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AN ENDEMIC RADIATION OF HYDROBIID SNAILS FROM ARTESIAN SPRINGS IN NORTHERN SOUTH AUSTRALIA: THEIR TAXONOMY, PHYSIOLOGY, DISTRIBUTION AND ANATOMY

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CONTENTS

ABSTRACT

Artesian springs between Marree and Oodnadatta contain an endemic fauna of hydrobiid snails that have undergone an adaptive radiation in which habitat partitioning and size displacement are clearly evident. Ten new species in two new endemic genera, *Fonscochlea* and *Trochidrobia*, are described. Three of the species of *Fonscochlea* are divided into a total of six geographic forms, which are not formally named. Two geographic forms are restricted to single springs, the remainder being found in several springs, spring groups, or complexes of springs. *Fonscochlea* is divided in to two subgenera, *Fonscochlea* s.s. containing five species and *Wolfgangia* with a single species.

Both genera are represented in most springs, with up to five taxa present in single springs in the Freeling Springs Group and in some of the other springs in the northern part of the spring system. As many as four taxa are present in most other springs. The pattern of one or two sympatric species of *Trochidrobia*, a large, amphibious species of

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Fonscochlea, one large aquatic species of *Fonscochlea* and a small aquatic species of *Fonscochlea* is established in most of the springs in the area. Some of the factors leading to the evolution and maintenance of this diversity are discussed.

A subjective classification, based on shell, opercular and anatomical characters, was tested phenetically using discriminate analysis.

Simple physiological experiments were carried out on some of the taxa to test for the effects of temperature, submergence, desiccation, increased salinity, reduced dissolved oxygen, and responses to light. All taxa showed a wide range of tolerance to salinity and temperature but the small animals were more susceptible to desiccation than the large ones. Varying responses to light and submergence were obtained but all taxa showed reduced activity in deoxygenated water.

The anatomy of the type species of both genera is described in detail. *Fonscochlea* is unique in having two equal-sized sperm sacs in the female that are probably derived from the bursa copulatrix and, as in *Trochidrobia*, which has a single sperm sac, the seminal receptacle is lost.

The endemic snails, together with the unusual endemic crustaceans sympatric with them, and their unusual community structure, give the springs special interest, both from the scientific and conservation viewpoints.

Key words: Mollusca, Hydrobiidae, springs, endemics, taxonomy, physiology, anatomy, speciation, sympatry, habitat partitioning

INTRODUCTION

The most nearly permanent type of water body in an arid environment is probably an artesian spring (Naiman, 1981). The habitat provided by an artesian spring in this situation is analogous to that of an island. Each spring is typically separated by arid land providing as marked a discontinuity of habitat as the sea does to terrestrial organisms. Artesian springs are typically permanent, within a moderate time scale, perhaps in the order of thousands to even millions of years for spring systems but tens to hundreds of years for individual springs, and usually provide a reasonable diversity of habitats. Given these conditions one might expect genetic differentiation of populations in separate springs and some habitat partitioning allowing similar species to coexist. Studies of the faunas of arid-zone artesian springs have sometimes revealed spectacular examples of speciation and habitat partitioning. The best documented examples are of the fishes of the western deserts in the United States and northern Mexico (Minckley, *et al.*, 1986), particularly of the Death Valley system (Soltz & Naiman, 1978). Studies of these fishes have provided insight into the nature of the speciation process (Turner, 1974; Soltz & Hirshfield, 1981), biogeography relative to drainage history (Hubbs & Miller, 1948; Hubbs *et al.*, 1974; Smith, 1978) and adaptation to diverse spring-fed habitats (Naiman & Soltz, 1981).

Natural water bodies in arid lands, such as springs, water in caves and marshes, are frequently refugia for relict biota. There are numerous examples, particularly amongst fishes and crustaceans, that are well documented. A spectacular example is the crocodiles in pools in the Ahaggar Mountains of Africa, now surrounded by vast desert areas (Cole, 1968). Springs sometimes support diverse faunas that might be partly relictual and partly endemic radiations. The hydrobiid snails of the Cuatro Cienegas Basin, Coahuila, Mexico, are presumably an example of such a fauna (Taylor, 1966a; Hershler, 1984, 1985).

Radiations of hydrobiid snails in springs in temperate climates are also known, examples including those in Florida (Thompson, 1968) and parts of Europe (e.g., Radoman, 1983). A spectacular radiation of the related family Pomatiopsidae in Southeast Asia has been well documented by Davis (1979).

Bayly and Williams (1973) note that extremely little is known about the biology of Australian springs. This is certainly true for the artesian springs associated with the Great Artesian Basin. Before this study commenced the only animals that had been studied in detail in artesian springs in arid Australia were the fishes (Glover & Sim, 1978a; Glover, 1982). Recent biological work is summarised by Ponder (1986).

The artesian springs in the arid north of South Australia (Figs. 1, 2) were only recently shown to contain a large and interesting biota (Mitchell, 1985; Symon, 1985; Ponder, 1985, 1986). To date the only invertebrates described from these mound springs are a phreatoicid isopod (*Phreatomerus latipes* (Chilton, 1922), an ostracode, *Nagarawa dirga* (DeDeckker, 1979), and a macrostomid flatworm, the first record of this order from Australia (Sluys, 1986). Both of the Crustacea are endemic to the springs and belong in monotypic subfamilies.

