987a, 1987b). However, several areas investigated in this study covered the region defined as the Burdekin gap (Bowen and parts of North-east Queensland), suggesting the `gap' may thus be composed of two (or more) contemporaneous barriers, which acted together as a single major barrier to vertebrate fauna, but not to hadroid camaenids, and presumably other invertebrates.

The gap roughly coincides with the Burdekin River, which passes through extensive savannah woodlands between the edge of the Great Dividing Range and the coast. The Burdekin now empties into the sea between Ayr and Home Hill, but during the Pleistocene its course was deflected northwards and it also opened into Bowling Green Bay (Hopley, 1970). The Haughton River, which is now separate from the Burdekin, was probably a tributary at that time (Hopley, 1970). The course of the Burdekin was not fixed, and changed several times during the Quaternary (Hopley, 1970).

Pleistocene littoral and estuarine deposits extend inland west of Ayr indicating one or more marine transgressions, which would have isolated patches of higher ground (e.g. Mt Elliot, Kelly's Mount, Stokes Range, Cape Bowling Green) (Hopley, 1970). During the Holocene, fluvial deposition prevented inland migration of the coastline along the northern edge of the Burdekin delta (Bowling Green Bay), but was not as great in the east, allowing the sea to encroach as far west as Ayr and Home Hill. Water levels were 4.5m above present sea level during the Pleistocene pluvials and approximately 37.5m below it during the glacials (Hopley, 1970).

A marine transgression at Edgecumbe Bay may have been the barrier which separated the Bowen area from mid-east Queensland (Fig. 8.6, d). Aquatic sediments up to 60m thick have been recorded from late Tertiary and Quaternary beds along the current edge of the bay (Clarke *et al*, 1971; Paine *et al*, 1974), suggesting that a water barrier existed for a considerable period.

The St Lawrence gap is associated with a series of coastal creeks and rivers, running from the coastal range to a area of swamp at Broad Sound. The boundaries of the mid-east and south-east Queensland areas, which the gap divides, are broadly separated, suggesting that the barrier which developed between them was wide. Although none of the rivers which occur in the gap is as large as the Normanby or Burdekin, the combined effect of at least six rivers from Clairview Creek to Herbert Creek, may have been similar. Sediments on the coastal plain are `moderately extensive' (Malone, 1970: 10), while plains to the west of the mountains are overlain by up to 120m of Tertiary and Quaternary sediments from low-energy regimes, extending to a depth of 1200m in the Duaringa Basin (Malone, 1970).

Dispersal hypotheses

Dispersal hypotheses suggest that ancestors of Australia's land snail fauna entered the continent from Indonesia during the Mesozoic and Tertiary (Solem, 1959, 1992, 1993; Stanisic, 1993). Several waves of invasion were postulated to explain the diversity of the snail fauna (Solem, 1959).

Disperal hypotheses are *ad hoc* narratives (each describes a pattern of dispersal for a single group) so cannot be tested. The biogeographic hypothesis presented in this study show that the distribution of increasingly advanced taxa is not linear, which is contrary to general ideas of centre of origin and dispersal (e.g. Darlington, 1959; Hennig, 1966; Briggs, 1973). The most primitive genus, *Meridolum*, occurs at the southernmost part of the clade's distribution, while the most advanced genera (*Bentosites*, *Temporena*, Gen. nov. A) are found in mid-east and south-east Queensland.

It is likely that the presence of camaenids in Australia and Asia reflects the Gondwanan origin of the land masses, with vicariance explaining the family's distribution rather than dispersal (see above).

Vicariance hypotheses

Previous vicariance hypotheses of eastern Queensland have been restricted to the relationships between the rainforests of Cape York Peninsula, Atherton Tablelands and eastern Queensland (e.g. Cracraft, 1982, 1986, 1991) or those of north-, mid- and south-east Queensland (e.g. Christidis & Schodde, 1991; Joseph, Moritz & Hugall, 1993). This study supported the hypothesis of Joseph, Moritz & Hugall (1993), in which rainforests of north-east Queensland were postulated to have been isolated first by the development of a barrier in the Townsville region, while mid- and south-east Queensland remained in contact for a longer period.

In examining broad-scale area relationships, these previous studies have treated each rainforest block as a homogeneous unit, separated from other units by semi-arid barriers. This study recognised that rainforest blocks were composite, each containing several distinct biogeographic areas (see below). It also included areas which had formerly been treated as barriers (e.g. Burdekin area).

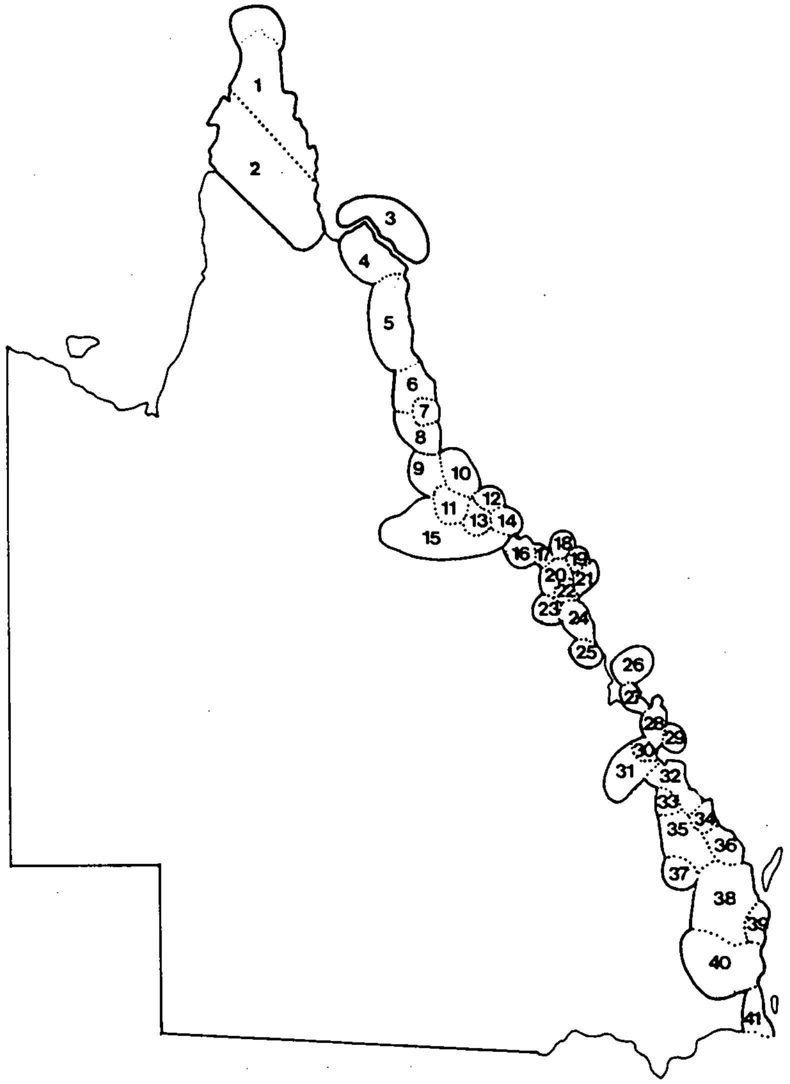


Fig. 8.5: Biogeographical areas defined in this study

1, Torres Strait and NE Cape York Peninsula; 2, SW Cape York Peninsula; 3, continental islands; 4, Cape Melville - Starcke; 5, Cooktown - Mossman; 6, Cairns - Innisfail; 7, Bellenden Ker Range; 8, Innisfail - Tully; 9, Kirrama; 10, Hinchinbrook; 11, Seaview and Paluma Ranges; 12, Palm Group; 13, Townsville; 14, Magnetic Island; 15, Western Ranges; 16, Inkerman; 17, Bowen; 18, Holbourne Island; 19, northern Whitsunday group; 20, Proserpine; 21, southern Whitsunday group; 22, Conway; 23, Eungella; 24, Seaforth - Koumala; 25, Denham Range; 26, Northumberland Islands; 27, Shoalwater Bay; 28, Byfield; 29, Keppel group; 30, Caves District; 31, Mt Morgan; 32, Gladstone; 33, DanDan - Bulburin; 34, Miriam Vale; 35, Monto; 36, Bundaberg; 37, Gayndah - Wondai; 38, Sunshine Coast hinterland; 39, Sunshine Coast; 40, Brisbane - Toowomba; 41, Gold Coast.

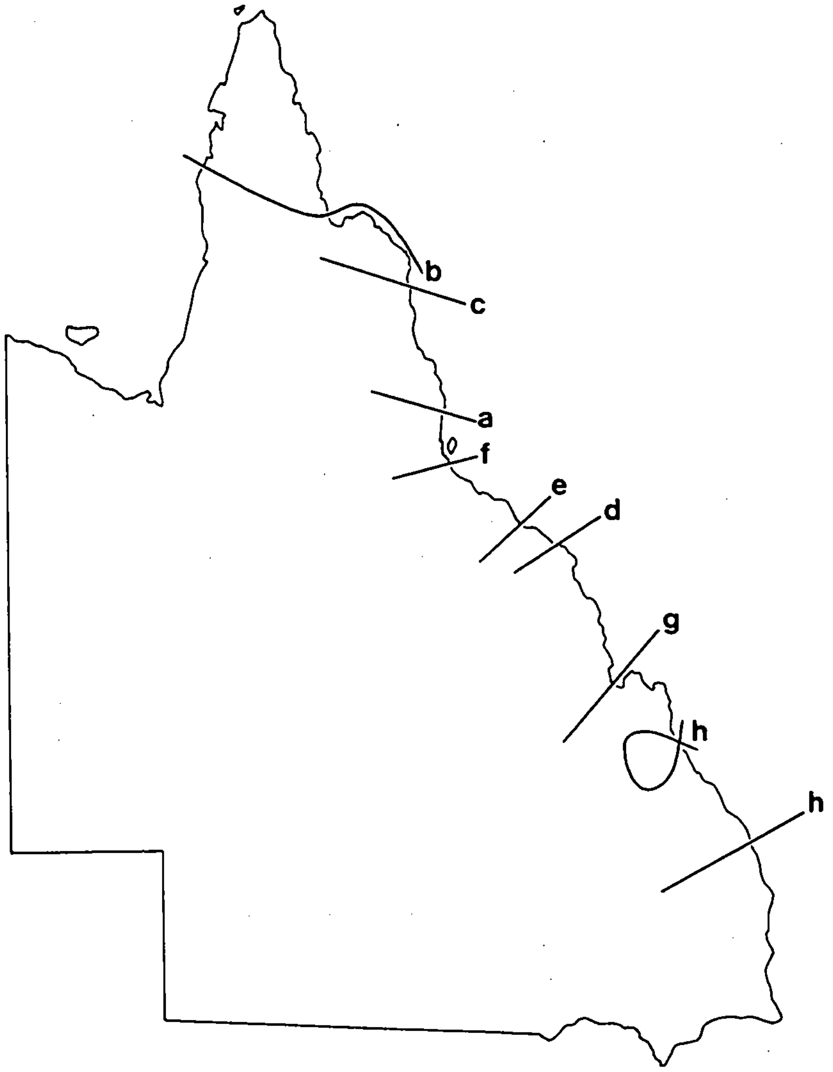


Fig. 8.6: Geographical scenario for eastern Queensland indicated by area cladogram (a-h indicate events discussed in this study).

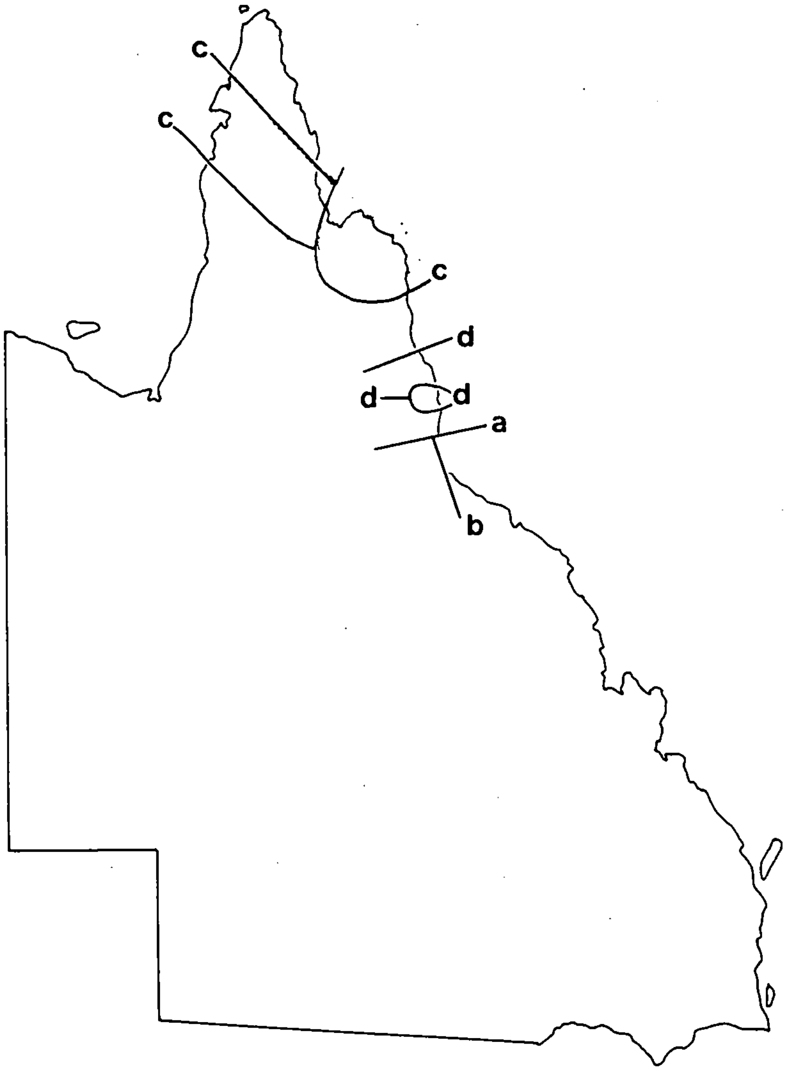


Fig. 8.7: Geographical scenario for Cape York Peninsula and the Wet Tropics indicated by area cladogram (a-d indicate events discussed in this study).

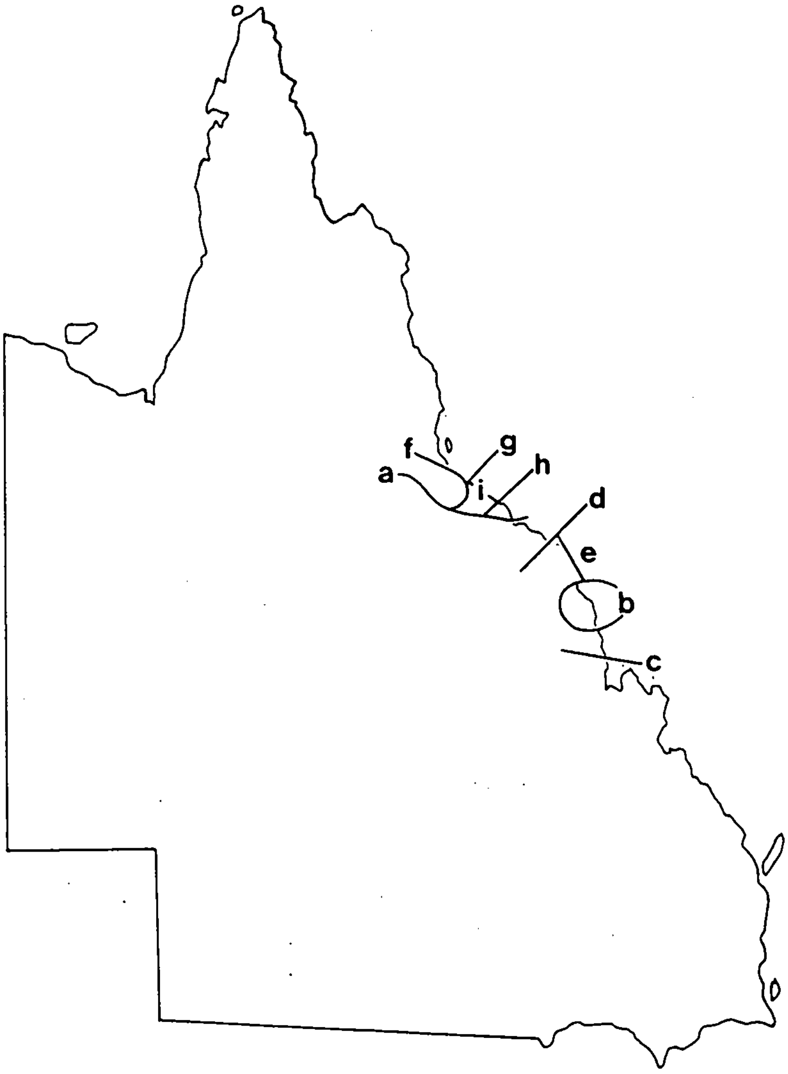


Fig. 8.8: Geographical scenario for north-east and mid-east Queensland indicated by area cladogram (a-i indicate events discussed in this study).