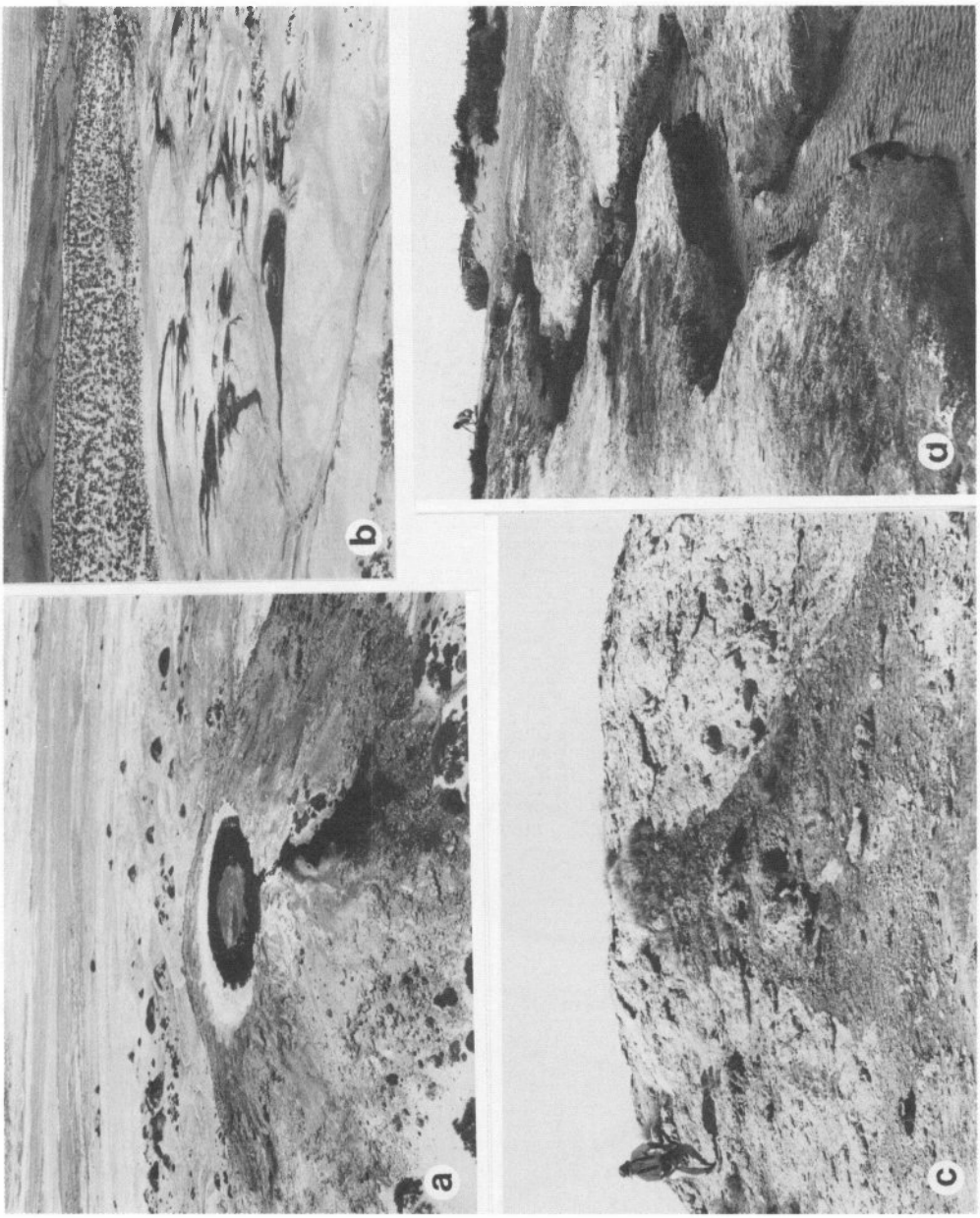


FIG. 1. Various springs in the Lake Eyre Supergroup showing some of the morphological diversity.
A. Blanche Cup Spring (Stns 8–12), a conical, calcareous mound spring with a crater-like pool.
B. Aerial view of part of Hermit Hill Spring Complex showing part of a spring group (Finniss Swamp West) composed of small ground-level springs and some low sand mounds.
C. Almost extinct mound in the Blanche Cup Complex, in the Horse Spring Group (stn 748). Snails and crustaceans are abundant in small seeps such as this.
D. The Bubbler Spring (stns 13–17), one of the largest flows in the Lake Eyre Supergroup.

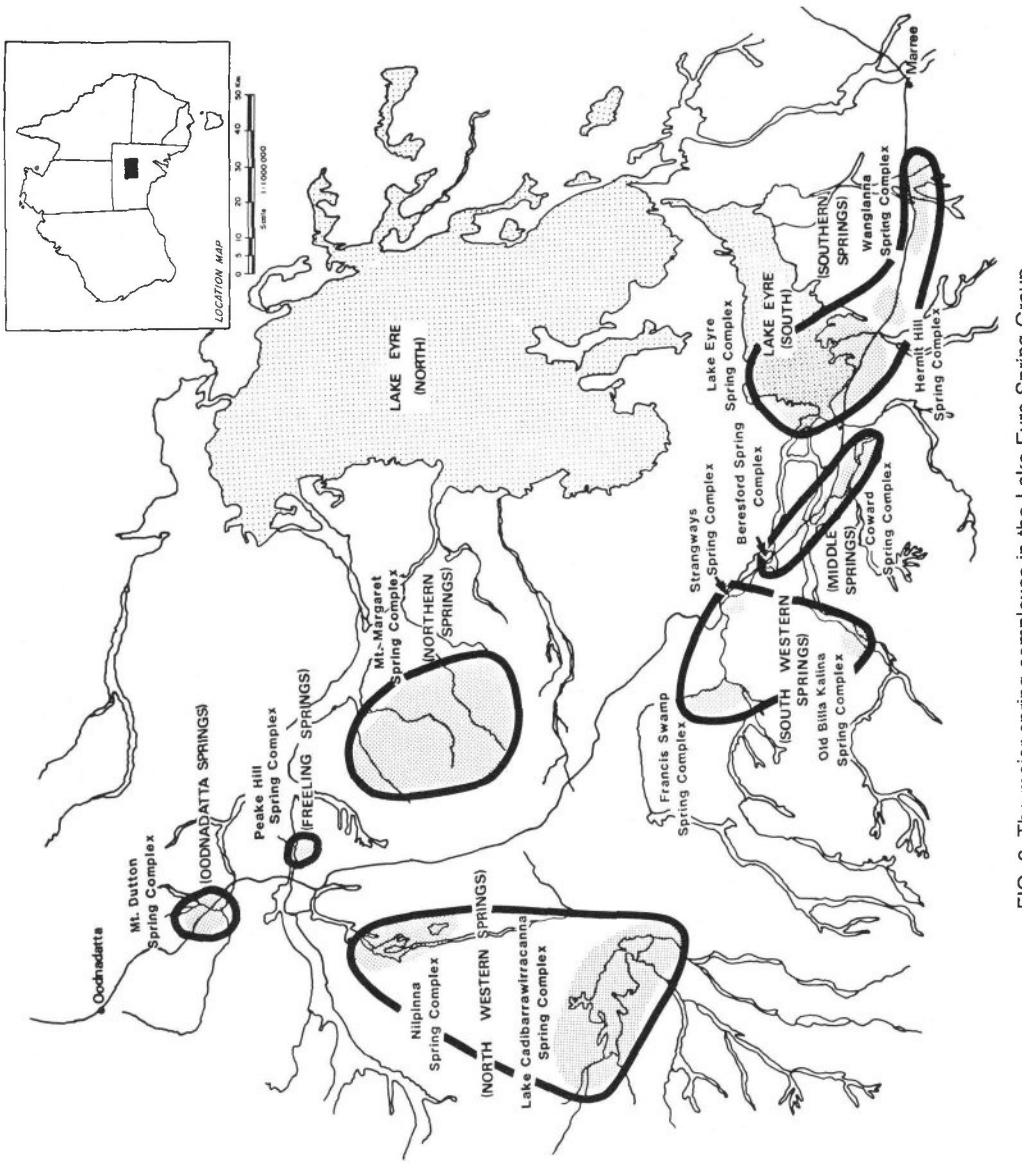


FIG. 2. The major spring complexes in the Lake Eyre Spring Group.