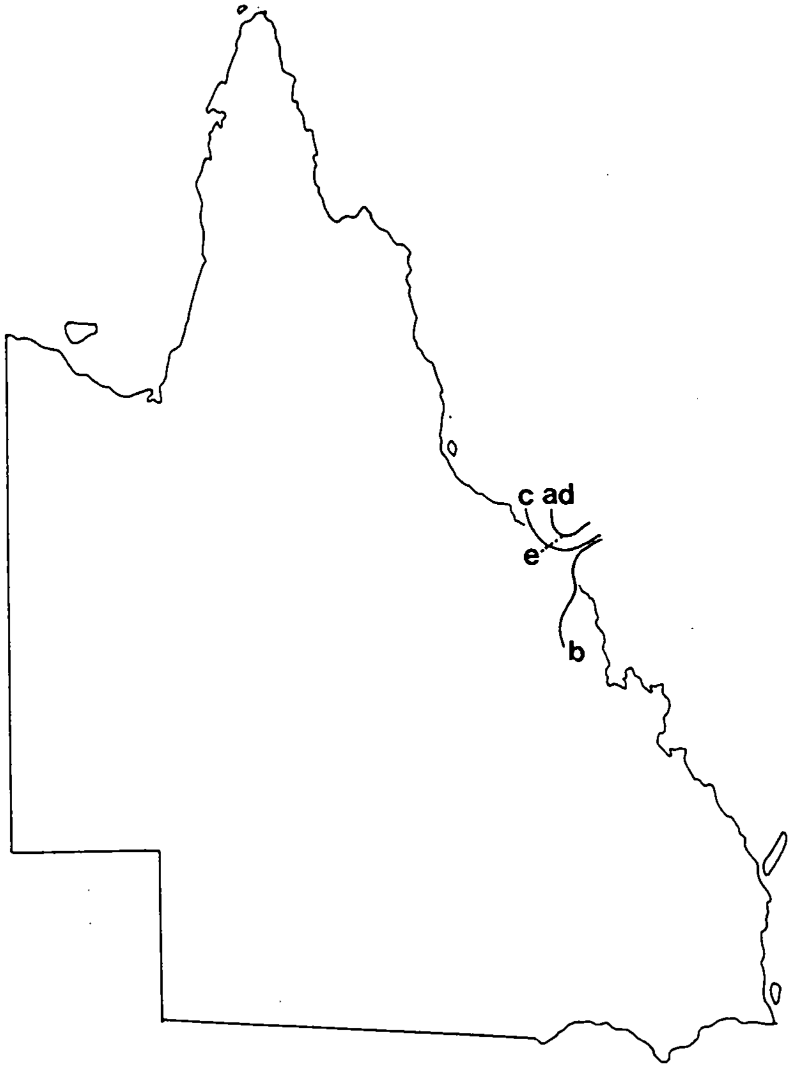


Fig. 8.9: Geographical scenario for Bowen and the Whitsunday group indicated by area cladogram (a-e indicate events discussed in this study).

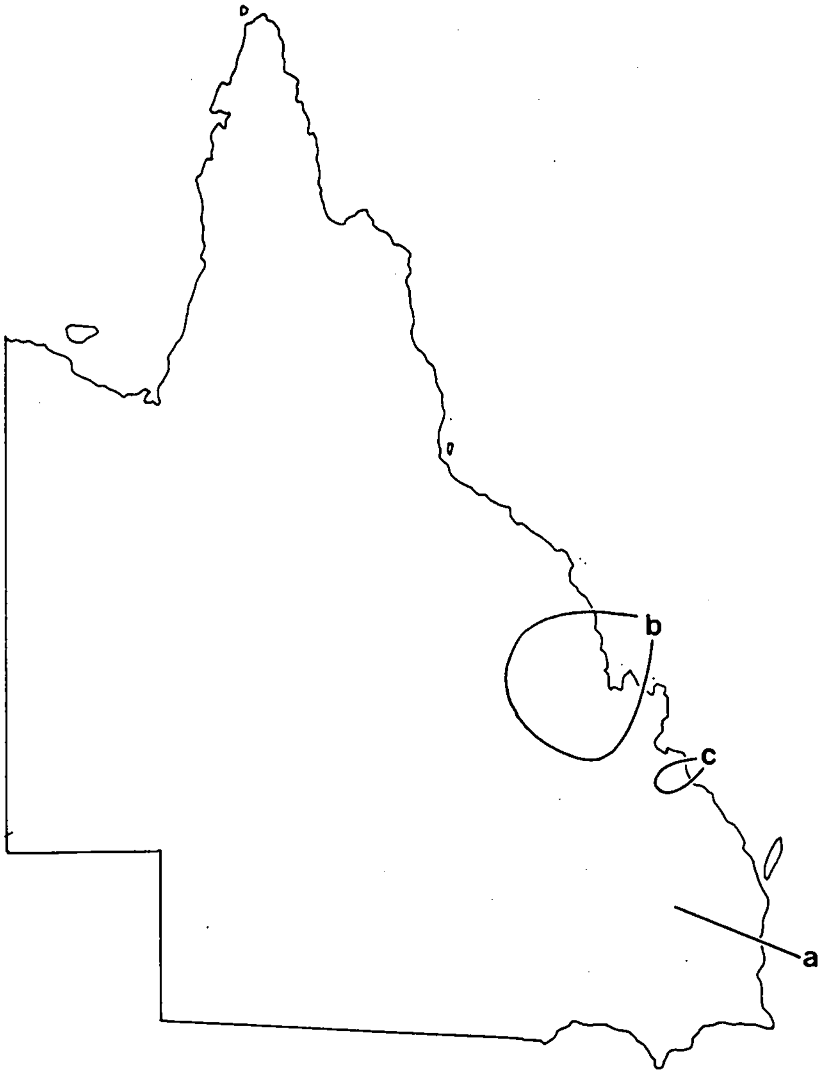


Fig. 8.10: Geographical scenario for south-east Queensland indicated by area cladogram (a-c indicate events discussed in this study).

Principal conclusions of this study

1. Camaenidae is a polyphyletic family, which can be separated into American and Australasian components.

2. Bradybaenidae is sister group to the Australasian Camaenidae.

3. Australasian Camaenidae has a Gondwanan origin.

4. South-east Asian terranes rifted from Australia later than current palaeogeographical hypotheses predict.

5. The headwart of Australasian Camaenidae is homologous to the bradybaenid headwart.

6. The camaenid headwart may not secrete pheromones, but may be important in determining day-length.

7. The hadroid camaenids form a coherent group, the phylogeny of which can be represented by cladistic analysis of conchological and anatomical data.

8. Species-specific genital morphology is not the result of reproductive character displacement.

9. Multiple mating may result in spermatophore displacement.

10. Eastern Queensland is composed of at least 41 distinct biogeographical areas.

11. The sequence of vicariance events in eastern Queensland may be determined by cladistic analysis of hadroid camaenid genera.

12. Major biogeographic barriers may be the result of marine transgressions or pluvial inundation.

All conclusions in this thesis are presented as hypotheses, which are available for testing. Phylogenetic hypotheses (1, 2, 7) are constructed on conchological and anatomical data and can be tested with molecular data. Biogeographical hypotheses (3, 4, 10, 11, 12) may be tested with cladistic analyses of other taxa, while the nature of biogeographic barriers (10) may be examined with palynological data. Hypotheses on the function of the headwart (5, 6) and the mechanics of copulation (8, 9) may be tested experimentally.

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Appendix 1
MATERIAL EXAMINED

***Hadra bipartita* (Férussac)**
Type material: *blighi* (holotype): Restoration Island, Queensland, Australian Museum, C100632; *webbi incallida* (holotype): adult shell, Atherton Tableland, Queensland, Australian Museum, C100633.

Other material: New Guinea: 4 dead adults (MV). North East Australia: 3 dead adults (MV); 2 dead adults, islands off coast (MV). Queensland: 8 dead adults (MV); 3 dead adults (MV); 2 dead adults (MV); 1 dead adult, 1 dead juvenile, 26.viii.1872 (MV); 2 dead adults, 26.viii.1872 (MV). North Queensland: 3 dead adults (MV); 3 dead adults (MV); 1 dead adult (MV); 2 dead adults (MV); 4 dead adults (MV). Torres Strait: 3 dead adults, ii.1874; 1 dead adult, islands near Cape York (MV); 2 dead adults, Cape York islands, 1.xi.1886 (MV); 4 dead adults, islands near Cape York, Cox Collection (AM C106684). Mount Cornwallis Island (9^{0}25'S, 142^{0}31'E): 3 dead adults (MV). Ugar (Stephens) Island (9^{0}30'S, 143^{0}33'E) and Bet Island (10^{0}9'S, 142^{0}49'E): 12 dead adults (AM C106685). Erub (Darnley) Island (9^{0}35'S, 143^{0}46'E): 2 dead adults, iii.1928 (MV). Massid (Yorke) Island (9^{0}44'S, 143^{0}26'E): 7 dead adults, 14 dead juveniles, in scrub bordering airstrip, 7.vii.1976 (AM C105224). Tudu (Warrior) Island (9^{0}48'S, 142^{0}57'E): 1 dead adult (AM C17945). Yam (Turtle-backed) Island (9^{0}54'S, 142^{0}46'E): 2 dead adults, iii.1928 (MV); 2 dead adults, iii.1928 (MV); 2 dead adults, iii.1928 (MV); 3 dead adults, 14 dead juveniles, in forest and rainforest behind village and airstrip, 7.vii.1976 (AM C105227). Murray Islands: 4 dead adults, 1 dead juvenile (MV F13555); 1 dead adult, ix.1927 (MV); 2 dead adults, iii.1928 (MV); 2 dead adults, iii.1928 (MV); 8 dead adults, iii.1928 (MV); 2 dead adults (MV); 1 dead adult, 2.ix.1945 (MV); 2 dead adults, 2.ix.1945 (AM C106688); 1 dead adult (AM C106750); 12 dead adults, numerous dead juveniles (AM C106677). Mobiag (Jervis) Island (9^{0}58'S, 142^{0}11'E): 3 dead adults, iii.1928 (MV). Moa (Banks) Island (10^{0}11'S, 142^{0}16'E): 2 dead adults, 2.vi.1969 (MV); 2 dead adults, (AM C106630). Cape York: 7 dead adults (MV); 2 dead adults, rainforest litte (MV); 2 dead adults (MV); 1 dead adult (MV); 1 dead adult (MV); 4 dead adults, xi.1873 (MV F4819); 1 dead adult, 2 dead juveniles (MV); 2 dead adults, 1.xi.1886 (MV); 2 dead adults, rainforest litter, 1944 (MV); 1 dead adult (MV F9728); 1 dead adult (MV F1035); 2 dead adults (MV); 2 dead adults (MV); 1 dead adult, 1 dead juvenile, 1954 (MV F18371); 2 dead adults (AM C17641); 4 dead adults (AM C106627). Gulf of Carpentaria: 1 dead adult, ii.1928 (MV). Somerset (10^{0}44'S, 142^{0}36'E): 3 dead adults, 1 dead juvenile, Blackwater Creek, rainforest, 9-12.vii.1976 (AM C105427). Bamaga (10^{0}53'S, 142^{0}24'E): 1 dead adult, 1966 (AM C117633). Cairncross Island (11^{0}14'S, 142^{0}55'E): 3 dead adults (AM C17646); 4 dead adults (AM C106699). Heathlands Homestead (11^{0}45'S, 142^{0}35'E): 1 dead adult, 20km north east of Heathlands Homestead on road to Captain Billy Beach, in log in rainforest, 13.vii.1980 (AM C122963). Pig Island

(11^{0}50'S, 143^{0}29'E): 2 dead adults, north end of Great Barrier Reef, in leaf litter in fig forest, 19.i.1973 (AM C90363). Weipa (12^{0}40'S, 141^{0}50'E): 9 dead juveniles, 50 miles south east of Weipa, York Downs Homestead, 12.vii.1980 (AM C122995). Iron Range (12^{0}44'S, 143^{0}17'E): 1 dead adult, 18 miles from Portland Roads, Weymouth Bay (AM). Claudie River (12^{0}46'S, 143^{0}17'E): 1 dead adult, 1940 (MV); 1 dead juvenile (MV); 6 dead adults, under logs and debris, xi-ii.1913-1914 (MV); 2 dead adults, i.1913 (MV); 3 dead adults, 2 dead juveniles (MV); 1 dead adult (MV). Leo Creek (13^{0}33'S, 143^{0}27'E): 2 dead adults, rainforest floor, marginal scrub, 14.x.1958 (AM C106623). Chester River (13^{0}40'S, 143^{0}29'E): 1 dead adult, 8.x.1958 (AM C106629). Coen (13^{0}52'S, 143^{0}12'E): 6 dead adults, 1922 (MV); 1 dead adult, Rocky River, in jungle, ii.1922 (MV); 2 dead adults, Rocky River camp, Cape York Expedition, 20.vi.1960 (AM C106628); 8 live juveniles, Rocky Creek (MV F23301). Flinders Island (14^{0}10'S, 144^{0}15'E): 2 dead adults, west side, open sclerophyll, 20.xii.1981 (AM C132734). Nymph Island (14^{0}39'S, 145^{0}15'E): 2 dead adults, 1 dead juvenile, 12.xii.1974 (AM C99327). Lizard Island (14^{0}40'S, 145^{0}28'E): 2 dead adults, 1861 (MV); 4 live adults, station 5, Lizard Island Expedition, iii.1975 (MV); 14 live adults, 1 live juvenile, station 3, Lizard Island Expedition, ii.1975 (MV); 1 dead adult, station 27, Lizard Island Expedition, 10.xiii.1975 (MV); 2 dead adults (MV); 2 dead adults (MV); 2 dead adults, 1 dead juvenile (MV F14351); 18 dead adults, 1 dead juvenile, south side of west point, in small patch of coastal scrub and grass, 1.xii.1974 (AM C99357). Hopevale (15^{0}18'S, 145^{0}07'E): 1 dead adult, 34 miles north of Cooktown, Lutheran Mission, 21.vi.1951 (AM). Cooktown (15^{0}30'S, 145^{0}16'E): 4 live adults, 200yds from river mouth, xii.1973 (MV); 1 dead adult (MV); 5 dead adults (MV); 2 dead adults, domestic gardens around rock edges, ii.1975 (MV); 1 dead adult (AM C1914); 1 dead adult (AM C5752). Home Rule (15^{0}44'S, 145^{0}18'E): 1 live juvenile (MV). Bloomfield River (15^{0}55'S, 145^{0}21'E): 8 dead adults, 9 dead juveniles, Ayton, 1976 (AM C104452). Donovan Creek (16^{0}00'55"S, 145^{0}26'40"E), rainforest, i.1989 (MTQ MO17468). Tachalbadger Creek (16^{0}01'40"S, 145^{0}26'50"E): 2 live juveniles, rainforest, 24.i.1989) (MTQ MO17466). Cape Tribulation (16^{0}05'S, 145^{0}29'E): 1 dead adult (MV). Alexandra Bay (16^{0}12'S, 145^{0}28'E): 2 dead adults, Inch Rock, 10.ii.1984 (AM C142972). Mount Alexandra (16^{0}15'S, 145^{0}28'E): 2 dead adults (AM C106661). Daintree (16^{0}15'S, 145^{0}19'E): 1 dead adult, Daintree River, in swamp at punt landing, 19.x.1987 (AM C110192). Wonga Beach (16^{0}28'S, 145^{0}23'E): 1 live adult, in scrub near beach, 20.x.1973 (MV); 1 live adult, near beach in scrub, 20.x.1973; 6 dead adults (MV); 3 dead adults, under palm leaves (MV); 15 dead adults, under palm leaves, 1976 (MV); 1 dead adult, 20.x.1973 (MV); 2 dead adults, 1 dead juvenile, under palm leaves on edge of beach, 1966 (AM). Mossman Gorge (16^{0}26'S, 145^{0}16'E): 1 dead adult, 20.x.1973 (MV):1 live adult, rainforest, on trees, 26.i.1989 (MTQ MO17467). Mossman (16^{0}21'S, 145^{0}15'E): 1 dead adult (MV); 8 dead adults, scrub (MV); 1 dead adult, rubbish tip near sugar mill, 25.vii.1972 (MV); 2 dead adults, 2 dead juveniles, rubbish tip near sugar mill, 25.vii.1972 (MV); 1 dead adult, scrub and leaf litter, 1980 (MV); 1 dead adult, sugar mill (MV); 1 dead adult (MV); 4 dead adults, 1 dead juvenile, beside sugar mill in scrubland, 17.x.1973 (MV). Windsor Tableland (16^{0}15'S, 145^{0}2'E): 3 dead adults, dry rainforest, 18.vii.1977 (MV). Port Douglas (16^{0}30'S, 145^{0}30'E): 5 dead adults, 1891 (MV). Kuranda (16^{0}49'S, 145^{0}38'E):

1 dead adult (MV); 1 dead adult, 6.x.1928 (MV). Cairns (16^{0}57'S, 145^{0}45'E): 1 dead adult (MV); 4 dead adults (MV); 1 dead adult (AM C8176); 1 dead adult, Lake Placid, 2.i.1959 (AM C106669); 2 dead adults, Edge Hill Scrub, under logs and damp bark on ground, x.1908 (AM C106658). Tinaroo (17^{0}10'S, 145^{0}33'E): 1 dead adult, Barron River (MV); 1 dead adult, under logs in jungle, xi.1908 (MV); 2 dead adults (MV); 1 dead adult, under logs in jungle xi.1908 (MV); 2 dead adults, 1908 (MV); 1 dead adult, 4.xi.1908 (MV); 7 dead adults (MV F1471); 2 dead adults, 1 dead juvenile, under logs on land cleared in 1899, xi.1908 (MV); 3 dead adults (MV F3019); 6 dead adults (MV F1469); 4 dead adults (MV); 6+ dead juveniles, xi.1908 (MV); 10+ dead juveniles (MV); 6 dead adults (MV F1470); 3 dead adults, Barron River (AM C106663). Lake Eacham (17^{0}17'S, 145^{0}37'E): 4 dead adults, 18.ix.1949 (AM C106668); 2 dead adults, Eacham Scrub (MV F14350). Lake Barrine (17^{0}15'S, 145^{0}38'E): 1 dead adult, 15.i.1977 (MV); 1 dead adult, in rainforest, 31.iii.1943 (AM C106681). Yungaburra (17^{0}16'S, 145^{0}35'E): 1 dead adult (MV); 6 dead adults (AM C106672); 4 dead adults, 1 dead juvenile (MV); 8 dead adults (MV F14347). Tolga (17^{0}13'S, 145^{0}29'E): 1 dead adult, under rubbish, 1976 (MV); 1 dead adult, under leaf litter (MV); 10 dead adults, under leaf litter, 1976 (MV); 4 dead juveniles, 30.x.1908 (MV F4873). Peeramon (17^{0}19'S, 145^{0}37'E): 1 live adult, 3 miles south of Peeramon, rainforest next to road, xi.1973 (MV). Atherton (17^{0}17'S, 145^{0}30'E): 1 dead adult (MV F6689). Wongabel State Forest (17^{0}16'S, 145^{0}28'E): 10 dead adults, 6 miles south of Atherton on Ravenshoe road, 14.vii.1964 (MV); 5 dead adults, 1 dead juvenile, 5 miles south of Atherton, iii.1959 (AM C106670). Bellenden Ker (17^{0}16'S, 145^{0}51'E): 1 live juvenile, Josephine Falls, on rock at night, 30.i.1988 (MTQ MO17388); 1 dead adult, top of Bartle Frere, 5287' (AM C106659); 1 dead adult, Josephine Falls, rainforest along track, 4.vi.1977 (AM C110200); 5 dead adults, Bellenden Ker Range (AM C76640). Innisfail (17^{0}33'S, 146^{0}5'E): 1 dead adult, municipal garden (MV F19784); 4 dead adults (MV); 1 dead adult, Johnstone River, Hawkins Creek, xi.1908 (MV); 2 dead adults, 3 dead juveniles, Coquette Point, forest floor under leaf mould, ii.1976 (MV); 6 dead adults (MV); 3 dead adults, xii.1959 (AM C106676). Babinda (17^{0}20'S, 145^{0}56'E): 1 dead adult, 1963 (AM C10660). Eubenangee (17^{0}27'S, 145^{0}58'E): 1 dead adult (MV F6688). Etty Bay (17^{0}34'S, 146^{0}5'E): 1 live juvenile, in garden of Natural History Museum, 31.i.1988 (MTQ MO17335). Tully (17^{0}56'S, 145^{0}56'E): 1 live juvenile, west of Tully, Jarrah Creek, 40-60m altitude, rainforest, under logs, 29.x.1988 (MTQ MO17465); 1 dead adult, 1 dead juvenile, 3.9km from Tully on Tully-Cardstone road, in mesophyll-*Pandanus*-vine forest, under logs, 2.vi.1977 (AM C110182). Kurrimine Beach (17^{0}47'S, 146^{0}06'E): 2 dead juveniles (MV); 1 dead adult, scrub in rainforest area under dead leaves, v.1978 (AM C110172); 2 live adults, 1 live juvenile, Kurrimine Beach Environmental Park, 24.ix.1988 (MTQ MO17470). Purtaboi Island (17^{0}57'S, 146^{0}09'E): 3 dead adults, 1 dead juvenile, 1955 (AM C106642).

***Hadra dunkiensis* (Forbes)**

Type material: *cadmus* (holotype): Goold Island, Queensland, Australian Museum C100664; *coxenae* (holotype): Johnson River, Queensland, Australian Museum C17634; *helga* (holotype): Hinchinbrook Island, Queensland, Australian Museum

C54464; *nicomede* (holotype): Cardwell, Queensland, Australian Museum C3515; *portus* (holotype): Port Douglas, Queensland, Australian Museum C100658.

Other material: Mt Carbine (16^{0}30'S, 145^{0}09'E): live, rocky outcrop *c.* 2.5km NE of Mt Carbine, remnant vine thicket (QM MO20697). Dunk Island (17^{0}55'S, 146^{0}10'E): 29 dead adults, viii.1977 (QM MO6926). Ingham (18^{0}39'S, 146^{0}10'E): 1 dead adult, 1 dead juvenile, Cardwell Range lookout, *ca.* 12km N of Ingham on Ingham - Cardwell road, rainforest/woodland, in cleared area, on ground and under rubbish, 15.x.1981 (QM MO11867).

Hadra barneyi **(Cox)**

Type material: *barneyi* (syntypes): 2 adult shells, off Cape Sidmouth, Claremont Group, Number 6 island (13^{0}50'S, 143^{0}42'E). Australian Museum, C55512.

Other material: Queensland: 2 dead adults (AM C17628). Torres Strait: 3 dead adults, island (AM C11729). Barney Island (10^{0}13'S, 142^{0}10'E): 6 dead adults, 1 dead juvenile (AM C106724). Cape York: 1 dead adult, rainforest, in forest debris, 1944 (MV F14467); 1 dead adult, ?main telegraph station (AM C106749). Bamaga (10^{0}53'S, 142^{0}50'E): 1 dead adult, v.1958 (MV F13552). Mapoon (11^{0}58'S, 141^{0}53'E): 1 dead adult (AM C106750). Weipa (12^{0}40'S, 141^{0}50'E): 4 dead adults, under bark, 1987 (MV); 3 dead adults, under bark, 1983 (MV); 1 dead adult, under logs in scrub (AM C106748); 3 dead adults, 9 dead juveniles, near junction of Hayes and Mission Rivers, "rainforest" on coast between administration area and townsite, near mangroves in soil beneath fallen logs, 17.vii.1972 (AM C88682). Batavia River (12^{0}40'S, 142^{0}40'E): 1 dead adult, headwaters, Wenlock (AM C106746); 1 dead adult (AM C10630); 1 dead adult, (AM C6650); 3 dead adults, 1 dead juvenile, Wenlock Downs (AM C106745); 3 dead adults, 2 dead juveniles (AM C10630). Archer River (13^{0}24'S, 142^{0}53'E): many dead juveniles, 2 miles south of Archer River, Cape York Expedition, 27.vi.1960 (AM C106743). Coen (13°52'S, 143^{0}12'E): 10 dead adults, 6 dead juveniles, *ca.* 56.5km N of Coen on Peninsula road, rocky outcrop/remnant vine thicket, under rocks, 16.ix.1988 (QM MO21300); 1 live adult, 2 live juveniles, *c.* 17km N of Coen on Peninsula Road, remnant vine thicket, under logs, 16.ix.1988 (QM MO21292); 2 dead adults, in forest, 1922 (MV); 1 dead adult (AM C106747); 4 dead juveniles, 10 miles east of Coen, Cape York Expedition, 21.vi.1960 (AM);4 dead juveniles, 16km east of Coen, 21.vi.1960 (AM); 3 dead juveniles, Silver Plains, Cape York Expedition, 23.vi.1960 (AM). Lankelly Creek (13^{0}54'S, 143^{0}14'E): 3 live adults, Lankelly Creek camp, NE of Coen, 21.viii.1977 (QM MO20988). Upper Massey Creek (13^{0}54'S, 143^{0}24'E): 2 live adults, NE of Coen, 18.viii.1977 (QM MO20987). Ebagoolah (14^{0}15'S, 143^{0}12'E): 1 dead adult (AM C106744).

Hadra bellendenkerensis **(Brazier)**

Type material: *beddomae* (holotype): adult shell, Cardwell range, 20 miles north west of Cardwell, in range, Rockingham Bay, 3500ft, Australian Museum, C17632;

bellendenkerensis (holotype): adult shell, Mount Bellenden Ker, *circa* 25 miles south of Cairns, Australian Museum, C17631; *castanea* (syntypes): adult shell, Queensland, collected by Dr Mjoberg, 1913, Australian Museum, C41901; *humoricola* (holotype): adult shell, Innisfail, Queensland, Australian Museum, C100630; *humoricola* (paratypes): 3 adult shells, Geraldton (= Innisfail), in dense scrub, under logs, collected by Sidney Jackson, 1908, Australian Museum, C106798; *pterinus* (holotype): adult shell, Lake Barrine, 25 miles SW of Cairns, Queensland, Queensland Museum, MO1769;

Other material: Endeavour River (15^{0}27'S, 145^{0}14'E): 1 dead adult (AM C106759). Home Rule (15^{0}44'S, 145^{0}18'E): 1 live juvenile, Mt Hedley, in closed forest, QNPWS, 13.xi.1974 (MV). Thornton Peak (16^{0}10'S, 145^{0}23'E): 1 live juvenile, 7.xi.1975 (MV). Daintree River (16^{0}15'S, 145^{0}19'E): 2 dead adults, 25 miles north of Mossman, x.1958 (AM 106772). Mt Alexander (16^{0}15'S, 145^{0}28'E): 1 dead adult (AM C106797). Kuranda (16^{0}49'E, 145^{0}38'S): 2 dead adults, 1 dead juvenile (AM C106755). Cairns (16^{0}57'S 145^{0}45'E): 2 dead adults (MV); 1 dead adult, 1891 (AM C106761); 1 dead adult, 1 dead juvenile, back of Carrington (AM C106762); 2 dead adults, inland from Cairns, i.1914 (AM C106754). Tinaroo (17^{0}10'S, 145^{0}33'E): 3 dead adults, 3 dead juveniles, under bark on ground in damp places, xi.1908 (AM C106757); 5 dead adults (MV F4832); 1 dead adult, SW of Cairns (AM C106756). Lake Eacham (17^{0}17'S, 145^{0}37'E): 1 dead adult (AM). The Crater (17^{0}26'S, 145^{0}19'E): 1 dead adult, under log, 1976 (MV). Yungaburra (17^{0}16'S, 145^{0}33'E): 6 dead adults, 1 dead juvenile (MV F14348); 4 dead adults (AM C106764). Tolga (17^{0}13'S, 145^{0}29'E): 1 dead adult, under log, 1976 (MV). Atherton (17^{0}17'S, 145^{0}30'E): 1 dead adult, Atherton High School, v.1965 (AM C106760). Wongabel State Forest (17^{0}19'S, 145^{0}31'E): 1 dead adult, 5 miles south of Atherton, iii.1959 (AM C106758). Little Mulgrave Scrub (17^{0}09'S, 145^{0}43'E): 2 dead adults, near Gordonvale (AM C76588). Mulgrave River (17^{0}10'S, 145^{0}53'E): 2 dead adults (AM C106795); 7 dead adults, 7 dead juveniles (AM C106774); 2 dead adults (AM C106752). Bellenden Ker (17^{0}16'S, 146^{0}5'E): 4 dead adults (SAM TD8401); 1 dead adult, 25 miles south of Cairns (AM C106753); 1 live juvenile, Broken Nose track, lower slopes, in litter, 30.i.1988 (MTQ MO17472). Babinda (17^{0}20'S, 145^{0}56'E): 1 dead adult, 1964 (AM C106796). Innisfail (17^{0}33'S, 146^{0}5'E): 2 dead adults, 4 others damaged (MV F1485); 2 dead adults (AM 106763); 1 dead adult, 2 dead juveniles, 14 miles south of Geraldton (= Innisfail), in dense scrub, xii.1908 (AM C106773). Herberton Range (17^{0}31'S, 145^{0}28'E): 1 dead juvenile, Evelyn Scrub, 4000', very scarce, 17.xi.1908 (MV F4831). Major Mountains (17^{0}31'S, 145^{0}28'E): 1 live adult, 1 live juvenile, southern slopes, Vine Creek, 27.x.1988 (MTQ MO17471). Tully (17^{0}56'S, 145^{0}56'E): 1 live adult, 1 live juvenile, west of Tully, Jarrah Creek, 40-60m altitude, rainforest, under logs, 29.x.1988 (MTQ MO17473). Mission Beach (17^{0}52'S, 146^{0}06'E): 1 dead adult, 10 miles from Mission Beach, under log on fern and sand (MV). Mt Pershouse (18^{0}14'6"S 145^{0}47'50"E): 1 live adult, under log (MTQ MO17460).

***Hadra rudis* (Hedley)**
Type material: *rudis* (syntypes): 2 adult shells, Tinaroo scrubs, SW of Cairns, Australian Museum, C106802.

Other material: Mt Bellenden Ker (17^{0}16'S, 145^{0}51'E): 1 live adult (QM MO11277); 1 dead adult (MTQ). Lake Eacham (17^{0}17'S, 145^{0}37'E): 1 dead adult (QM MO6915). Palmerston NP (17^{0}37'S, 145^{0}47'E): 1 dead adult (MTQ).

***Sphaerospira fraseri* (Griffith & Pidgeon)**
Type material: *fraseri feriarum* (holotype): adult shell, Stradbroke Island, Queensland, Australian Museum, C45024; *fraseri flavescens* (holotype): adult shell, Currumbin Creek, Queensland, Australian Museum C100634; *fraseri permuta* (holotype): adult shell, Clarence River, New South Wales, Australian Museum, C106830; *parallela* (holotype): adult shell, North Pine River, Blackall Range, Queensland, Australian Museum, C100645.

Other material: Bunya Mountains (26^{0}51'S, 151^{0}35'E): 2 live adults, 1 live juvenile, 4-5.xii.1960 (AM). Palmwoods (26^{0}41'S, 152^{0}58'E): 1 live adult, in garden, 25.x.1972 (QM MO5711). Yarraman State Forest (27^{0}00'S, 152^{0}00'E): 2 live adults, 2 live juveniles (AM). Moreton Island (27^{0}15'S, 152^{0}00'E): 1 live adult, 0.5 miles from Tangalooma, very dry scrubby wallum, under log, iii.1972 (QM MO5703). Mt Glorious (27^{0}20'S, 152^{0}46'E): 1 live adult, 0.75 mile NW of Mt Glorious café, under palm frond in rainforest, 28.x.1970, (QM MO4336); 1 live adult, 3 miles NW of Mt Glorious café, under palm in forest, 28. x.1970 (QM MO4336); 1 dead adult, 1987 (QM MO19300); 6 live adults, 1 live juvenile, 3-4.ii.1961 (AM). Mt Nebo (27^{0}24'S, 152^{0}47'E): 2 live adults, Boombana National Park, 7.x.1976 (QM MO23557); 1 live adult, *ca.* 4 miles SE of Mt Nebo, under log on ground *Araucaria* notophyll vine forest, 15.x.1975 (AM). Brookfield (27^{0}30'S, 152^{0}55'E): 1 live adult, dry sclerophyll forest, 12.ii.1972 (QM MO5704). Stradbroke Island (27^{0}30'S, 153^{0}24'E): 1 live adult, Dunwich, under bark on tree, vi.1971 (AM). Goat Island (27^{0}31'S, 153^{0}23'E): live adults, in rotting tree trunk, x.1971 (AM C83687). Toowoomba (27^{0}34'S, 151^{0}57'E): 1 dead juvenile, Redwood Park, vine thicket, pitta anvil, 23.x.1983 (QM MO13997); 2 dead adults (SAM TD8373). Mt Flinders (27^{0}49'S, 152^{0}49'E): 1 live adult, Mt Flinders foothills, dry sclerophyll forest, under piece of wood on bank of creek, 22.x.1971 (QM MO5707). Whian Whian State Forest (28^{0}36'S, 153^{0}22'E): 1 live adult, rainforest, 5-6.x.1975 (AM). New England: 1 live adult, 25.v.1973 (AM).