Gastropod molluscs were reported from the mound springs by Mitchell (1980, unpublished; 1985) who, on the advice of Dr. B. Smith, to whom the material was sent for identification, recognized the presence of three or possibly four species referable to three or four genera. DeDeckker (1979) also refers to these snails as undescribed endemics, on Smith's advice. We cannot find any earlier references to these species in the literature, despite their being conspicuous and abundant in most of the springs. A few of the early explorers noticed the small fish found in some springs (see review by Glover & Sim, 1978b).

Some of the more accessible mound springs were visited in the latter part of the 1970's by several biologists who made some collections, those of W. Zeidler of the South Australian Museum being the most significant. His collections and those sent to Dr. B. Smith were made available to one of us (W.F.P.) and field work was carried out in 1981 by W.F.P. and Zeidler. The result of that field investigation, and an additional one the same year by Zeidler, showed the existence of an apparent endemic fauna of hydrobiid snails of considerable diversity.

The available information on the mound-spring fauna was reviewed in an Environmental Impact Statement (E.I.S.) for the Olympic Dam Project (Kinhill-Stearns Roger, 1982) and in a supplement to this E.I.S. (Kinhill-Stearns, 1983). The review in the supplement included some new information on the hydrobiid snails provided by two of us (W.F.P., B.W.J.). Because the Olympic Dam Project required water from a borefield located near a large spring complex at Hermit Hill (Fig. 2; Appendix 1, Fig. 62), further biological and hydrological studies were carried out to assess the importance of the flora and fauna associated with these springs. This paper has been developed from the report resulting from those studies. A summary of the results of the hydrobiid work appears in the report prepared for Roxby Management Services on the mound springs (Ponder & Hershler, 1984).

The importance of the springs and the need for their conservation has been stressed by Casperton (1979), Harris (1981), Symon (1985) and Ponder (1985, 1986). This view has also been strongly supported by the evidence accumulated in the reports prepared as a result of the Olympic Dam Project (Kinhill-Stearns Roger, 1982, Kinhill-Stearns, 1983, 1984). The World Wildlife Fund has recently provided funds to fence some springs.

The snails present in the mound springs are members of the Hydrobiidae, a worldwide family of prosobranch gastropods that are part of the large, predominantly marine superfamily Truncatelloidea. The hydrobiids were probably derived from brackish-water ancestors in the middle part of the Mesozoic (Ponder, 1988) and some members of the family are still restricted to brackish-water environments. To date the family is known to be represented in Australia by about nine genera and approximately 35 named species, excluding those from the mound springs, although recent unpublished work by W.F.P. shows that this fauna is actually much larger.

The adaptations of organisms to the diverse and often extremely harsh aquatic environments in deserts are of interest to physiologists as well as ecologists and evolutionary biologists. While a variety of taxa are usually found in such waters, only the desert fishes are well studied in terms of their ecology and physiology (see summaries, Deacon & Minckley, 1974; Soltz & Naiman, 1978; Naiman & Soltz, 1981). In areas in which hydrobiid snails have radiated extensively in desert waters, particularly spring systems of North and Central America (Taylor, 1966a, b; Hershler, 1985; Hershler & Landye, 1988) and Australia (Ponder, 1986), their frequent local diversity and high densities suggest that they are trophically important members of desert aquatic communities. Yet there is a paucity of data concerning their ecology and virtually nothing is known of their physiology. Tolerances to the environmental parameters that often achieve extreme levels in desert waters (e.g., salinity, temperature), have not been studied for any spring-dwelling hydrobiid species, although some work on South African species of *Tomichia,* of the related family Pomatiopsidae, has been done (Davis, 1981).

This paper commences with an introductory section outlining the main features of the mound springs. The rest of the paper is divided into three sections. The first deals with the taxonomy of the hydrobiid snails, followed by a detailed account of the anatomy of the type species of the two genera found in the springs. The results of the physiological work done in the field are presented in the third section.

The mound springs—a brief description

Geomorphology and water chemistry: The artesian mound springs of South Australia are aligned in an arc running from the far northern

part of the state at Dalhousie Springs, north of Oodnadatta, around the south of Lake Eyre to Lake Frome and Lake Callabonna on the eastern side of the Flinders Ranges. Additional artesian springs are found in western Queensland and were found in the north-west of New South Wales, but these are now mostly extinct (personal observations by W.F.P. and M.A. Habermehl, pers. comm.), presumably as a result of water extraction from the basin by the pastoral industry. The springs are natural discharges from the aquifers formed from the Jurassic and Cretaceous sedimentary rocks of the Great Artesian Basin (see Habermehl, 1980, 1982, for geological details). They occur in a variety of forms, the most common being small mounds resulting from groundwater precipitates, mainly carbonates, and fine sediments derived from the aquifer and confining beds. Wind-blown debris and plant material also contribute to the mound formation. The mounds are composed primarily of hard travertine or of sediment, or layers of both. They range from virtually flat to large mounds several tens of meters high. The larger mounds are the older springs, the ground-level springs the youngest (Ponder, 1986: Fig. 4). More detailed descriptions of the springs are provided by Watts (1975), Habermehl (1982), Thomson and Barnett (1985), and Ponder (1986). The South Australian mound springs are the most active and numerous of the artesian springs fed by the Great Artesian Basin (Habermehl, 1982) and are now the best known biologically. The little that is known of Queensland artesian springs is summarised by Ponder (1986).