***Sphaerospira blomfieldi* (Cox)**
Type material: *blomfieldi* (syntypes): 2 adult shells, Port Curtis, Miriam Vale, Cox Collection, Australian Museum C106782; *blomfieldi latior* (holotype): adult shell, Mary River, Queensland, Australian Museum, C100641; *mortenseni* (holotype): adult shell, Parnassus Range, north of Byfield, Queensland, Australian Museum C57807;

Other material: Parnassus Range (22^{0}49'S, 150^{0}35'E): 3 live adults, 3 live juveniles, upper reaches of Nob Creek road, low notophyll vine forest, under logs, 12.v.1988 (QM MO19682). Gavial Creek (23^{0}25'S, 150^{0}32'E): 1 live adult, mesophyll vine forest, among rocks, 10.v.1988 (QM MO19868). Bouldercombe Creek (23^{0}34'S, 150^{0}28'E): 3 dead adults, Mt Usher, *ca.* 2km SW of Bouldercombe, rainforest, among leaf litter, 28.vi.1982 (QM MO12851). Raglan (23^{0}43'S, 150^{0}49'E): 10 live adults, in hollow logs, 15.xi.1981 (QM MO11480). Ulam Range (23^{0}53'S, 150^{0}37'E): 1 dead adult, 9 miles NE of Mt Morgan, in rotten log (QM MO4165). Mt Morgan (15^{0}04'S, 150^{0}44'E): 1 live adult, *ca.* 7km E of Mt Morgan, microphyll vine thicket, under logs, 10.v.1988 (QM MO19769); 6 dead adults, 3 dead juveniles, *ca.* 7km E of Mt Morgan, notophyll vine forest, on ground, 11.vii.1980 (QM MO8266). Mt Moore (24^{0}02'S, 151^{0}05'E): 18 dead adults, west side, in patch of scrub, in vine thicket, 5.ix.1982 (QM MO13210). Miriam Vale (24^{0}20'S, 151^{0}34'E): 1 dead adult, under log (MV); 20 dead adults, under log (MV); 3 dead adults (MV). Kroombit Tops (24^{0}22'S, 151^{0}03'E): 5 dead adults, 1 dead juvenile, 9-10.xii.1983 (QM MO15028). Colosseum Creek (24^{0}23'S, 151^{0}27'E): 5 dead adults, rainforest along creek, 6.x.1982 (QM MO13267); 7 dead adults, under logs and rubbish, riverine rainforest, *C. australe*, 14.x.1981 (QM MO11857). Mt Colosseum (24^{0}25'S, 151^{0}35'E): 2 dead adults, rainforest, under rotten logs, 6.vii.1982 (QM MO12861). Blackman's Creek (24^{0}26'S, 151^{0}25'E): 1 dead adult, 5.ix.1982 (QM MO13187). Dawe's Range (24^{0}28'S, 151^{0}07'S): 2 dead adults, 1 dead juvenile, mesophyll vine forest/*Araucaria*, 4.ix.1982 (QM MO12639). Granite Creek (24^{0}31'S, 151^{0}30'E): 1 live adult, west of rest area, off Bruce Highway, 26.ix.1983 (QM MO14006); 3 dead adults, beside creek bed, 7.xii.1983 (QM MO14673). Builyan (24^{0}32'S, 151^{0}23'E): 8 dead adults, 1 dead juvenile, *ca.* 1.8km E of Builyan Railway Station, on Builyan - Gladstone road, next to river bank, rainforest, between rocks, 15.vii.1980 (QM MO10315). Ban Ban Springs (24^{0}41'S, 151^{0}51'E): 3 dead adults, *ca.* 2.8km E of Ban Ban Springs on Ban Ban - Biggenden road, remnant bottle tree low mesophyll vine forest, litter, 16.vii.1980 (QM MO11152). Kalpowar State Forest (24^{0}42'S, 151^{0}21'E): 2 dead adults, Mt Fort William, notophyll vine forest, 4.ix.1982 (QM MO12604); 2 dead adults, rainforest walk, mesophyll vine forest/*Araucaria*, 4.ix.1982 (QM MO12584); 4 dead adults, 2 dead juveniles, vine thicket/scrub, 4.ix.1982 (QM MO13139); 15 dead adults, Fireclay Road, mesophyll vine forest/*Araucaria*, litter, 15.vii.1980 (QM MO11068). Bundaberg (24^{0}52'S, 152^{0}21'E): 2 dead adults, The Hummock, amongst rock and leaf litter in thorny scrub on hillside, 6.xii.1983 (QM MO14693). Gin Gin (25^{0}00'S, 151^{0}57'E): 13 dead adults, 2 dead juveniles, *ca.* 28km SSW of Gin Gin on Gin Gin - Gayndah Road, *Araucaria*/notophyll vine forest, on ground and in litter, 9.vii.1980 (QM MO7965). Limestone Creek State Forest (25^{0}15'S, 151^{0}55'E): 3 dead adults, 3.ix.1982 (QM MO13018); 4 dead adults, *ca.* 1.5km N of turnoff to state forest, 3.ix.1982 (QM MO12475). Dallarnil (25^{0}23'S, 152^{0}03'E): 2 dead adults, under logs, (QM MO6826). Mt Woowoonga (25^{0}26'S, 152^{0}06'E): 6 dead adults, mesophyll vine forest/*Araucaria*, 3.ix.1982 (QM MO12438). Mt Goonaneman (25^{0}26'S, 152^{0}08'E): 3 dead adults, rainforest, 670m, 3-7.xi.1980 (QM MO9823). Mt Biggenden (25^{0}32'S, 151^{0}50'E): 3 dead adults, 4 dead juveniles, semi-evergreen vine thicket, 3.ix.1982 (QM MO11966); 6 dead adults, limestone outcrop, notophyll vine forest, on ground and in litter, 8.vii.1980 (QM MO7962). Coalstoun Lakes (25^{0}36'S, 151^{0}54'E): 5 dead adults, semi-evergreen vine thicket, 2.ix.1982 (QM MO12392). Walla Range (25^{0}38'S, 151^{0}50'E): 10 dead adults, 1 dead juvenile, 3.ix.1982 (QM MO12428). Mt Guyra NP (25^{0}49'S, 152^{0}35'E): 3 dead adults, mesophyll vine forest/notophyll vine forest/*Araucaria* (QM MO12081). Mt Bauple (25^{0}49'S, 152^{0}37'E): 3 live adults, xi.1987 (QM MO19033). Mudlo Gap State Forest (26^{0}01'S, 152^{0}14'E): 11 dead adults, mesophyll vine forest/*Araucaria*, 2.ix.1982 (QM MO12338). Wondai (26^{0}19'S, 151^{0}53'E): 15 dead adults (QM MO5828). Clifton Range State Forest (26^{0}34'S, 152^{0}16'E): 3 dead adults, 1 dead juvenile, SW of Fairlie's Knob, vine thicket/*Araucaria*, 2.ix.1982 (QM MO12383).

Sphaerospira informis **(Mousson)**

Type material: *informis dietrichae* (holotype): adult shell, Mt Dryander, Queensland, Australian Museum, C100649; *informis fringilla* (holotype): adult shell, Finch Hatton, 50 miles west of Mackay, Australian Museum, C100639.

Other material: Proserpine (20^{0}24'S, 148^{0}35'E): 1 dead adult (MV). Cathu (20^{0}49'S, 148^{0}38'E): 1 live juvenile, 25-30 miles S of Proserpine, Mt Crofton, 3000' (QM MO4695). Mt Ossa (20^{0}58'S, 148^{0}49'E): 1 dead adult (MV). Eungella (21^{0}08'S 148^{0}30'E): 1 dead adult (MTQ MO17518); 1 dead adult, Crediton Track, in creek leaf litter in rainforest, 9.viii.1988 (MTQ MO17375); 1 live juvenile, Palm Walk, under log by day, 4.x.1988 (MTQ MO17475); 13 dead adults, Palm Walk, 800m alt., complex notophyll vine forest, xi.1976 (QM MO6824); 7 dead adults, 6 dead juveniles, Broken River, notophyll vine forest, 5.vii.1982 (QM MO11704); 3 dead adults, Diggings Road, notophyll vine forest, 8.vi.1982 (QM MO11750); 1 live juvenile, Mt William, 915m, at night, 18.i.1988 (MTQ MO17334); 2 dead adults, 2 dead juveniles, 8km south of Eungella, rainforest, on ground, 28.vi.1982 (QM MO12841). Calen (20^{0}54'S, 148^{0}48'E): 6 dead adults, numerous dead juveniles, *c.* 17.5km south west of Calen on Calen - Mt Charlton road, notophyll vine forest, 6.vi.1982 (QM MO11717); 2 live adults, between St Helen's Creek and Mt Charlton, in rotting log in rainforest, 25.vii.1980 (QM); 1 dead adult, south of Calen, between Mt Charlton and St Helens Creek, in hollow log, 7.xii.1980 (QM MO14175). Mackay (21^{0}8'S 149^{0}11'E): 1 dead adult (SAM TD8375); 2 dead adults, 8 dead juveniles, *c.* 36.7km north of Mackay on Mackay - Seaforth road, notophyll vine forest(?), on hillside, 3.vi.1982 (QM MO11692); 3 dead adults, Pioneer River (SAM D3030). Sarina (21^{0}26'S, 149^{0}13'E): 7 dead adults, 2 dead juveniles, *c.* 15km south of Sarina, Sarina Range, Bell's Gap, notophyll vine forest, 7.vi.1982 (QM MO11735).

Sphaerospira **sp. nov.**

Type material: Holotype, live adult, width = 33.1mm, height = 31.4mm, whorls = 5.5. Mid-east Queensland, SW of Gladstone, Dan Dan Scrub. Queensland Museum, number to be designated. Paratype, live adult, width = 33.2mm, height = 31.8mm, whorls = 5.25. Same locality as holotype. Queensland Museum, MO5150.

Bentosites macleayi (Cox)

Type material: *macleayi* (syntypes): 2 adult shells, Port Denison, Queensland, Australian Museum, C107277; *macleayi wardiana* (holotype): adult shell, Hayman Island, Queensland, Australian Museum, C100650; *macleayi wardiana* (paratypes): 4 adult and juvenile shells, Hayman Island, Queensland, collected by M. Ward, Australian Museum, C107259.

Other material: North eastern Australia: 1 dead adult (MV). Queensland: 3 dead adults (MV); 2 dead adults (MV); 3 dead adults (MV); 2 dead adults (MV F8535); 5 dead adults (MV), 10 dead adults (SAM TD8370). North Queensland: 3 dead adults, 1 dead juvenile, 1.ix.1936 (MV). Port Denison: 2 dead adults (QM MO5831); 5 dead adults (MV); 2 dead adults (MV). Bowen district: 1 dead adult (AM). Bowen (20^{0}0'S, 148^{0}16'E): 2 dead adults (QM MO5829), 8 dead adults (QM MO5830). Border Island (20^{0}10'S, 149^{0}2'E): 2 dead adults, in gullies, vi.1981 (QM MO11476). Dent Island (20^{0}21'S, 148^{0}56'E): 1 dead adult, 22.v.1934 (MV). Hayman Island (20^{0}03'S, 148^{0}53'E): 7 dead adults, numerous juveniles and fragments, in leaf litter, ii.1982 (QM MO11518); 1 live juvenile, in resort garden, active at night, 21.1.1989 (MTQ MO17478); 1 dead adult, in talus slope by marina, 21.1.1989 (MTQ); 6 dead adults, 1 dead juvenile, under stones in gully among ferns, 22.x.1946 (AM C105554); 1 dead adult (AM C98040); 1 dead adult (AM C72496); 10 dead adults, 3 dead juveniles (AM C107279); 11 dead adults, numerous dead juveniles, (AM C57052); 18 dead adults, 5 dead juveniles (AM C107287). Henning and Dent Islands: 2 dead adults, 1 dead juvenile (AM C107278). Henning Island (20^{0}19'S, 148^{0}56'E): 6 dead adults, 5 dead juveniles (AM C57044); 1 dead adult, 1 dead juvenile (AM C76558). Hook Island (20^{0}9'S, 148^{0}57'E): 7 dead adults, in low woodland, 10m, xii.1976 (QM MO6862); 2 dead adults, 1 dead juvenile, vi.1988 (MTQ MO17356); 4 live adults, Nara Inlet, rainforest and open forest on steep rocky slope, 9.iii.1988 (MTQ MO17344); 2 dead adults (MV); 1 dead adult (AM C76534); 5 dead adults (AM C107258). Whitsunday Island (20^{0}15'S 149^{0}4'E): 1 dead adult, vi.1988 (MTQ MO17357); 1 live juvenile, Joe's Beach, on trunk of tree, 2m above ground, 27.iv.1988 (MTQ MO17347); 6 dead adults (AM C107276); 4 dead adults, Cid Harbour, in trees on beach front on side of mountain (AM C95423); 2 dead adults, 1 dead juvenile (AM C76557). Lindeman Island (20^{0}27'S, 149^{0}02'E): 6 dead adults, 6 dead juveniles (AM C107280). Cumberland Islands (20^{0}15'S, 149^{0}12'E - 20^{0}50'S, 149^{0}35'E): 5 dead adults (AM C17626). No locality: 7 dead adults (AM C107256).

Bentosites yulei (Forbes)

Type material: *findera* (holotype): adult shell, Port Mackay, Queensland, Australian Museum, C100657; *rainbirdi* (holotype): adult shell, Mt Dryander, Port Denison, Queensland, Australian Museum, C107708; *starena* (holotype): adult shell, Whitsunday Island, Queensland, Australian Museum, C100635; *thorogoodi* (holotype): adult shell, Proserpine River, Queensland, Australian Museum, C100636.

Other material: Port Denison: 2 dead adults (SAM TD8384). Bowen (20^{0}00'S, 148^{0}16'E): 7 dead adults, near Bowen (?Mt Dryander) (QM MO6877). Mt Dryander (20^{0}15'S, 140^{0}35'E): 9 dead adults (SAM TD8383). Mt Julian (20^{0}23'S, 148^{0}37'E): 1 dead adult, 6.ix.1989 (JW1521). Proserpine (20^{0}24'S, 148^{0}35'E): 2 dead adults, under logs (QM MO11675); 2 dead adults, banks of Gregory River, under rocks and logs, 2.ix.1980 (QM MO8906); 5 dead adults, 2 dead juveniles, *c.* 19km north of Proserpine, near Gregory River (20^{0}17'S, 148^{0}35'E), NVF/MVF, 6.iii.1982 (QM MO11726); 2 dead adults (MV); 7 dead adults (MV); 2 dead adults (MV); 5 dead adults (MV); 3 dead adults (MV); 1 dead adult, scrub, 1981 (MV); 7 dead adults, scrub (MV). Kelsey Creek (20^{0}26'S, 148^{0}28'E): 6 live adults, under logs, vi.1971 (MV); 2 dead adults, ii.1971 (QM MO4475). Cannonvale (20^{0}17'S, 148^{0}42'E): 3 dead adults, Brandy Creek Road, 7km south of Cannonvale (JW1491). Gregory (23^{0}58'S, 145^{0}03'E): 1 dead adult, 11km west of Cannonvale (JW1501). Conway Range NP (20^{0}31'S 148^{0}53'E): 1 live adult, under logs in scrub (tree climbers in wet weather), 20.xi.1970, (QM MO4388); 1 live adult, 1 live juvenile, 2m altitude, closed forest, 18.i.1975 (QM MO5872); rainforest, 1 live adult (MTQ MO17476); in rainforest, under logs, 1 live adult, 2 live juveniles, 2.x.1988 (MTQ); 1 live adult, 2m above sealevel, on ground in leaf litter in closed forest, 18.i.1975 (MV); 1 dead adult, circuit track, 16.ix.1989 (JW1513). Long Island (20^{0}23'S, 148^{0}52'E): 1 live adult, 200-300m along track from Happy Bay, 20.iv.1988 (MTQ MO17348). Hook Island (20^{0}07'S, 148^{0}55'S): 1 live juvenile, Nara Inlet, rainforest and open forest on steep slopes, 9.iii.1988 (MTQ MO17345). Whitsunday Island (20^{0}15'S, 149^{0}00'E): 1 live juvenile, under pile of stones, 27.iv.1988 (MTQ MO17346); 1 live juvenile, Sawmill Beach, at base of tree at edge of foredunes, 27.iv.1988 (MTQ MO17349). West Molle Island (20^{0}15'S 148^{0}49'E): 5 dead adults, low *Araucaria* vine forest, xii.1976 (QM MO6876). Cape Hillsborough (20^{0}54'S, 148^{0}59'E): 2 dead adults, rainforest, under bark of dead trees, 26.vi.1982 (QM MO12846). Seaforth (19^{0}33'S, 147^{0}27'E): 1 dead adult, under logs, 2.ix.1980 (QM MO8907). Mackay (21^{0}09'S, 149^{0}11'E): 1 dead adult, 6 dead juveniles, *c.* 36.7km north of Mackay on Mackay - Seaforth road, NVF (?), hillside, 3.viii.1982 (QM MO11693).

Bentosites mulgravensis **(Brazier)**

Type material: *banfieldi* (holotype): adult shell, Dunk Island, Queensland, Australian Museum, C100652; *bellaria* (holotype): adult shell, Hinchinbrook Island, Queensland, Australian Museum, C100629; *cookensis* (holotype): adult shell, "Cooktown" (= Brooke Island, Rockingham Bay, Queensland, *vide* Iredale), Australian Museum, C100661; *hubbardi* (holotype): adult shell, Johnstone River, Queensland, Australian Museum, C100688; *mulgravensis* (holotype): adult shell, Mulgrave Island, Torres Strait, Australian Museum, C17616; *palmensis* (syntype): adult shell, Great North Palm Island, north of Townsville, Queensland, Australian Museum, C107674; *palmensis meridionalis* (suntypes): 3 adult shells, Great South Palm Island, Queensland, Australian Museum, C11113; *russelli* (holotype): adult shell, North Barnard Island, Queensland, Australian Museum, C100662.

Other material: Kurrimine Beach (17^{0}47'S, 146^{0}06'E): 2 live adults, rainforest, 28.v.1970 (MV). Mission Beach (17^{0}52'S, 146^{0}06'E): 8 dead adults, under palm curls (MV); 8 dead adults (MV).

Bentosites rawnesleyi (Cox)

Type material: *bala* (holotype): adult shell, Magnetic Island, Queensland, Australian Museum, C100644; *rawnesleyi* (syntypes): 5 adult shells, Mt Elliot, Port Denison, Queensland, Australian Museum, C107680.