Dalhousie Springs, to the north of Oodnadatta, yields about 95% of the natural discharge from the Great Artesian Basin in South Australia (Williams, 1979; Williams & Holmes, 1978). These springs are, however, outside the present study area, as are some small springs east of Marree to the north and east of the northern Flinders Ranges. Some of these springs contain endemic invertebrates, including hydrobiids, and these will be dealt with elsewhere. The springs included in this report (Fig. 2; Appendix 1) are located mainly on the Warrina, Billa Kalina and Curdimurka 1:250,000 map sheets and a few on the Oodnadatta sheet. They form a zone about 400 km long and as much as 20 km wide between Marree and Oodnadatta (Fig. 2) and are referred to as the Lake Eyre group by Habermehl (1982) and the Lake Eyre Supergroup by Ponder (1986).

The morphology of the springs in the Lake Eyre Supergroup is diverse (Fig. 1). The springs range from surface seeps (Fig. 1b) to low, conical mounds (Fig. 1a, c) or even small hills. The mounds consist of sand, silt and clay, often cemented by carbonate and overlain by layers of carbonate (Habermehl, 1980, 1982). The cemented mounds often persist for considerable periods after the springs that formed them have ceased to flow, but the unconsolidated mounds erode rapidly. Some mounds have a crater-like, water-filled depression at the top (Fig. 1a), while others have rounded domes (Fig. 1c); both types typically have one or more outlets. Some of the larger, dome-like mounds (e.g., Kewson Hill and the Elizabeth Springs mound) have several small seeps issuing from them.

Discharges from most of the springs are small, ranging from about 0.5 litre per second to 7.5 litres per second at the Bubbler Spring (Fig. 1d) (Cobb, 1975; Williams, 1979; Habermehl, 1982). Despite this, discharge from some springs is sufficient to maintain flows for several hundred metres or, more rarely, a kilometre or more, providing a well-vegetated wetland habitat. Other springs have such a small discharge that they do not maintain an outflow, having only a pool or small swampy area at the head. Others are merely permanently damp patches that might flow occasionally. Some small springs in the Hermit Hill complex (Fig. 1b) have been observed flowing on some occasions and are dry on others. The Lake Eyre Supergroup has a total estimated discharge of 100–200 litres per second (Habermehl, 1982), compared with 670 litres per second for Dalhousie Springs (A.F. Williams, 1974; Williams & Holmes, 1978).

The depth of the water in the pools and outflows rarely exceeds 2–3 cm and is usually only a few millimetres. The pools and outflows usually contain sedges but rarely true aquatic vegetation apart from algae. The outflows are usually narrow trickles with a firm, sandy base and, in the case of the hard mounds, calcareous rock.

Our observations indicate that the area of outflow diminishes in summer, presumably owing to increasing evaporation, and some observations suggest that periods of high barometric pressure coincide with reduced water flow (C. Woolard, pers. comm.).

Williams and Holmes (1978) have estimated that a spring with a small discharge typical of many of the springs in the Lake Eyre

Supergroup, shown on the Curdimurka map sheet, would take about 1000 years to deposit sufficient calcium carbonate to build a hemispherical mound three metres high. On this basis some of the larger mounds, such as Kewson Hill, might, even with substantially increased flow rates, take several tens of thousands of years to form. Forbes (1961) has shown, however, that drilling on mounds in this vicinity reveals that a substantial portion of the mound is formed by the deposition of sand and clay rather than "limestone", suggesting that the calculations by Williams and Holmes (1978) might be invalid.

Analyses of the water from the springs in the Lake Eyre Supergroup have been given by Cobb (1975), Williams (1979) and Kinhill-Stearns (1984) and summarized by Habermehl (1982). Sodium and bicarbonate are the major ions in springs in the eastern part of the Lake Eyre group whereas in springs in the western part the bicarbonate component is small and sodium and chloride ions predominate over calcium and sulphate. Total dissolved solids in most springs range from 2000–4000 ppm, with a few in excess of 5000 ppm, and pH from about 7.1 to 8.1, although a field pH of up to 9.95 has been recorded in recent surveys. The temperatures in the spring vents are constant throughout the year and show a slight increase from east to west ranging from upper teens to mid-twenties (°C) in the east to upper twenties in the west. The salinity increases toward the discharge areas of the Great Artesian Basin.

A few springs in the Lake Eyre Supergroup might not originate from the waters of the Great Artesian Basin aquifer, or show significant mixing with sulphate-rich ground-water, as their hydrochemistry is atypical. These springs are located on the faulted edge of the basement rocks and include Kerlatroaboorntallina Spring, Talton Springs, Edith Spring, Dead Boy Spring and Pigeon Hill Springs, the last two in the Hermit Hill Complex. None of these springs contains the typical mound spring invertebrates.

Exploitation of the water from the Great Artesian Basin has resulted in a drop of the potentiometric surface by several tens of metres in heavily developed areas (Habermehl, 1980). Even by the turn of the century the sinking of bores near some springs had greatly reduced or extinguished their flow (Pittman & David, 1903).

At present, a new steady-state condition appears to have been reached in which total recharge and discharge are approaching equilibrium again (Habermehl & Seidel, 1979; Habermehl, 1980), and little change is expected to occur in the discharge rates of the springs provided no new well development takes place.

Spring groups and complexes: The mound springs in the Lake Eyre Supergroup are not distributed evenly and for the purposes of this report can be divided into several major spring complexes. Within each of these complexes spring groups can be identified. A spring complex can be defined as a large cluster of springs separated from adjacent spring clusters by several tens of kilometres. Smaller groups of springs, either within a complex or an isolated group, can be referred to as spring groups. For example, Hawker Springs can be called a spring group within the Mt. Margaret Spring Complex. In the Hermit Hill Spring Complex there are several spring groups, e.g., Finniss Swamp West (= West Finniss), Hermit Hill Springs Proper and Old Woman Springs. The following classification of spring complexes in the Lake Eyre Supergroup is essentially that proposed by Kinhill-Stearns (1984) (Fig. 2). Table 1 lists the springs, grouped in complexes, containing hydrobiids.

To facilitate discussion we have arranged these spring complexes into seven informal systems (Fig. 2), the arrangement being biased towards the distribution of the hydrobiid fauna. Detailed maps for each spring area are given in Appendix 1 and these are referred to in the list below.

1. The Oodnadatta Springs.

Mt. Dutton Spring Complex. The few small springs on the Oodnadatta Map Sheet that lie southeast of Oodnadatta (Appendix 1, Fig. 63).

2. The Freeling Springs:

The Peake Hill Spring Complex. Includes the Freeling Springs and a few small springs to the north and northwest of Mt. Denison (Appendix 1, Figs. 58, 63B).

3. The Northern Springs:

Mount Margaret Spring Complex. Includes the large, scattered group of springs to the east of Mt. Margaret, as well as the Peake and Denison Ranges (Appendix 1, Fig. 59).

4. The North Western Springs:

a) Nilpinna Spring Complex. A few scattered, small, springs to the west of the Marree-Oodnadatta Road and west of the Mt. Margaret Spring Complex (Appendix 1, Fig. 58).

TABLE 1. Distribution of taxa in springs and spring complexes. x = present (living), s = shells only

SPRING OR SPRING GROUP	*F. zeidleri* form A	*F. zeidleri* form B	*F. aquatica* form A	*F. aquatica* form B	*F. accepta* form A	*F. accepta* form B	*F. accepta* form C	*F. variabilis* form A	*F. variabilis* form B	*F. variabilis* form C	*F. billakalina*	*F. conica*	*T. punicea*	*T. smithi*	*T. minuta*	*T. inflata*	SPRING COMPLEX
Southern Springs																	
Welcome group	x				x							x	x				Wangianna
Davenport group	x				x							x	x				Spring Complex
Old Woman group	x					x						x	x				
West Finniss group	x					x						s	x				
Hermit Springs group	x					x							x				
Old Finniss group	x					x							x				Hermit Hill
Dead Boy Spring						x							x				Spring Complex
Sulphuric group						x							x				
Bopeechee Spring						x							x				
Venable Spring	s					s						s	s				
Priscilla Spring	s					s						s	s				Lake Eyre
Centre Island Spring	s																Spring
Emerald Spring							x										Complex
Middle Springs																	
Horse East group	x		x									x	x				
Horse West group	x		x									x	x				
Strangways Spring	x		x									x	x				
Mt. Hamilton Spring	x		x										x				Blanche Cup
Blanche Cup group (785, 787)	x		x									x	x				Spring
Blanche Cup Spring	x		x					x					x				Complex
Blanche Cup group (786)	x		x					x					x				
Little Bubbler Spring	x		x					x					x				
The Bubbler Spring	x		x					x					x				
Coward Springs Railway Bore	x							x									
Coward Springs group	x		x									x	x				
Kewson Hill group	x		x									x	x				Coward Spring
Julie group	x		x									x	x				Complex
Elizabeth group	x		x									x	x				
Jersey group	x		x									x	x				
Warburton group	x		x									x		x			Beresford Spring
Beresford group	x		x									x		x			Complex
South-Western Springs																	
Strangways group	x		x								x			x			Strangways Spring Complex
Billa Kalina group	x		x								x			x			Old Billa Kalina
Fenced Spring	x		x								x			x			Spring
Welcome Bore Spring	s										s						Complex
Margaret Spring	s		s								s			s			Francis Swamp
Francis Swamp group	x		x								x			x			Spring
Loyd Bore spring	x		x								x			x			Complex
Northern Springs																	
Brinkley Spring	x		x											x			
Hawker group	x		x						x					x			
Twelve Mile group	x		x						x					x	x		Mt. Margaret
Outside group	x		x						x					x	x		Spring
Fountain group	x		x						x					x	x		Complex
Big Perry Spring	x		x						x					x	x		
Spring Hill Spring	s																
Freeling Springs																	
Freeling group	x			x						x					x	x	Peake Hill Spring
North of Freeling Spring															x		Complex
Oodnadatta Springs																	
Big Cadnaowie		x															Mt. Dutton Spring Complex

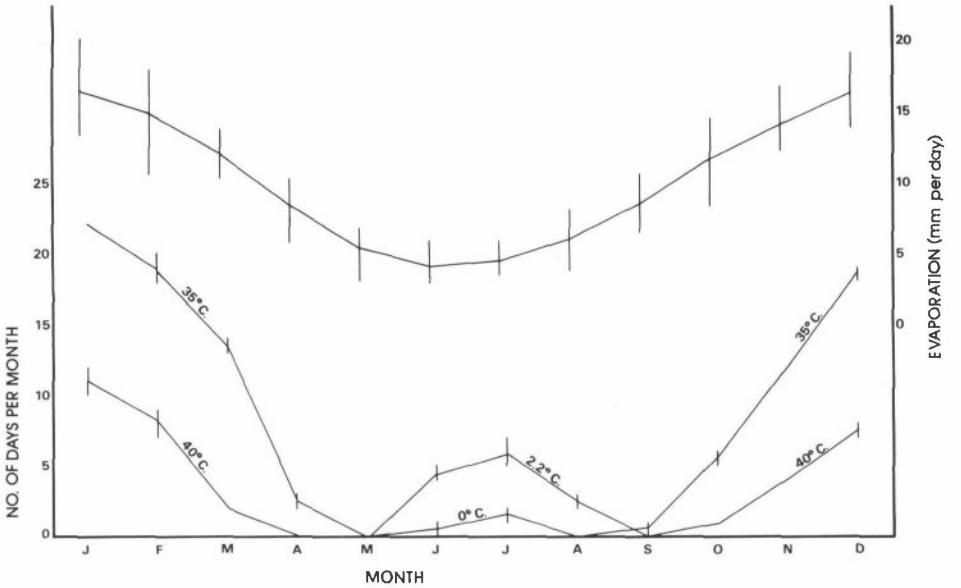


FIG. 3. Temperature and evaporation data for Marree and Oodnadatta. Mean daily evaporation, for each month, is given only for Oodnadatta, 1968–1982. The temperature data are for Marree, 1957–1982, and Oodnadatta, 1940–1982 together (with error bars indicating the range that the two encompass) and consists of number of days/month with temperatures >40° C., number of days/month with temperatures >35° C., number of days/month with temperatures <0° C., and number of days/month with temperatures <2.2° C.

b) Lake Cadibarrawirracanna Spring Complex. A widely scattered group of springs west of William Creek; the most westerly of all the spring complexes (Fig. 2; Appendix 1, Fig. 58).

5. The South Western Springs:

a) Francis Swamp Spring Complex. A large group of springs south of William Creek (Appendix 1, Fig. 60).

b) Old Billa Kalina Spring Complex. A scattered group of springs south of Francis Swamp on the northern side of Margaret Creek (Appendix 1, Fig. 60).

c) Strangways Spring Complex. A compact group of mostly extinct carbonate mounds to the east of Francis Swamp (Appendix 1, Fig. 59).