Other material: Many Peaks Range (19^{0}12'S, 146^{0}45'E): 6 live adults, vine thicket on rock outcrop, under rocks, 16.x.1988 (MTQ MO17463). Mt Elliot (19^{0}28'S, 146^{0}55'E): 2 live adults, under logs, 8.iv.1980 (QM MO7291). Herveys Range (19^{0}29'S, 146^{0}35'E): 1 live adult, Thornton's Gap, 25.i.1975 (MV). Mingela (19^{0}53'S, 146^{0}38'E): 13 live adults, 4km east of Fanning River Station, in cave litter, viii.1988 (MTQ MO17398). Giru (19^{0}34'S, 147^{0}13'E): 2 live adults, Haughton River crossing, 11.v.1987 (QM MO20211); 9 live adults, Haughton River, 8 miles north of Giru, 1976 (QM MO5874); 14 adults, 1 juvenile, Haughton River, in hollow logs, i.1976 (QM MO5842).

Bentosites zebina (Brazier)

Type material: *zebina* (holotype): adult shell, Douglas River, Queensland. Australian Museum C17614.

Other material: Mt Fox (18^{0}51'S, 145^{0}48'E): live adults, under leaf litter, 11.vi.1980 (QM MO8021). Cleveland Bay (19^{0}13'S, 146^{0}55'E): 4 dead adults (AM C107648); 1 dead adult (AM C107647). Herveys Range (19^{0}29'S, 146^{0}35'E): 2 dead adults, west side (MV). Townsville (19^{0}16'S, 146^{0}49'E): live adults, hills on road to Ingham, north of Townsville, under stones, 11.vi.1980 (QM MO7989); 2 live adults, summit of Mt Stuart, TV station, 1.i.1976 (MV); 1 dead adult, 11.iii.1910 (AM C107649); 3 dead adults (QM MO1875); 1 dead adult, Castle Hill (AM C76531); 1 dead adult, Castle Hill (AM C76546); Melton Hill, in garden under leaf litter (MTQ MO17343); 4 dead adults, Melton Hill (AM C76542); 2 dead adults, 3 dead juveniles, Melton Hill (AM C76585). Wando Vale (19^{0}40'S, 144^{0}54'E): numerous dead adults viii.1977 (QM MO6821). Sellheim (20^{0}00'S, 146^{0}25'E): 1 km south of Sellheim, living in rotting tree stumps, 21.viii.1988 (MTQ MO17397); 6 dead adults, 1km south of Sellheim, 21,.viii.1988 (JW354). Tucker's Range (20^{0}03'S, 146^{0}33'E): 2 dead adults, 28km east of Charters Towers (JW1308). Fanning River Station (19^{0}44'S, 146^{0}26'E): dead, Big Scrub (MTQ MO17515); dead (MTQ MO17512); dead (MTQ MO17514); 2 dead adults, homestead (JW889). Mingela (19^{0}53'S, 146^{0}38'E): 5 dead adults, *c.* 28km north west of Mingela on Mingela to Hervey's Range road, 8.vi.1987 (QM MO20201). Calcium (19^{0}41'S, 146^{0}50'E): 4 dead adults, 1.5km west of township, 5.viii.1989 (JW1293); 2 dead adults, upstream from Calcium on Charters Towers road, under stones, v.1978 (AM C110173); 2 dead adults, on Charters Towers road, under bark on trees, v.1978, (AM C110166); 4 live adults, in hollow fence posts, near limestone quarry (MTQ MO17474). Rishton Scrub (20^{0}09'S, 146^{0}32'E): 6 dead adults, 2 dead juveniles, 30km east south east of Charters Towers (JW1077). Ayr (19^{0}34'S, 147^{0}24'E): 2 dead adults, Douglas River at its junction with the Burdekin (AM C107650); 2 dead adults, Burdekin River (AM C107648); 3 dead adults, Burdekin River, near Ayr, in hollow logs (QM MO6822). Clare (19^{0}45'S, 147^{0}14'E): 15 live adults, 2 live juveniles, banks of Burdekin River, 14.vi.1987 (QM MO2146).

Bentosites mazee (Brazier)

Type material: *mazee* (holotype): adult shell, Waterview (= Seaview) Range Scrubs, Cardwell, Australian Museum, C107693.

Other material: Coane Range (19^{0}05'S, 146^{0}05'E): 1 live adult, 6 miles SE of Hidden Valley, on Paluma road, 14.vii.1974 (MV). Paluma Range (19^{0}05'S, 146^{0}17'E): 1 live adult, *ca.* 6km west of Paluma in *Eucalyptus grandis* wet sclerophyll, under log, 15.v.1983 (QM MO13415); 1 live adult, 1 live juvenile, off road to Taravale, approx. 5 miles from Paluma, 9.ii.1975 (MV). Mt Spec (19^{0}10'S, 146^{0}34'E): 1 live adult, under leaf litter at edge of scrub, 11.vi.1980 (QM MO8020).

Bentosites gavisa Iredale

Type material: *birchi* (holotype): adult shell, Proserpine River, Queensland, Australian Museum, C100651.

Other material: Whitsunday Island (20^{0}15'S, 149^{0}00'E): 1 dead adult (AM C107283); 1 dead adult (AM C17624). Shute Harbour (20^{0}18'S, 148^{0}48'E): 1 dead adult, in thick scrub at base of mountain (AM C72495). Upper Proserpine River (20^{0}24'S, 148^{0}48'E): 2 dead adults, 20 miles NW of Proserpine (AM C107287). Conway (20^{0}31'S, 148^{0}53'E): 2 live adults, under logs in scrub, xii.1970 (QM MO4416). Repulse Bay: 6 live adults, 4 live juveniles, Wilson Beach, 1.v.1975 (AM C161762); live adults, Wilson Beach, on trees, 2.v.1975 (AM).

Bentosites sp. nov.

Type material: Holotype, live adult, scrub S of Pine Mt, on Sarina-Clermont road, c. 50 km SW of Sarina, Queensland (21^{0}46'30"S, 148^{0}50'30"E), semi-evergreen vine thicket, in logs and hollow trees, coll. J. Stanisic, D. Potter, N. Potter, 22.v.1990, Queensland Museum MO54878. Paratypes, same collection details as holotype. Queensland Museum, MO36234

Varohadra oconnellensis (Cox)

Type material: *oconnellensis* (syntypes): 3 adult shells, Port Denison, Queensland, Australian Museum, C107735; *oconnellensis caroli* (holotype): adult shell, Lindeman

Island, Queensland, Australian Museum C100648; *oconnellensis jacksoni* (holotype): adult shell, Finch Hatton, 50 miles west of Mackay, Queensland, Australian Museum, C100647.

Other material: Port Denison: 4 dead adults, 2 damaged shells (?Port Mackay), (QM MO5821); 2 dead adults, O'Connell River (SAM TD8392); 2 dead adults (SAM TD8391). Bowen (20^{0}0'S, 148^{0}16'E): 2 dead adults (AM C17623). Mt Dryander (20^{0}15'S, 140^{0}35'E): 12 dead adults, O'Connell River (AM C107732). Proserpine (20^{0}24'S, 148^{0}35'E): 2 live adults, x.1968 (MV). Lindeman Island (20^{0}27'S, 149^{0}02'E): 28 dead adults, 16 juveniles, NW side (AM C107731); 1 dead adult, 20.ix.1923 (AM C49559); 1 dead adult, 1 dead juvenile (AM C107739); 3 dead adults (AM C107740). Cathu (20^{0}49'S, 148^{0}38'E): 1 dead adult, 30 miles south of Proserpine (QM MO5012); 1 dead adult, 25-30 miles south of Proserpine, Mt Crofton, 3000' (QM MO4698). Cape Hillsborough (20^{0}54'S, 148^{0}59'S): 1 live adult, 2m above sea level, grass in open and closed forest, QNPWS, 8.i.1975 (MV); 4 dead adults, 1957 (AM C105540). Mt Ossa (20^{0}58'S, 148^{0}49'E): 2 dead adults (MV); 1 live adult, Ossa Creek, 26.xii.1980 (QM MO20986). Mount de Moleyns (21^{0}07'S, 148^{0}56'E): 3 dead adults, 20 miles West of Mackay, 1956 (AM C107733). Black Mountain (21^{0}07'S, 149^{0}12'E): 1 dead adult, 10 miles north east of Mackay (AM C107734). Mackay (21^{0}08'S, 149^{0}11'E): 1 dead adult, 3 dead juveniles (QM MO5820); 3 dead adults, 1 dead juvenile, Pioneer River scrubs, West of Mackay, 1908 (AM C107736); 2 dead adults, Pioneer River scrubs, 1908 (AM C31234); 1 dead adult (AM C1908). Finch Hatton (21^{0}9'S, 148^{0}38'E): 8 dead adults, 1 dead juvenile, living in dry wood of rotten trees in jungle, viii.1908 (AM); 7 dead adults, 2 dead juveniles, Finch Hatton scrubs, viii.1908 (AM C107737). Eton (21^{0}16'S, 148^{0}59'E): 2 dead adults, 10 miles West of Mackay, under log (QM MO5822). Hatfield's Gap (21^{0}36'S, 149^{0}12'E): 2 live adults, W of Koumala, 17.vi.1987 (QM MO19984). No locality: 1 dead adult (AM); 6 dead adults (AM C107738).

Gen. nov. A *incei* (Philippi)

Type material: *aureedensis* (holotype): adult shell, Aureed Island, Torres Strait, Australian Museum, C17604; *bernhardi* (holotype): adult shell, Rockhampton, Queensland, Australian Museum, C100671; *challisi* (syntypes): 8 adult shells, L. Island, Broad Sound, Queensland, Australian Museum, C17597; *curtisiana exedra* (holotype): adult shell, Boyne Island, Port Curtis, Queensland, Australian Museum, C100672; *keppelensis* (holotype): adult shell, North Keppel Island, Queensland, Australian Museum, C100656; *keppelensis degener* (holotype): adult shell, South Keppel Island, Queensland, Australian Museum, C100655.

Other material: Pine Islet (21^{0}39'S, 150^{0}13'E): 1 dead adult, xii.1987 (QM MO19147). Clairview Beach (22^{0}7'S, 149^{0}33'E): 1 dead adult, 2.vi.1987 (QM MO19970). Yeppoon (23^{0}07'S, 150^{0}44'E): 5 live adults, Mulambin Beach, ix.1970 (MV). 4 live adults, Mulambin Beach, found under logs about 1 mile from beach front, iii.1972 (QM MO5011). Wartburg (24^{0}30'S, 151^{0}56'E): Matchbox Range district, 2 dead adults, 1987 (QM MO17058). Ambrose (23^{0}47'S, 150^{0}55'E): 3 live adults, 1 dead adult, Ambrose limestone quarry, under rocks and logs, open scrub/remnant vine thicket, 10.vii.1980 (QM MO8160). Iveragh (24^{0}08'S, 151^{0}27'E): 2 dead adults, under logs (QM MO6791). Bororen (24^{0}15'S, 151^{0}30'E): 2 live adults, under rotten log (QM MO4141); under rotten log, 3 dead adults, 1 dead juvenile (QM MO4142). Miriamvale (24^{0}20'S, 151^{0}34'E): 1 live adult, 8km SE of Miriamvale on Miriamvale - Colosseum road, notophyll vine forest, under logs and debris, 9.viii.1980 (QM MO20985); 2 dead adults (MV). Curtis Island (23^{0}30'S, 151^{0}04'E): 10 live adults, found under loose bark on trees, xi.1971 (QM MO4908); 14 dead adults, under loose bark on trees, xi.1971 (QM MO4909).

Gen. nov. A *appendiculata* (Reeve)

Type material: *bayensis* (holotype): adult shell, Wide Bay, Queensland, Australian Museum, C17595; *bayensis reducta* (holotype): adult shell, Tenningering (Mt Perry), Bundaberg, Queensland, Australian Museum, C100653; *thatcheri* (holotype): adult shell, Mt Bersaker, Rockhampton, Queensland, Australian Museum, C100659.

Other material: Berserker Range (23^{0}20'S, 150^{0}35'E): 2 dead adults (QM MO1469); 1 dead adult (QM MO1468). Mt Dick (20^{0}07'S, 144^{0}35'E): live, under rocks (QM MO4147); 3 dead adults, Lakes Creek, under rocks (QM MO4147); 4 dead adults, Lakes Creek, under logs, near creek in scrub country, 2.vii.1982 (QM MO12854); 1 dead adult, foot of Mt Dick, under rocks (QM MO4148). Rockhampton (23^{0}22'S, 150^{0}31'E): 2 dead adults, Koongal, in garden under rubbish (QM MO6796). Mt Archer (23^{0}20'S, 150^{0}35'E): 2 dead adults, Frenchville, under bricks on farm, ii.1980 (QM MO7224). Mount Morgan (150^{0}04'S, 145^{0}04'E): 27 dead adults, 11 dead juveniles, ca. 7km E of Mt Morgan, notophyll vine forest, on ground, 11.vii.1980 (QM MO8267); 36 dead adults, 14 dead juveniles, ca. 7km due E of Mt Morgan on road to St Mary's Falls, semi-evergreen vine thicket, 29.vi.1982 (QM MO11636); 2 dead adults, ca. 7km E of Mt Morgan, near top of St Mary's Falls, microphyll vine forest, 29.vi.1982 (QM MO13109); 2 live adults, Ulam Ranges, 9 miles NE of Mt Morgan, under rocks (QM MO4146); 2 live adults, Ulam Range, 10 miles NE of Mt Morgan, in hollow log (QM MO4396); 1 dead adult, side of Mt Usher, Bouldercombe, 10 miles NE of Mt Morgan, under rocks (QM MO6806); 2 dead adults, Milne Collection (MV); 4 live adults, 10 miles NE of Mt Morgan (MV). Ambrose (23^{0}47'S, 150^{0}55'E): 4 dead adults, 3 dead juveniles, Ambrose limestone quarry, under rocks and logs, open scrub, remnant vine thicket, 10.vii.1980 (QM MO8159). Mt Larcom (23^{0}49'S, 151^{0}04'E): 3 dead adults, foothills Yarwun (QM MO14769). Bracewell (23^{0}54'S, 150^{0}54'E): 3 dead adults, limestone outcrop, 31.x.1977 (QM MO6808); 42 dead adults, 18 dead juveniles, ca. 2km W of Bracewell, limestone outcrop, semi-evergreen vine thicket, between boulders, 10.vii.1980 (QM MO8136). Calliope (24^{0}00'S, 151^{0}12'E): 57 dead adults, 13 dead juveniles, Dan Dan Scrub, ca. 30km SW of Calliope, semi-evergreen vine thicket/Araucaria, 5.ix.1982 (QM MO12217). Mt Moore (24^{0}02'S, 151^{0}05'E): 40 dead adults, 6 dead juveniles, in patch of scrub in vine thicket, 5.ix.1982 (QM MO13211). Bororen (24^{0}15'S, 151^{0}30'E): 2 dead adults, Oakey Creek, Turkey District, 21.iv.1985

(QM MO15951). Miriam Vale ($24^0$20'S, $151^0$34'E): 10 dead adults, under leaf litter (MV). Kroombit Tops ($24^0$22'S, $151^0$03'E): 2 dead adults, dry creek near forestry camp, 11-15.xii.1983 (QM MO14676). Colosseum ($24^0$24'S, $151^0$37'E): 5 dead adults, 6 dead juveniles, Motel Colosseum, beside road under debris, 6.ix.1982 (QM MO12167). Mt Colosseum ($24^0$25'S, $151^0$35'E): 5 dead adults, 1 dead juvenile, rainforest, under logs, rocks and bark of trees, 6.vii.1982 (MO12859). Colosseum Creek ($24^0$24'S, $151^0$28'E): 13 dead adults, 12 dead juveniles, ca. 9km S of Miriam Vale, under logs and rubbish, riverine rainforest, *C. australe*, 14.x.1981 (QM MO11859); 1 dead adult, 1 dead juvenile, rainforest along creek, 6.ix.1982 (QM MO13266); 1 dead adult, ca. 16km S of Miriamvale, under logs and rubbish (Stn 87), riverine rainforest, C. australe, 14.x.1981 (QM MO13292). Many Peaks Range ($24^0$18'S, $151^0$23'E): 1 dead adult, 2 dead juveniles, Eastern Boyne River, 5.ix.1982 (QM MO13193). Builyan ($24^0$32'S, $151^0$23'E): 1 dead adult, 4 dead juveniles, ca. 18km E of Builyan railway station on Builyan - Gladstone road, between rocks next to river bank, rainforest, 15.vii.1980 (QM MO10316). Bundaberg ($24^0$52'S, $152^0$21'E): 13 dead adults, the Hummock, amongst rocks and leaf litter in thorny scrub on hillside, 6.xii.1983 (QM MO14695). Gin Gin ($25^0$00'S, $151^0$57'E): 31 dead adults, 6 dead juveniles, ca. 28 miles SSW of Gin Gin on Gin Gin - Gayndah road, *Araucaria*/notophyll vine forest, on ground in leaf litter, 9.viii.1980 (QM MO7966). Woodgate NP ($25^0$09'S, $152^0$35'E): 1 dead adult, sandy area, thick acacia regrowth, 18.xii.1973 (QM MO6799); 1 dead adult, on sandy road (QM MO6810). Biggenden ($25^0$31'S, $152^0$04'E): 4 dead adults, Mt Biggenden, ca. 8km SW of Biggenden, semi-evergreen vine thicket, 3.ix.1982 (QM MO11967). Coalstoun Lakes NP ($25^0$36'S, $151^0$54'E): 5 dead adults, 1 dead juvenile, semi-evergreen vine thicket, 2.xi.1982 (QM MO12391). Gayndah ($25^0$38'S, $151^0$36'E): 2 dead adults (QM MO6805).