6. The Middle Springs:

a) The Beresford Spring Complex. Two main springs associated with two very large, extinct mounds, North and South Beresford Hills (Appendix 1, Figs. 60, 61).

b) Coward Spring Complex (Appendix 1, Fig. 61) includes the springs between Coward Springs and Hamilton Hill.

7. The Southern Springs:

a) Lake Eyre Spring Complex. A few springs on the southern and southwestern sides of Lake Eyre South and on islands in this lake (Appendix 1, Figs. 61, 62).

b) Hermit Hill Spring Complex. Several large groups of springs in the vicinity of Hermit Hill (Appendix 1, Fig. 62).

c) Wangianna Spring Complex. Includes the Welcome and Davenport Spring Groups, as well as the degraded Wangianna Spring (Appendix 1, Figs. 62, 63B).

Climate: Basic meteorological data for this region are presented in Fig. 3. Note the frequency of summer days with >40° C temperatures. Annual rainfall at Marree varied from 39.3–379.9 mm for the 21 years between 1957–1982, and at Oodnadatta from 54.3–465.8 mm for the 20 years between 1958–1982. Evaporation is exceedingly high, usually >10mm/day (Fig. 3) and, for a given year, typically exceeds precipitation by a factor of 10 or more (data for Oodnadatta and Marree were provided by the Bureau of Meteorology).

MATERIALS AND METHODS

Taxonomy

Taxonomic rationale: Because the mound springs are isolated from one another, each population has the potential to contain a unique genome that, given sufficient time, isolation and selective pressure, could develop into separate taxa. It was impractical to analyse all populations but a representative, non-random selection (Appendix 2, Tables 18–21) was made and these populations were treated as separate units in the statistical analyses to prevent bias towards the initial subjective split into species units.

The method that we have used to distinguish taxa is essentially phenetic. The phenetic grouping of populations by discriminate analysis is used as an aid for recognizing taxa but because strict acceptance of phenetic classifications, we believe, can be misleading, a subjective element was also introduced, generally on the side of caution. The rather large number of characters measured were statistically tested for differences between the recognised taxa. Most taxa are distinguished by at least one major set of characters (e.g., opercular, shell or reproductive) that are statistically significantly different ($p < 0.01$) from the phenetically closest taxon. It is our belief that the classification that we present is conservative and in all probability, by using techniques such as electrophoresis, genetic differences not easily recognised in the phenotype will be detected, and additional subdivision required. An electrophoretic program is planned that will test the classification adopted here and investigate some of the questions raised in the discussion.

Cladistic methods were not applied in this study because species discrimination depended largely on measurements, which would lead to difficulty in adequately defining character states.

Thorpe (1976) has discussed the practical and theoretical problems involved with sampling and analysing the phenetic differences among populations. He points out that there are two aspects to the problem of sampling, obtaining enough specimens to take account of local variation and surveying enough localities to represent the geographical area under consideration. We believe that our samples come close to meeting these requirements, especially as far as the shell and opercular data are concerned. Certainly the amount of variance obtained in most characters within even the wider-ranging taxa is generally small.

There are some inherent problems in working with hydrobiids because their shells are simple, unicoloured, rather featureless and small. Measurements of a number of shell parameters provide a picture of the shell that can be statistically analysed to detect subtle differences that occur between taxa. The opercular characters of species of *Fonscochlea* have proved to be useful. The number and relative development of the pegs on the inner surface of the operculum are the most useful opercular characters. These pegs are apparently a mechanism to increase the surface area for the attachment of the columellar muscles. The anatomical characters were much more difficult and time-consuming to study and, consequently, smaller numbers of individuals were examined. Important and obvious anatomical differences occur between the species of *Trochidrobia,* but within the two primary groups of *Fonscochlea* the anatomical differences are small and show high variance. Non-quantified characters, such as the pigmentation patterns on the head, were considered when constructing our classification, although in some taxa head-foot pigmentation showed considerable intra- and inter-population variation. Ratios were calculated using a number of measurements in all three data sets of shell, operculum, anatomy, in an attempt to reduce size-dependent differences and generate shape variables. These were used in the initial screening of the data to assist with the delineation of taxa.

Species are recognized in those cases in which, first, there were one or more morphological differences, which we judge to be significant, between the individuals in one taxon compared with the most similar taxon, and/or second, the taxa, recognisable by one or more differences, are sympatric and congeneric. Sympatric in this sense is used to include taxa living not only within the same spring but in closely associated springs (within a few hundred metres) in the same spring group (i.e. parapatry).

Subspecies have not been recognised but geographic forms have been identified where, within a taxon recognised as a species, there are one or more differences judged to be of significance between allopatric populations, i.e. from different spring groups. These forms are apparently of infraspecific status but whether they should be formally named must

await an analysis using biochemical methods. Nevertheless we have set out a formal diagnosis and description of each of these forms so that future investigation can more readily focus on some of the more important geographic differences that occur in the species that we recognise. In each case in which more than one form is recognised, form A is the typical form.

Materials: Specimens were collected by sifting sediment with a plastic hand sieve having a mesh size of approximately 1 mm, and by washing vegetation and solid objects (stones, bones, wood) into a bowl. Sieve contents were tipped into a bowl and excess water drained out. Snails and crustaceans usually sank to the bottom of the bowl and were collected in bulk. Although care was taken, some of the crustaceans, but very few molluscs, were lost during this process by their floating out with the excess water. The material was preserved in 5–10% formalin neutralised with excess $NaHCO_3$, after relaxation with menthol crystals for 10–12 hours.

For most springs, separate collections were taken at the head of the spring, at the upper part of the outflow, and at the middle part of the outflow. Collections were also often taken at the lower outflow and elsewhere, depending on the type and size of spring and amount of time available. Separate samples were sometimes taken from the water edge and middle of the flow, otherwise the sampling combined these zones.

Before sorting, samples were sieved in the laboratory through a 1 mm mesh to minimize any size bias produced by use of hand sieves during collecting. Samples were sorted under a low-power binocular microscope. If the sample was especially large, it was subsampled by removing all animals from a portion of the sample after thorough mixing, until a maximum of 600 individuals of any one species had been counted. The specimens were sorted into species and the counts of number of individuals for each species were used to give approximate percentage frequencies. Adults and subadults only were used in the percentage frequency analyses as identification of juveniles to species was difficult and time-consuming. Empty shells were ignored in counting. The results obtained by the analyses of qualitative samples have several limitations that are discussed below.

Most of the material on which this report is based is housed in the Australian Museum (AMS). The holotypes, some paratypes and some other representative specimens are in the South Australian Museum, Adelaide (SAM). A representative collection is housed in the United States National Museum of Natural History, Washington, D.C.

Methods: Series of 20–25 adult (occasionally more) snails were randomly selected from given samples for morphological analyses in the following manner. The sample was placed into a Petri dish, the bottom of which was divided into a grid of 50 equal-sized and numbered squares. A random number table was used to select grid squares. All adult snails, excluding highly eroded specimens, were removed from each selected square until the desired number of specimens was obtained. Shells were measured with either a Wild dissecting microscope (M5 or M7) fitted with an ocular micrometer, or with a Houston Instruments Hipad Digitizer linked to a Morrow Microdecision (MD2) computer. For measurements using the former method, a shell was first affixed to a piece of plastic clay, apex pointing directly upwards, so that protoconch diameter (PD, Fig. 4c) could be measured and counts made of protoconch and teleoconch whorls (PW, TW). The shell was then reoriented to the standard position, i.e. aperture facing upwards (Fig. 4a) and measurements made of shell height (SH), shell width (SW), aperture height (AH), aperture width (AW), and length of the body whorl (BW, Fig. 4a). For most shells measured using this method, a Wild M-5 microscope was used with 10× eyepieces, and 12× (large species) or 25× (small species) magnification for all shell features except protoconch diameter (50×). The variance in shell measurements using the ocular micrometer, as determined by repeated measurements of a given feature on a single specimen, was approximately 0.05 mm.

For measurements using the digitizing pad, shells were oriented in the positions described above and placed under a Wild M-5 dissecting microscope. The shell image was projected onto the digitizing pad by a drawing apparatus attached to the microscope. Shell features were measured by placing the cursor, equipped with a cross-hair, over standardized points of the shell in a predetermined sequence, with coordinate data sent to the computer at these points by pressing the cursor button, using the point, not stream, mode. In addition to the six meristic variables listed above, the width of the first half-whorl of

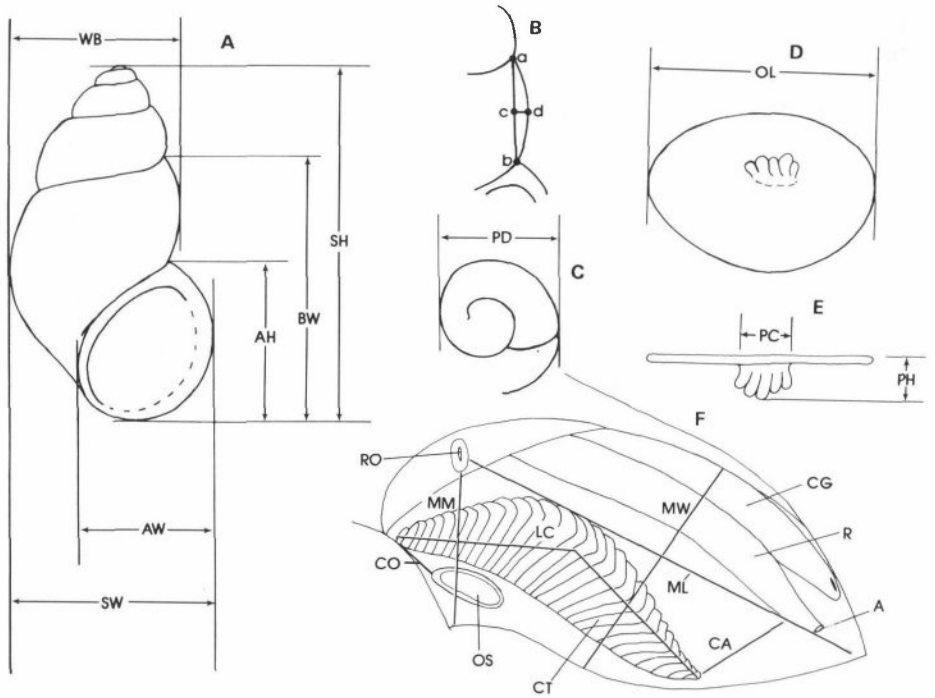


FIG. 4. Shell and operculum, showing various measurements.
A. Shell. AH, aperture height; AW, aperture width; BW, height of body whorl; SH, shell height; SW, shell width; WB, width of body whorl.
B. Shell showing measurements taken for convexity calculation (see methods).
C. Protoconch. PD, protoconch diameter.
D. Operculum, inner side. OL, opercular length.
E. Operculum, side view. PC, length of calcareous area; PH, peg height.
F. Pallial cavity, showing selected measurements of pallial structures.
A, anus; CA, distance from anus to ctenidium; CG, capsule gland; CO, distance between posterior end of osphradium and posterior end of ctenidium; CT, ctenidium; LC, length of ctenidium; ML, maximal length of pallial cavity; MM, minimal length of pallial cavity; MW, width of pallial cavity; OS, osphradium; R, rectum; RO, renal opening.

the body whorl (WB, Fig. 4a) and convexity of the penultimate whorl (CV; see below) were also measured using the Hipad. The Hipad was significantly more accurate than the above method, with repeated measurements varying by less than 0.02 mm. After a shell was measured it was cracked and the snail sexed by examination of the anterior portions of the genital tracts.

After sexing, opercula were removed from the same groups of snails used for shell measurements. Because measurements taken of the opercula of species of *Trochidrobia* did not provide useful data, these have been excluded from the analyses. The following methods apply to the opercula of species of *Fonscochlea*. Opercula were measured using a Wild M-5 dissecting microscope equipped with an ocular micrometer, with 10× eyepieces and 50× magnification. Opercula were first fixed flat onto a piece of plastic clay with the side that was attached to the foot facing upwards. The opercular length was measured (OL, Fig. 4d) and the calcareous pegs were counted. Then the opercula were stood on edge, with the pegs projecting beneath the operculum (Fig. 4e), enabling the length of the calcareous deposit (PC) and the height of the tallest peg (PH) to be measured.