Gen. nov. A *mattea* (Iredale)

Type material: *incei mattea* (holotype): adult, Rockhampton, Queensland, Australian Museum, C100642.

Other material: Rockhampton ($23^0$22'S, $150^0$31'E): live, 14 Hartley Street, suburban garden, A. Boorman, vi.1972 (QM MO5122); live, Park Avenue, near Fitzroy River, under dead bark (QM MO4215). Mt Morgan ($23^0$38'S, $150^0$29'E): 7 dead adults, 2 dead juveniles, sclerophyll on edge of notophyll vine forest, on ground, 11/vii/1980 (QM MO8268); 5 dead adults, 3 dead juveniles, ca 7km due E of Mt Morgan on road to St Mary's Falls, semi-evergreen vine thicket, 29/vi/1982 (QM MO11635). Dee River ($23^0$43'S, $150^0$23'E): 13 dead adults, 3 dead juveniles (QM MO1290); 11 dead adults, Dee River crossing, ca 9.5km S of Mt Morgan on Mt Morgan - Biloela road, remnant vine thicket, 29/vi/1982 (QM MO11616). Ambrose ($23^0$47'S, $150^0$55'E): 29 dead adults, Ambrose limestone quarry, under logs and rocks, open scrub/remnant vine thicket, 10/vii/1980 (QM MO8158). Gladstone ($23^0$51'S, $151^0$16'E): 4 dead adults, Aukland St, on lawn, 18/ii/1982 (QM MO14176). Biloela ($24^0$24'S, $150^0$31'E): 5 dead adults, 7 dead juveniles, ca 50km N of Biloela on Dululu - Biloela road, bottle-tree scrub, open forest, under logs and bark, 14/vii/1980 (QM MO10312); 6 dead adults, 1 dead juvenile, ca 54km S of Biloela on Biloela - Monto road, semi-evergreen vine thicket, rocky outcrop, leaf litter, 14/vii/1980 (QM MO10314). Dawes Range ($24^0$25'S, $151^0$02'E): 1 dead adult, microphyll vine forest/*Araucaria*, 4/ix/1982 (QM MO12640). Auburn River NP: 1 dead adult, 21/iv/1987 (QM MO17050). Gayndah ($25^0$38'S, $151^0$36'E): 14 dead adults, 12 dead juveniles, ca 2km W of Gayndah on Gayndah - Hinesville road, bottle-tree scrub, semi-evergreen vine thicket, 16/vii/1980 (QM MO11527). Coolola State Forest ($26^0$12'S, $153^0$03'E): 1 dead adult, Camp Milo, vicinity of forestry buildings, open eucalypt, partly cleared, 20/i/1972 (QM MO5014); 7 dead adults, 3 dead juveniles, Camp Milo, vicinity of forestry buildings, open eucalypt, partly cleared, 20/i/1972 (QM MO5013); 1 dead adult, Camp Milo, vicinity of forestry buildings, open eucalypt, partly cleared, 21/iv/1972 (QM MO5078). Ban Ban Springs ($25^0$41'S, $151^0$51'E): 10 dead adults, 4 dead juveniles, ca 2.8km E of Ban Ban Springs on Ban Ban - Biggenden road, in litter, remnant bottle-tree low microphyll vine forest, 16/vii/1980 (QM MO11151). Barambah Creek ($26^0$20'S, $152^0$12'E): 6 dead adults, 8 dead juveniles, 1/ix/1982 (QM MO12988). Coringa ($25^0$20'S, $151^0$58'E): 1 dead adult, 1 dead juvenile, ca 1.5km W of Coringa Community Hall, under rocks and logs in lightly timbered country, vi/1981 (QM MO14180). Noosa Heads ($26^0$23'S, $153^0$04'S): 2 dead adults, 9 dead juveniles, tree partly burnt on ground, *Casuarina* forest (QM M)1446) Montville ($26^0$41'S, $152^0$54'E): 1 dead adult, 2 dead juveniles (QM MO6784) Tweed River: 2 dead adults (QM MO6776).

Temporena whartoni **(Cox)**

Type material: *whartoni* (paratypes): 2 adult shells, Port Denison, Queensland, Australian Museum, C107646.

Other material: Queensland: 6 dead adults (AM C31512); 3 dead adults (MV); 2 dead adults, iv.1909 (MV); 2 dead adults, xi. 1874 (MV); 1 dead adult (MV). North Queensland: 3 dead adults (MV). Port Denison: 2 dead adults (MV). Bowen ($20^0$00'S, $148^0$14'E): 2 dead adults (AM C3683). Holbourne Island ($19^0$44'S, $148^0$22'E): 7 dead adults, "Holbrook Island" (SAM D11377); 2 dead adults, in low scrub under slabs or phosphate and dead coral (MV); 4 dead adults, in low scrub under slabs of phosphate and dead coral (MV); 2 dead adults, 28.vii.1945 (AM C107644); 2 dead adults, under pieces of dead coral and phosphate slabs, v.1978 (AM C110174); 47 dead adults, 11 dead juveniles, under coral blocks, 19.ix.1923 (AM C49555).

Temporena coxi **(Crosse)**

Type material: *croftoni* (syntypes): 5 adult shells, Hydrometer River, west of Mackay, Queensland, Australian Museum, C107614; *forbesii* (syntypes): 4 adult shells, Port Denison, Queensland, Australian Museum, C107603; *probleema* (holotype): adult, Hamilton Island, Whitsunday Group, Queensland, Australian Museum, C100660; *volgiola fortasse* (holotype): adult shell, Lindeman Island, Whitsunday Group, Queensland, Australian Museum, C100640.

Other material: Mt Inkerman (19^{0}45'S, 147^{0}30'E): 3 dead adults (MV). Proserpine (20^{0}24'S, 146^{0}35'E): 5 dead adults, scrub, 1982 (MV); 1 dead adult (MV). Cannonvale (20^{0}17'S, 148^{0}42'E): 2 dead adults (MV); 1 dead adult (MV). St Helen's Beach (20^{0}50'S, 148^{0}50'E): 7 live adults, under loose bark on tree, 20.xi.1970 (MV). Mirani (21^{0}10'S, 148^{0}52'E): 2 dead adults (MV).

***Temporena etheridgei* (Brazier)**
Type material: *etheridgei* (paratype): adult shell, Andromache River, near Bowen, Queensland, Australian Museum, C17625.

Other material: Mt Inkerman (19^{0}45'S, 147^{0}30'E): 1 dead adult (MV). Proserpine (20^{0}24'S, 148^{0}35'E): 4 dead adults (MV). Conway NP (20^{0}31'S, 148^{0}53'E): live adults, ca 1.7 miles from Proserpine, in scrub near beach, on trees and in scrub on leaves and dead limbs, iv.1974 (AM). Mt Jukes (21^{0}00'S, 148^{0}57'E): 3 live adults, xi.1971 (AM).

***Temporena macneilli* (Iredale)**
Type material: *macneilli* (holotype): adult shell, Double Island, off Bowen, Queensland, Australian Museum, C100646; *saxicola* (holotype): adult shell, Stone Island, Port Denison, Queensland, Australian Museum, C100669.

Other material: Port Denison: 1 dead adult (QM MO68888). Elliot River (19^{0}55'S, 147^{0}51'E): 15 dead adults, 10 dead juveniles, river crossing, 14.vi.1987 (QM MO20199). Bowen (20^{0}00'S, 148^{0}14'E): 2 dead adults, on rocky hillsides, xii.1970 (QM MO4444); 1 dead adult, Rose Bay, found under bark on dead trees (QM MO6887). Langford Island (20^{0}05'S, 148^{0}52'E): 2 dead adults, in turkey's nest, 7.ix.1981 (QM MO11474). Euri Creek (20^{0}08'S, 148^{0}01'E): 7 dead adults, 4 dead juveniles, 14.vi.1987 (QM MO19909). Border Island (20^{0}10'S, 149^{0}02'E): 2 dead adults, in gullies, vi.1981 (QM MO11477). Longford Creek (20^{0}19'S, 148^{0}22'E): 5 dead adults + fragments (QM MO20189).

Gen. nov. B *rockhamptonensis* (Cox)
Type material: *planibasis* (holotype): adult shell, Rockhampton, Queensland, Australian Museum, C17612; *rockhamptonensis* (syntypes): 4 adult shells, Rockhampton, Queensland, under dead timber, Australian Museum, C100638; *rockhamptonensis decreta* (holotype): adult shell, Mt Etna Caves district, Rockhampton, Queensland, Australian Museum, C100643; *rockhamptonensis pallida* (holotype): adult shell, Rockhampton, Queensland, Australian Museum, C264;

Other material: Mt Etna (23^{0}09'S, 150^{0}27'E): 2 live adults, limestone outcrop, microphyll vine forest, in leaf litter and under rocks, 13.vii.1980 (QM MO8821); 6 dead adults, Johannsen's Caves, semi-evergreen vine thicket, 30..vi.1982 (QM MO11648); 2 live adults, Johannsen's Caves, limestone outcrop, microphyll vine forest, under rocks and in leaf litter, 13.vii.1980 (QM MO9132). Rockhampton (23^{0}22'S, 150^{0}31'E): 2 dead adults (SAM TD8387).

Gen. nov. B sp. nov.
Type material: Holotype, live adult, Bulburin State Forest (24^{0}30'S,151^{0}33'E), 6 miles east of Many Peaks, Queensland, in rainforest under logs, collected by G. and S. Monteith, 5.iv.1972. Queensland Museum, MO5708. Paratypes, live adult, north of Gin Gin, *ca.* 8 km west of Granite Creek rest area (24^{0}30'S, 151^{0}41'E), off Bruce Highway, Queensland, collected by B. Carless, 26.ix.1983. Queensland Museum, MO14005; live adult, Granite Creek (24^{0}30'S, 151^{0}41'E), Queensland, collected by K.R. McDonald, 9.xii.1973. Queensland Museum, MO 5743.

Zyghelix forsteriana **(Reeve)**
Type material: none available, presumed lost (Smith, 1992).

Other material: North Australia: 1 dead adult (MV) Queensland: 1 dead adult (MV). Great Barrier Reef: island, 6 dead adults (MV). Cape York: 1 dead adult, 1 dead juvenile (MV F1545); 1 dead adult (MV); 2 dead adults (MoV). Starcke River (14^{0}53'S, 145^{0}04'E): 4 live adults, 39 dead adults, 16 dead juveniles, *c.* 12.5km from Starcke River on Starcke River to Starcke Station road, vine thicket/rocky outcrop, under and between rocks, 13.ix.1988 (QM MO21241).

Pallidelix sardalabiata **Cox**
Mt Dryander (20^{0}15'S, 140^{0}35'E): Holotype, 1 dead adult (BMNH 1880.12.11.12.)

Helix (Hadra) stephensoniana **Brazier**
Port Denison: Holotype, 1 dead adult (AM C100666).

Helix arthuriana **Cox**
L. Island: probable paratypes, 5 dead adults (AM C31506)

Gnarosophia nitifica **Iredale**
"Cape York": holotype, 1 dead adult, AM C100628; paratypes, 2 dead adults (AM C107646).

Varohadra halleyae **Iredale**
Lindeman Island (20^{0}27'S, 149^{0}02'E): holotype, 1 dead adult (AM C100654); paratypes, 2 dead adults (AM C57051).

***Hadra wilsoni* Solem**
Youwanjela Creek, Upper Prince Regent River, Prince Regent River Reserve (15^{0}34'S, 125^{0}25'E): holotype, 1 dead adult, B.R. Wilson & P. Smith, 20.x.1974 (WAM 1500.78)

American Camaenidae
***Pleurodonte marginella* (Gmelin)**
Cuba: 11 live adults, D.A. Welch, 1931 (ANSP A09373)

***Pleurodonte anomala* (Pfeiffer)**
Jamaica, Mandeville (18^{0}02'N, 77^{0}32'W): 9 live adults, Manchester Parish, H.B. Baker!, 14.vi.1933 - 5.vii. 1933 (ANSP A12354).

***Eurycratera jamaicensis* (Gmelin)**
Jamaica, Mandeville (18^{0}02'N, 77^{0}32'W): 3 live adults, Manchester Parish, H.B. Baker!, 15.vi.1933 - 2.ix. 1933 (ANSP A12674).

***Eurycratera aspera* (Férussac)**
Jamaica, Montego Bay (18^{0}26'N, 78^{0}05'W): 10 live adults, Sandy Bay, E.A. Andrews, 10.vii.1932 (ANSP A13390)

***Zachrysia auricoma* (Férussac)**
Cuba, Oriente Province (20^{0}50'N, 75^{0}44'W): 11 live adults, S.N. Rhoads! (ANSP A13375).

Bradybaenidae
***Bradybaena similaris* (Férussac)**
Atherton (17^{0}17'S, 145^{0}30'E): numerous live adults, in household garden, K.R. McDonald & B.J. Scott, 12.xi.1993. Christmas Island: numerous live adults, Drumsite, in household garden, S.M. Slack-Smith, 22.ii.1987 (WAM 131-90).

APPENDIX 2
Phylogenetic and biogeographic analyses

Superfamily Helicoidea

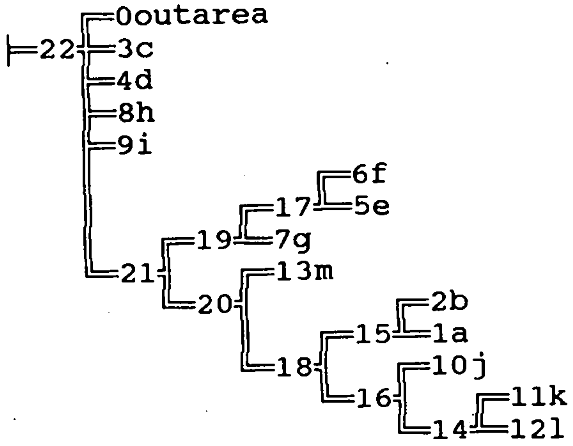
Phylogenetic analysis

```
ccode 0.0 seconds
ccode
   0   1   2   3   4   5   6   7   8   9  10  11
  1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[
ccode 0.0 seconds
ie length 33 ci 57 ri 53 trees 110
ie 1.0 seconds
xsteps file 0 from ie 110 trees
xsteps 0.2 seconds
ccode
    0    1    2    3    4    5    6    7    8    9   10   11
   5-[ 10-[ 10-[ 10-[ 10-[ 10-[  4-[  0-[  0-[  3-[ 10-[  3-[
ccode 0.0 seconds
ie length 198 ci 61 ri 64 trees 1
ie 0.3 seconds
tplot file 0 from ie 1 tree
    ┌═0zonites
├═19┼═8sagda
    │   ┌═10vitrinidae
    └═18┤   ┌═9helicarion
        └═17┤   ┌═6polygyra
            └═16┤       ┌═5amplirhaga
                │   ┌═13┴═3bradybae
                └═15┤   ┌═7haplotre
                    └═14┤   ┌═4pleurodont
                        └═12┤   ┌═1helix
                            └═11┴═2helminth
tplot 0.3 seconds
xsteps file 0 from ie 1 tree
tree 0
character 0
  11  12  13  14  15  16  17  18  19
 01+ 01+   3  03  03   0   0   0   0
character 1
 11 12 13 14 15 16 17 18 19
  1  1  1  1  1  0  0  0  0
character 2
 11 12 13 14 15 16 17 18 19
  0  0  1  0  0  0  0  0  0
```

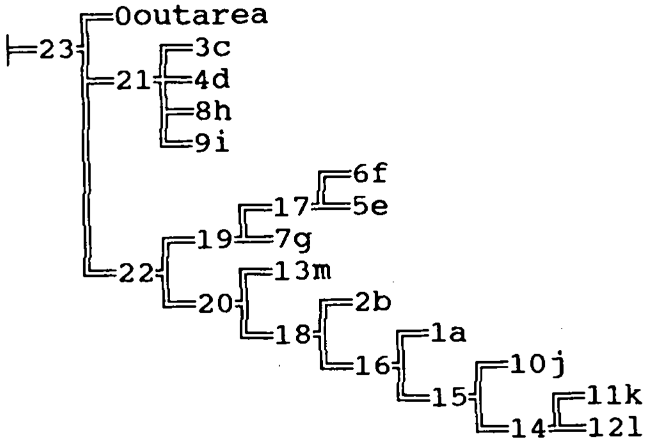
```
character 3
 11 12 13 14 15 16 17 18 19
  1  1  0  1  0  0 03 03 03
character 4
 11 12 13 14 15 16 17 18 19
  0  0  1  1  1  1  1  0  0
character 5
 11 12 13 14 15 16 17 18 19
  1  0  0  0  0  0  0  0  0
character 6
 11 12 13 14 15 16 17 18 19
  2  1  1  1  1  1  1  1  0
character 7
 11 12 13 14 15 16 17 18 19
  0  0  0  0  0  0  0  0  0
character 8
 11 12 13 14 15 16 17 18 19
  0  0  0  0  0  0  0  0  0
character 9
   11   12   13   14   15   16   17   18   19
    0    0 012    0   01   01    0    0    0
character 10
 11 12 13 14 15 16 17 18 19
  1  1  1  1  1  1  0  0  0
character 11
 11 12 13 14 15 16 17 18 19
  1  0  0  0  0  0  0  0  0
xsteps 0.5 seconds
xsteps file 0 from ie 1 tree
tree 0 length 198 ci 61 ri 64
character/steps/ci/ri
    0    1    2    3    4    5    6    7    8    9   10   11
    5    1    2    3    2    4    3    2    2    4    2    3
   60  100   50  100   50   50   66   50   50   50   50   33
   33  100   50  100   75   33   66    0    0    0   50   33

xsteps 0.2 seconds
```

```
ie length 24 ci 79 ri 87 trees 24
ie 5.5 seconds
tplot file 0 from ie 24 trees
tree 0
    ╔═0outarea
╞═22╬═3c
    ╠═4d
    ╠═8h
    ╠═9i
    ║           ╔═6f
    ║       ╔═16╩═5e
    ║   ╔═19╩═7g
    ╚═21╣       ╔═2b
        ║   ╔═17╩═1a
        ╚═20╣   ╔═13m
            ╚═18╣   ╔═12l
                ╚═15╣   ╔═10j
                    ╚═14╩═11k
tree 1
    ╔═0outarea
╞═23╣   ╔═3c
    ╠═21╬═4d
    ║   ╠═8h
    ║   ╚═9i
    ║           ╔═6f
    ║       ╔═16╩═5e
    ║   ╔═19╩═7g
    ╚═22╣       ╔═2b
        ║   ╔═17╩═1a
        ╚═20╣   ╔═13m
            ╚═18╣   ╔═12l
                ╚═15╣   ╔═10j
                    ╚═14╩═11k
tree 2
    ╔═0outarea
╞═22╬═3c
    ╠═4d
    ╠═8h
    ╠═9i
    ║           ╔═6f
    ║       ╔═17╩═5e
    ║   ╔═19╩═7g
    ╚═21╣   ╔═13m
        ╚═20╣   ╔═2b
            ╚═18╣   ╔═1a
                ╚═16╣   ╔═10j
                    ╚═15╣   ╔═11k
                        ╚═14╩═12l
```

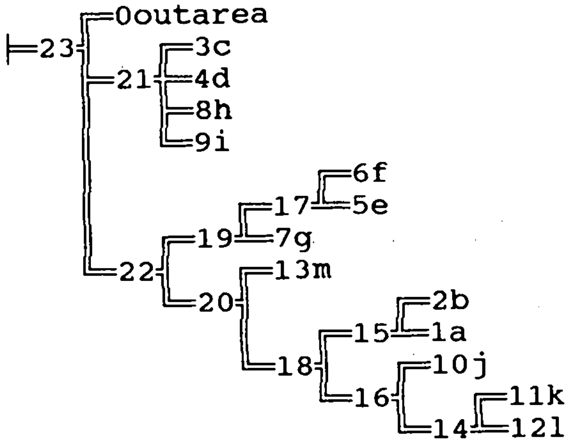
tree 3



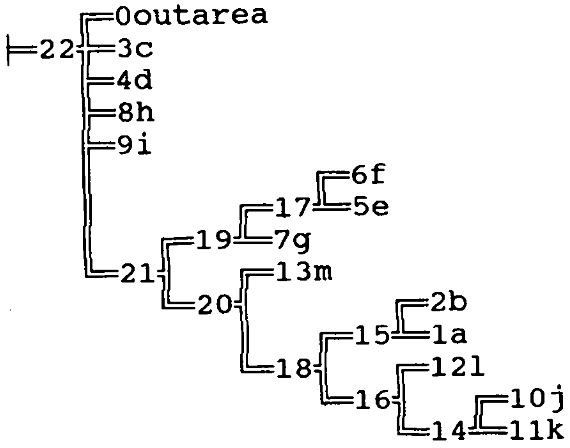
tree 4



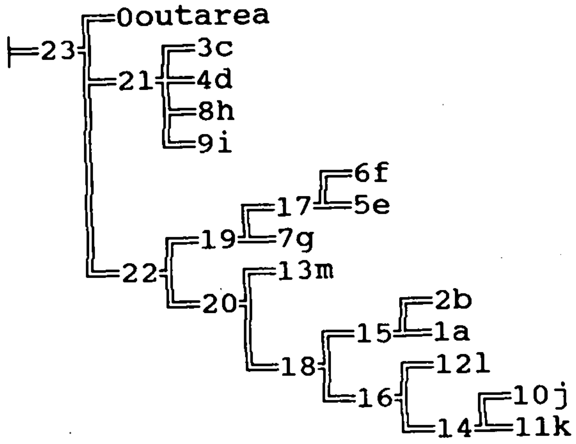
tree 5



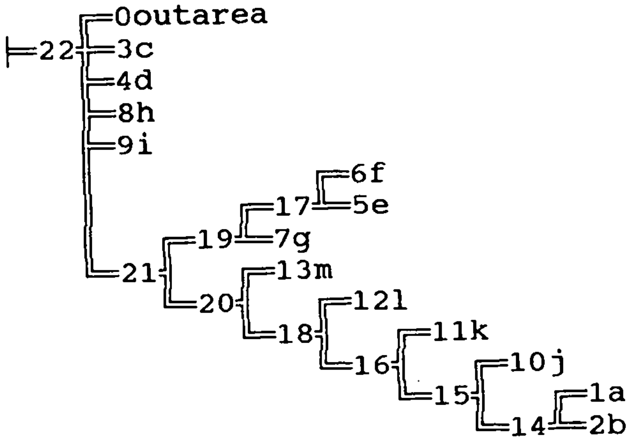
tree 6



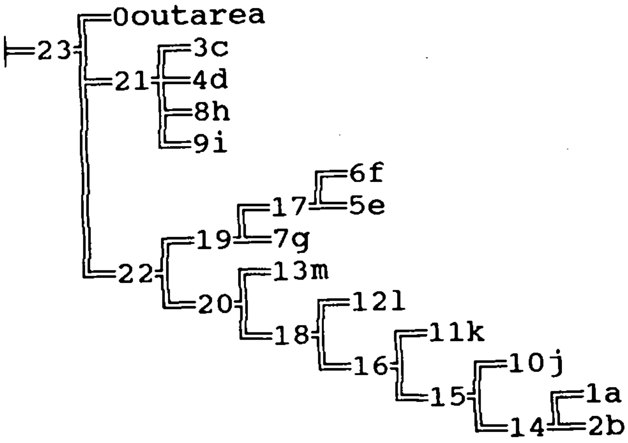
tree 7



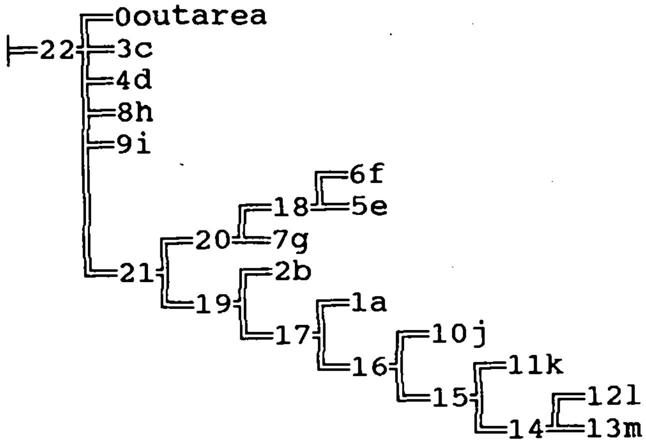
tree 8



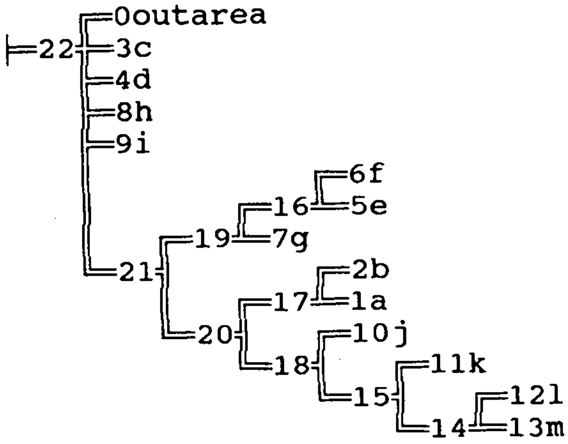
tree 9



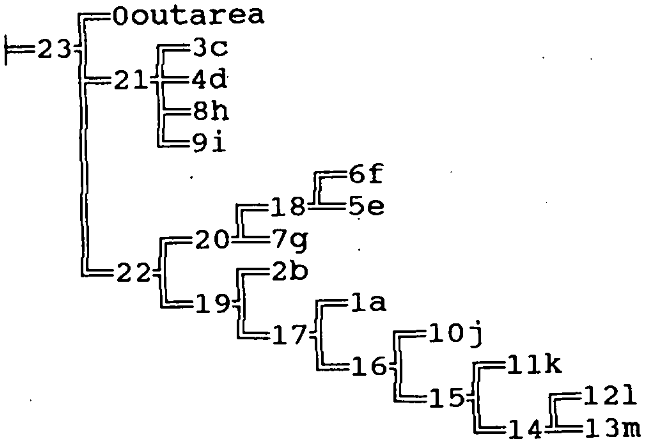
tree 10



tree 11



tree 12



```
tree 13
     ┌=0outarea
├=23┤    ┌=3c
     ├=21┼=4d
     │    ├=8h
     │    └=9i
     │              ┌=6f
     │         ┌=16┴=5e
     │    ┌=19┴=7g
     └=22┤          ┌=2b
          │    ┌=17┴=1a
          └=20┤    ┌=10j
               └=18┤
                    │    ┌=11k
                    └=15┤
                         │    ┌=12l
                         └=14┴=13m
tree 14
     ┌=0outarea
├=22┼=3c
     ├=4d
     ├=8h
     ├=9i
     │              ┌=6f
     │         ┌=16┴=5e
     │    ┌=19┴=7g
     └=21┤          ┌=2b
          │    ┌=17┴=1a
          └=20┤         ┌=11k
               │    ┌=14┴=10j
               └=18┤    ┌=12l
                    └=15┴=13m
tree 15
     ┌=0outarea
├=23┤    ┌=3c
     ├=21┼=4d
     │    ├=8h
     │    └=9i
     │              ┌=6f
     │         ┌=16┴=5e
     │    ┌=19┴=7g
     └=22┤          ┌=2b
          │    ┌=17┴=1a
          └=20┤         ┌=11k
               │    ┌=14┴=10j
               └=18┤    ┌=12l
                    └=15┴=13m
```

```
tree 16
        ╔═0outarea
╞═21════╬═3c
        ╠═4d
        ╠═8h
        ╠═9i
        ║                   ╔═6f
        ║           ╔═17════╩═5e
        ║    ╔═19═══╩═7g
        ╚═20═╣      ╔═2b
             ║      ║       ╔═12l
             ╚═18═══╬═16════╩═13m
                    ║       ╔═1a
                    ╚═15════╣       ╔═10j
                            ╚═14════╩═11k
tree 17
        ╔═0outarea
╞═22════╬═3c
        ╠═4d
        ╠═8h
        ╠═9i
        ║                   ╔═6f
        ║           ╔═16════╩═5e
        ║    ╔═19═══╩═7g
        ╚═21═╣              ╔═13m
             ║      ╔═18════╩═12l
             ╚═20═══╣       ╔═2b
                    ╚═17════╣       ╔═1a
                            ╚═15════╣       ╔═10j
                                    ╚═14════╩═11k
tree 18
        ╔═0outarea
╞═22════╬═3c
        ╠═4d
        ╠═8h
        ╠═9i
        ║                   ╔═6f
        ║           ╔═16════╩═5e
        ║    ╔═19═══╩═7g
        ╚═21═╣              ╔═13m
             ║      ╔═18════╩═12l
             ╚═20═══╣               ╔═2b
                    ║       ╔═14════╩═1a
                    ╚═17════╣       ╔═10j
                            ╚═15════╩═11k
```

```
tree 19
    ╔═0outarea
╞═22╣   ╔═3c
    ╠═20╬═4d
    ║   ╠═8h
    ║   ╚═9i
    ║           ╔═6f
    ║       ╔═17╩═5e
    ║   ╔═19╩═7g
    ╚═21╣   ╔═2b
        ╚═18╣   ╔═12l
            ╠═16╩═13m
            ║   ╔═1a
            ╚═15╣   ╔═10j
                ╚═14╩═11k
tree 20
    ╔═0outarea
╞═23╣   ╔═3c
    ╠═21╬═4d
    ║   ╠═8h
    ║   ╚═9i
    ║           ╔═6f
    ║       ╔═16╩═5e
    ║   ╔═19╩═7g
    ╚═22╣       ╔═13m
        ║   ╔═18╩═12l
        ╚═20╣   ╔═2b
            ╚═17╣   ╔═1a
                ╚═15╣   ╔═10j
                    ╚═14╩═11k
tree 21
    ╔═0outarea
╞═23╣   ╔═3c
    ╠═21╬═4d
    ║   ╠═8h
    ║   ╚═9i
    ║           ╔═6f
    ║       ╔═16╩═5e
    ║   ╔═19╩═7g
    ╚═22╣       ╔═13m
        ║   ╔═18╩═12l
        ╚═20╣       ╔═2b
            ║   ╔═14╩═1a
            ╚═17╣   ╔═10j
                ╚═15╩═11k
```

```
tree 22
    ╔═0outarea
╞═21╬═3c
    ╠═4d
    ╠═8h
    ╠═9i
    ║             ╔═6f
    ║        ╔═14═╩═5e
    ║   ╔═18═╩═7g
    ╚═20╣
        ║        ╔═2b
        ║   ╔═15═╩═1a
        ╚═19╣    ╔═10j
            ╠═16═╩═11k
            ║    ╔═12l
            ╚═17═╩═13m
tree 23
    ╔═0outarea
╞═22╣   ╔═3c
    ╠═20╬═4d
    ║   ╠═8h
    ║   ╚═9i
    ║             ╔═6f
    ║        ╔═14═╩═5e
    ║   ╔═18═╩═7g
    ╚═21╣
        ║        ╔═2b
        ║   ╔═15═╩═1a
        ╚═19╣    ╔═10j
            ╠═16═╩═11k
            ║    ╔═12l
            ╚═17═╩═13m
tplot 3.8 seconds
nelsen file 0 from ie 24 trees
nelsen 0.0 seconds
tplot file 0 from nelsen 1 tree
    ╔═0outarea
╞═18╬═3c
    ╠═4d
    ╠═8h
    ╠═9i
    ║       ╔═13m
    ║       ╠═12l
    ║       ╠═11k
    ║       ╠═10j
    ║   ╔═15╬═2b
    ║   ║   ╚═1a
    ╚═17╣   ╔═7g
        ╚═16╣    ╔═5e
            ╚═14═╩═6f
tplot 0.1 seconds
```

Hadroid camaenids

Phylogenetic analysis

```
ccode
   0   1   2   3   4   5   6   7   8   9  10  11
 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[
ccode 0.0 seconds
ccode 0.0 seconds
ie length 23 ci 60 ri 67 trees 5
ie 0.1 seconds
tplot file 0 from ie 5 trees
tree 0
    ╔═0bradybaena
├═18╣═1meridolum
    ║   ╔═2varohadra
    ╚═17╣═3miniwilli
        ║   ╔═4zyghelix
        ╚═16╣   ╔═5hadra
            ╚═15╣       ╔═7sphaerospi
                ║   ╔═12╩═6thersites
                ╚═14╣   ╔═8bentosites
                    ╚═13╣   ╔═9figuladra
                        ╚═11╩═10temporena
tree 1
    ╔═0bradybaena
├═19╣═1meridolum
    ║           ╔═3miniwilli
    ║       ╔═16╩═2varohadra
    ╚═18╣   ╔═4zyghelix
        ╚═17╣   ╔═5hadra
            ╚═15╣       ╔═7sphaerospi
                ║   ╔═12╩═6thersites
                ╚═14╣   ╔═8bentosites
                    ╚═13╣   ╔═9figuladra
                        ╚═11╩═10temporena
tree 2
    ╔═0bradybaena
├═18╣═1meridolum
    ║   ╔═4zyghelix
    ╚═17╣   ╔═2varohadra
        ╚═16╣═3miniwilli
            ║   ╔═5hadra
            ╚═15╣       ╔═7sphaerospi
                ║   ╔═12╩═6thersites
                ╚═14╣   ╔═8bentosites
                    ╚═13╣   ╔═9figuladra
                        ╚═11╩═10temporena
```

```
tree 3
    ╔═0bradybaena
╞═19╬═1meridolum
    ║   ╔═4zyghelix
    ╚═18╣       ╔═3miniwilli
        ║   ╔═15╩═2varohadra
        ╚═17╣   ╔═5hadra
            ╚═16╣       ╔═7sphaerospi
                ║   ╔═12╩═6thersites
                ╚═14╣   ╔═8bentosites
                    ╚═13╣   ╔═9figuladra
                        ╚═11╩═10temporena
tree 4
    ╔═0bradybaena
╞═19╬═1meridolum
    ║   ╔═4zyghelix
    ╚═18╣   ╔═3miniwilli
        ╚═17╣   ╔═2varohadra
            ╚═16╣   ╔═7sphaerospi
                ╚═15╣   ╔═6thersites
                    ╚═14╣   ╔═5hadra
                        ╚═13╣   ╔═8bentosites
                            ╚═12╣   ╔═9figuladra
                                ╚═11╩═10temporena

best fits
character/steps/ci/ri
   0   1   2   3   4   5   6   7   8   9  10  11
   3   1   2   2   1   2   2   2   1   2   2   1
  66 100  50  50 100 100  50  50 100  50  50 100
   0 100  66  75 100 100  50   0 100  75   0 100

worst fits
character/steps/ci/ri
   0   1   2   3   4   5   6   7   8   9  10  11
   3   2   2   2   1   3   2   2   2   3   2   1
  66  50  50  50 100  66  50  50  50  33  50 100
   0  50  66  75 100  75  50   0  66  50   0 100

xsteps 0.3 seconds
nelsen file 0 from ie 5 trees
nelsen 0.0 seconds
tplot file 0 from nelsen 1 tree
    ╔═0bradybaena
╞═15╬═1meridolum
    ║   ╔═2varohadra
    ╚═14╬═3miniwilli
        ╠═4zyghelix
        ║   ╔═5hadra
        ╚═13╬═6thersites
            ╠═7sphaerospi
            ║   ╔═8bentosites
            ╚═12╣   ╔═9figuladra
                ╚═11╩═10temporena
```

```
tplot 0.1 seconds
xsteps file 0 from nelsen 1 tree
tree 0
character 0
 11 12 13 14 15
  0  0  0  0  0
character 1
 11 12 13 14 15
  1  1  1  1  0
character 2
 11 12 13 14 15
  0  1  1  0  0
character 3
 11 12 13 14 15
  0  0  1  1  0
character 4
 11 12 13 14 15
  1  1  1  1  0
character 5
 11 12 13 14 15
  1  1  1  0  0
character 6
 11 12 13 14 15
  0  0  0  0  0
character 7
 11 12 13 14 15
  0  0  0  0  0
character 8
 11 12 13 14 15
  1  1  1  0  0
character 9
 11 12 13 14 15
  1  1  1  0  0
character 10
 11 12 13 14 15
  0  0  0  0  0
character 11
 11 12 13 14 15
  1  1  0  0  0
```

```
ie length 22 ci 86 ri 89 trees 6
ie 0.1 seconds
tplot file 0 from ie 6 trees
tree 0
     ╔═0outarea
╞═19═╬═11k
     ║    ╔═1a
     ╚═18═╣    ╔═2b
          ╠═16═╩═3c
          ║    ╔═4d
          ╚═17═╣    ╔═5e
               ╚═15═╣    ╔═6f
                    ╚═14═╣    ╔═7g
                         ╚═13═╣    ╔═8h
                              ╚═12═╬═9i
                                   ╚═10j
tree 1
     ╔═0outarea
╞═19═╬═11k
     ║              ╔═3c
     ║         ╔═14═╩═2b
     ║    ╔═16═╩═1a
     ╚═18═╣    ╔═4d
          ╚═17═╬═5e
               ║    ╔═6f
               ╚═15═╣    ╔═7g
                    ╚═13═╣    ╔═8h
                         ╚═12═╬═9i
                              ╚═10j
tree 2
     ╔═0outarea
╞═20═╬═11k
     ║              ╔═3c
     ║         ╔═15═╩═2b
     ║    ╔═17═╩═1a
     ╚═19═╣    ╔═4d
          ╚═18═╣    ╔═5e
               ╚═16═╣    ╔═6f
                    ╚═14═╣    ╔═7g
                         ╚═13═╣    ╔═8h
                              ╚═12═╬═9i
                                   ╚═10j
```

```
tree 3
     ╔═0outarea
╞═20═╬═11k
     ║              ╔═3c
     ║         ╔═14═╩═2b
     ║    ╔═17═╩═1a
     ╚═19═╣         ╔═5e
          ║    ╔═15═╩═4d
          ╚═18═╣    ╔═6f
               ╚═16═╣    ╔═7g
                    ╚═13═╣    ╔═8h
                         ╚═12═╬═9i
                              ╚═10j
tree 4
     ╔═0outarea
╞═19═╬═11k
     ║              ╔═3c
     ║         ╔═13═╩═2b
     ║    ╔═16═╩═1a
     ╚═18═╣         ╔═6f
          ║    ╔═14═╬═5e
          ║    ║    ╚═4d
          ╚═17═╣    ╔═7g
               ╚═15═╣    ╔═8h
                    ╚═12═╬═9i
                         ╚═10j
tree 5
     ╔═0outarea
╞═20═╬═11k
     ║              ╔═3c
     ║         ╔═14═╩═2b
     ║    ╔═17═╩═1a
     ╚═19═╣              ╔═5e
          ║         ╔═12═╩═4d
          ║    ╔═15═╩═6f
          ╚═18═╣    ╔═7g
               ╚═16═╣    ╔═8h
                    ╚═13═╬═9i
                         ╚═10j
tplot 0.8 seconds
nelsen file 0 from ie 6 trees
nelsen 0.0 seconds
tplot file 0 from nelsen 1 tree
     ╔═0outarea
╞═17═╬═11k
     ║    ╔═1a
     ╚═16═╣    ╔═2b
          ╠═14═╩═3c
          ║    ╔═4d
          ╚═15═╬═5e
               ╠═6f
               ║    ╔═7g
               ╚═13═╣    ╔═8h
                    ╚═12═╬═9i
                         ╚═10j
tplot 0.1 seconds
```

Hadra

Phylogenetic analysis

```
ccode 0.0 seconds
ccode
  0   1   2   3   4   5   6   7   8   9  10  11
 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[
ccode 0.0 seconds
ie length 20 ci 65 ri 56 trees 1
ie 0.1 seconds
tplot file 0 from ie 1 tree
   ╔═0forsterian
╞═9╬═4bellendenk
   ║   ╔═3barneyi
   ╚═8╣   ╔═5rudis
       ╚═7╣   ╔═1bipartita
          ╚═6╩═2dunkiensis
tplot 0.1 seconds
xsteps file 0 from ie 1 tree
tree 0
character 0
 6 7 8 9
 0 1 1 1
character 1
 6 7 8 9
 0 0 0 0
character 2
 6 7 8 9
 0 0 1 1
character 3
  6   7   8   9
 01  01  01  01
character 4
 6 7 8 9
 0 0 0 1
character 5
 6 7 8 9
 0 0 0 0
character 6
 6 7 8 9
 1 1 1 0
character 7
 6 7 8 9
 0 0 0 0
```

```
character 8
 6 7 8 9
 0 0 0 1
character 9
  6   7   8   9
  1   1  01  01
character 10
 6 7 8 9
 0 1 1 1
character 11
 6 7 8 9
 0 0 1 1
xsteps 0.3 seconds
xsteps file 0 from ie 1 tree
tree 0 length 20 ci 65 ri 56
character/steps/ci/ri
   0    1    2    3    4    5    6    7    8    9   10   11
   2    2    1    3    1    1    2    2    1    2    2    1
  50   50  100   33  100  100   50  100  100   50   50  100
  50    0  100    0  100  100   50  100  100    0   50  100
```

Biogeographic analysis

```
ccode
   0    1    2    3    4    5    6    7    8
 1+[  1+[  1+[  1+[  1+[  1+[  1+[  1+[  1+[
ccode 0.0 seconds
ie length 10 ci 90 ri 85 trees 1
ie 0.3 seconds
tplot file 0 from ie 1 tree
       ┌=0outarea
├=13┤      ┌=8h
       ├=12┴=9i
       │      ┌=1a
       └=11┼=2b
              ├=3c
              │     ┌=4d
              └=10┼=5e
                    ├=6f
                    └=7g
tplot 0.1 seconds
```

Sphaerospira

Phylogenetic analysis

```
ccode 0.0 seconds
ccode
   0   1   2   3   4   5   6
 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[
ccode 0.1 seconds
ie length 9 ci 77 ri 50 trees 2
ie 0.1 seconds
tplot file 0 from ie 2 trees
tree 0
   ╔═0thersites
╞═7╬═2blomfieldi
   ║  ╔═3informis
   ╚═6╣  ╔═1fraseri
      ╚═5╩═4sp_nov
tree 1
   ╔═0thersites
╞═7╬═1fraseri
   ║  ╔═3informis
   ╚═6╣  ╔═2blomfieldi
      ╚═5╩═4sp_nov
tplot 0.1 seconds
xsteps file 0 from ie 2 trees
tree 0
character 0
 5 6 7
 0 0 0
character 1
 5 6 7
 0 0 1
character 2
 5 6 7
 0 1 1
character 3
 5 6 7
 0 0 0
character 4
 5 6 7
 1 1 1
character 5
 5 6 7
 0 0 0
```

```
character 6
 5 6 7
 0 0 0
tree 1
character 0
 5 6 7
 1 0 0
character 1
 5 6 7
 0 0 0
character 2
 5 6 7
 1 1 1
character 3
 5 6 7
 0 0 0
character 4
 5 6 7
 1 1 0
character 5
 5 6 7
 0 0 0
character 6
 5 6 7
 0 0 0
xsteps 0.3 seconds
xsteps file 0 from ie 2 trees
tree 0 length 9 ci 77 ri 50
character/steps/ci/ri
    0   1   2   3   4   5   6
    2   1   1   1   2   1   1
   50 100 100 100  50 100 100
    0 100 100 100   0 100 100

tree 1 length 9 ci 77 ri 50
character/steps/ci/ri
    0   1   2   3   4   5   6
    1   2   2   1   1   1   1
  100  50  50 100 100 100 100
  100   0   0 100 100 100 100

best fits
character/steps/ci/ri
    0   1   2   3   4   5   6
    1   1   1   1   1   1   1
  100 100 100 100 100 100 100
  100 100 100 100 100 100 100

worst fits
character/steps/ci/ri
    0   1   2   3   4   5   6
    2   2   2   1   2   1   1
   50  50  50 100  50 100 100
    0   0   0 100   0 100 100
```

```
TREE 0
ccode
   0   1   2   3   4   5   6
 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[
ccode 0.1 seconds
ie length 8 ci 87 ri 66 trees 1
ie 0.0 seconds
tplot file 0 from ie 1 tree
   ╔═0outarea
╞═7╬═3c
   ║  ╔═1a
   ╚═6╣  ╔═2b
      ╚═5╩═4d
tplot 0.0 seconds
```

```
TREE 1

ccode
   0   1   2   3   4   5   6
 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[
ccode 0.0 seconds
ie length 7 ci 100 ri 100 trees 1
ie 0.1 seconds
tplot file 0 from ie 1 tree
   ╔═0outarea
╞═7╬═4d
   ║  ╔═1a
   ╚═6╣  ╔═2b
      ╚═5╩═3c
tplot 0.1 seconds
```

Bentosites

Phylogenetic analysis

```
ccode 0.0 seconds
ccode
   0    1    2    3    4    5    6    7    8    9
 1-[  1-[  1-[  1-[  1-[  1-[  1-[  1-[  1-[  1-[
ccode 0.1 seconds
ie length 21 ci 47 ri 56 trees 1
ie 0.2 seconds
tplot file 0 from ie 1 tree
     ╒═0fraseri
╞═15╪═5macleayi
    │   ╒═3zebina
    ╘═14┤   ╒═2yulei
        ╘═13┤   ╒═8sp. nov.
            ╘═12┤   ╒═7gavisa
                ╘═11┤   ╒═4mazee
                    ╘═10┤  ╒═1mulgravens
                        ╘═9╧═6rawnesleyi
tplot 0.1 seconds
xsteps file 0 from ie 1 tree
tree 0
character 0
  9 10 11 12 13 14 15
  0  0  0  0  0  0  0
character 1
  9 10 11 12 13 14 15
  1  1  1  1  1  1  1
character 2
  9 10 11 12 13 14 15
  1  0  0  0  0  0  0
character 3
  9 10 11 12 13 14 15
  1  1  0  0  0  0  1
character 4
  9 10 11 12 13 14 15
  0  0  0  1  1  1  0
character 5
  9 10 11 12 13 14 15
  1  1  1  0  0  0  0
```

```
character 6
  9 10 11 12 13 14 15
  1  1  1  1  1  0  0
character 7
  9 10 11 12 13 14 15
  1  1  1  1  1  0  0
character 8
  9 10 11 12 13 14 15
  1  1  0  0  0  0  0
character 9
  9 10 11 12 13 14 15
  1  1  1  1  0  0  0
xsteps 0.3 seconds
xsteps file 0 from ie 1 tree
tree 0 length 21 ci 47 ri 56
character/steps/ci/ri
   0   1   2   3   4   5   6   7   8   9
   3   2   3   2   2   1   2   1   2   3
  33  50  33  50  50 100  50 100  50  33
   0   0  33  66  50 100  66 100  66  33
```

Biogeographic analysis

```
ccode
   0   1   2   3   4   5   6   7   8   9  10  11  12  13  14
 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[
ccode 0.1 seconds
ie length 17 ci 88 ri 90 trees 1
ie 0.0 seconds
tplot file 0 from ie 1 tree
    ╔═0outarea
├═19╣═5e
    ║   ╔═9i
    ╚═18╣   ╔═10j
        ╚═17╣       ╔═8h
            ║   ╔═15╩═7g
            ╚═16╣   ╔═2b
                ╚═14╣   ╔═1a
                    ╚═13╣   ╔═6f
                        ╚═12╣   ╔═3c
                            ╚═11╩═4d

 tplot 0.1 seconds
```

Temporena

Phylogenetic analysis

```
ccode 0.0 seconds
ccode
  0   1   2   3   4   5   6
 1-[ 1-[ 1-[ 1-[ 1-[ 1-[ 1-[
ccode 0.0 seconds
ie length 11 ci 63 ri 42 trees 2
ie 0.0 seconds
tplot file 0 from ie 2 trees
tree 0
   ╔═0figuladra
╞═7╣═1whartoni
   ║  ╔═3coxi
   ╚═6╣  ╔═2macneilli
      ╚═5╩═4etheridgei
tree 1
   ╔═0figuladra
╞═7╣  ╔═1whartoni
   ╠═5╩═2macneilli
   ║  ╔═3coxi
   ╚═6╩═4etheridgei
tplot 0.1 seconds
xsteps file 0 from ie 2 trees
tree 0
character 0
 5 6 7
 1 1 1
character 1
 5 6 7
 1 1 0
character 2
 5 6 7
 1 1 1
character 3
  5  6  7
 01 01  0
character 4
 5 6 7
 1 1 1
```

```
character 5
 5 6 7
 0 1 1
character 6
 5 6 7
 0 1 1
tree 1
character 0
 5 6 7
 0 1 1
character 1
  5   6   7
 01   1 01
character 2
 5 6 7
 0 1 1
character 3
 5 6 7
 0 1 0
character 4
  5   6   7
 01   1 01
character 5
 5 6 7
 1 1 1
character 6
 5 6 7
 1 1 1
xsteps 0.3 seconds
xsteps file 0 from ie 2 trees
tree 0 length 11 ci 63 ri 42
character/steps/ci/ri
    0   1   2   3   4   5   6
    2   1   2   2   2   1   1
   50 100  50  50  50 100 100
    0 100   0   0   0 100 100

tree 1 length 11 ci 63 ri 42
character/steps/ci/ri
    0   1   2   3   4   5   6
    1   2   1   1   2   2   2
  100  50 100 100  50  50  50
  100   0 100 100   0   0   0

best fits
character/steps/ci/ri
    0   1   2   3   4   5   6
    1   1   1   1   2   1   1
  100 100 100 100  50 100 100
  100 100 100 100   0 100 100

worst fits
character/steps/ci/ri
    0   1   2   3   4   5   6
    2   2   2   2   2   2   2
   50  50  50  50  50  50  50
    0   0   0   0   0   0   0
```

```
TREE 0

ccode
  0   1   2   3   4   5   6
 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[
ccode 0.0 seconds
ie length 8 ci 87 ri 88 trees 4
ie 0.1 seconds
tplot file 0 from ie 4 trees
tree 0
    ┌═0outarea
├═12┼═3c
    │   ┌═5e
    └═11┼═7g
        │      ┌═4d
        │   ┌═8┴═2b
        └═10┤  ┌═1a
            └═9┴═6f
tree 1
    ┌═0outarea
├═13┼═3c
    │       ┌═7g
    │   ┌═11┴═5e
    └═12┤      ┌═4d
        │   ┌═8┴═2b
        └═10┤  ┌═1a
            └═9┴═6f
tree 2
    ┌═0outarea
├═12┼═3c
    │      ┌═4d
    │   ┌═9┴═2b
    └═11┤   ┌═5e
        └═10┼═7g
            │  ┌═1a
            └═8┴═6f
tree 3
    ┌═0outarea
├═13┼═3c
    │       ┌═4d
    │   ┌═10┴═2b
    └═12┤      ┌═6f
        │   ┌═8┴═1a
        └═11┤  ┌═5e
            └═9┴═7g
```

```
tplot 0.4 seconds
nelsen file 0 from ie 4 trees
nelsen 0.0 seconds
tplot file 0 from nelsen 1 tree
    ╔═0outarea
╟═11╬═3c
    ║    ╔═5e
    ╚═10╬═7g
         ║   ╔═2b
         ╠═8╩═4d
         ║   ╔═1a
         ╚═9╩═6f
tplot 0.1 seconds
```

```
TREE 1

ccode
   0   1   2   3   4   5   6
 1+[ 1+[ 1+[ 1+[ 1+[ 1+[ 1+[
ccode 0.0 seconds
ie length 7 ci 100 ri 100 trees 1
ie 0.0 seconds
tplot file 0 from ie 1 tree
     ╔═0outarea
╟═11╣     ╔═1a
     ╠═10╬═5e
     ║    ╠═6f
     ║    ╚═7g
     ║   ╔═3c
     ╚═9╣   ╔═2b
         ╚═8╩═4d
tplot 0.1 seconds
```