Specimens were dissected after their shells were dissolved in Bouin's solution. Dissections were done while the animals were pinned out in a black wax-bottomed dish filled with a solution of 50–70% Bouin's solution

and water. Pallial and head structures were measured after the pallial roof and visceral coil were removed from the head/foot/neck. The digestive gland and gonad were then measured, followed by the other reproductive organs and stomach. All measurements were made, in the latter part of the study, with a crossed measuring reticule, divided into 200 segments on each line, in a 25× eyepiece using 31× magnification on the Wild M-7, or 25× magnification on the Wild M-5. In the early stages of the project a single line reticule, divided into 120 segments, in a 10× eyepiece, was used at 31× magnification on the Wild M-7. All measurements were converted into millimeters and used for calculation of ratios by the computer (see below).

The mean, standard deviation and variance were calculated for each attribute by sex for each population, using the microcomputer. All data files generated from the microcomputer were reformatted into data matrices based upon species and attribute groups and transmitted via a modem to disk storage on a mainframe computer, initially the CSIRO Cyber computer but more recently the NSW Data Processing Bureau Burroughs 7700. The Statistical Package for the Social Sciences was used to generate descriptive statistics (subprogram BREAKDOWN), test homogeneity of variances with both Bartlett's and Cochran's C-test, and perform two-tailed, single classification analyses of variance with the subprogram ONEWAY for each attribute. Missing data were ignored. In the cases in which groups of populations displayed significant heterogeneity of variance for given attributes, the data were transformed using either a log or arcsine transformation prior to analysis of variance. Student-Newman-Keuls test (SNK) and the Scheffe test were used to compare means using 0.05 and 0.001 probability levels. For all tests, significance was checked using the tables of critical values in Rohlf and Sokal (1969). Tests for sexual dimorphism were carried out using the subprogram ONEWAY on selected attributes for all species groups at probability levels of 0.05 and 0.001. Because some characters in some species proved to be sexually dimorphic, the male and female data were analysed separately.

Multivariate analysis was undertaken using discriminate function analysis (MDA) (hereafter referred to as discriminate analysis) using the BIOSTAT package of programs (Pimentel & Smith, 1986). Because there are problems in using ratios in multivariate analyses (Brookstein *et al.*, 1985) and closely correlated measurements a reduced set of measurements was used in the discriminate analyses [*Fonscochlea:* shell: SH, SW, AH, TW; operculum (not used with *F. zeidleri*): OL, PH, PC, PN; *Trochidrobia:* SH, SW, AH, AW, BW, TW, PD]. Discriminate analyses were run for each species group at the population level with sexes separate, and populations grouped into species and/or geographic forms of species with sexes separate and sexes combined. Anatomical data sets were run in the same way with two species groups in which anatomical data were used primarily to discriminate some of the species and geographic forms (*Trochidrobia* spp.; female genital measurements: GO, CG, AG, BC, WB, DB, CV, DV; "large aquatic" species of *Fonscochlea;* pallial measurements: LC, WC, FC, AC, HC, LO, WO, DO, CO, with sexes combined because of small numbers for each station).

Because of space constraints the univariate statistical analyses of the measurement data are not provided, nor are the details of the measurements obtained for every population. In the case of those data utilized in discriminate analysis, however, the results of an SNK test ($P<0.05$) are given for each character. It is hoped to utilize further the extensive set of measurement data in conjunction with a planned electrophoretic program. A summary of the measurement data is given in Appendix 2, Tables 18–21.

Characters: For descriptions of the taxa and analyses of morphological variation, the characters listed below were quantified for samples of snails from given populations.

The characters of the shell that were measured (Fig. 4A–C) are:

Maximal diameter of protoconch (PD).

Number of protoconch whorls (PW).

Number of teleoconch whorls (TW).

Shell height (SH), maximal length of shell along shell axis.

Shell width (SW), maximal width of shell perpendicular to shell axis.

Length of body whorl (BW), length from the suture, at junction of penultimate and body whorls.

Width of body whorl (WB), maximal diameter of first half-whorl of body whorl.

Height of aperture (AH), maximal length parallel to shell axis.

Width of aperture (AW), maximal width perpendicular to shell axis.

Convexity (CV), shortest distance from line

connecting sutures at junction between penultimate and body whorls to most abaxial point on whorl outline (Fig. 4B:c–d), divided by length of line connecting the two sutures (Fig. 4B:a–b).

The following ratios were generated from the shell measurements and used in the data analysis: protoconch diameter/shell height (PD/SH); shell width/shell height (SW/SH); aperture height/shell height (AH/SH); aperture height/length of body whorl (AH/BW); aperture width/width of body whorl (AW/WB); and an estimation of the degree to which the outer lip of the aperture protrudes beyond the outline of the junction of the penultimate and body whorl (WB/SW).

The opercular characters determined were:

Opercular length (OL), the maximal length of the operculum.

Number of opercular whorls (OW); determined for species of *Trochidrobia* only.

Number of pegs (PN) (i.e. number of separate calcareous projections); determined for species of *Fonscochlea* only, as were the following opercular characters.

Maximal height of pegs (PH), including thickness of operculum itself.

Length of calcareous smear (PC), length of calcareous deposit associated with pegs.

Several anatomical characters were determined. All measurements are maximal widths, lengths etc. unless otherwise stated. Characters of the head/foot and general body are:

Length of snout (LS), distance from eye to snout tip.

Length of tentacles (LT), distance from eye to tentacle tip.

Length of buccal mass (BM), measured after removal from snout.

Length of radular sac behind buccal mass (RS), length of portion of radular sac protruding from posterior end of buccal mass.

Length of digestive gland (LD), measured along its mid-upper surface following the coil.

Length of gonad (LG), measured as above.

Length of the digestive gland anterior to gonad (DG).

In the case of the pallial cavity all measurements were taken with the pallial cavity removed and flattened out (Fig. 4F). Characters are:

Maximal and minimal lengths of pallial cavity (ML, MM), distance from renal opening to given points along edge of cavity (Fig. 4F).

Width of pallial cavity (MW), taken as width of cavity approximately perpendicular to rectum (large species of *Fonscochlea*) (Fig. 4F) or as width along mantle edge (small species of *Fonscochlea*, and *Trochidrobia* spp.).

Number of ctenidial filaments (FC).

Length of ctenidium (LC), following curvature of ctenidium (Fig. 4F).

Width of ctenidium (WC), maximal width along long axis of filaments.

Gill apex (AC), width of ctenidium from left side to position of filament apex.

Filament height (HC), height of a filament at widest part of ctenidium.

Length and width of osphradium (LO, WO).

Distance between posterior tip of osphradium and posterior tip of ctenidium (CO) (Fig. 4F).

Shortest distance between osphradium and edge of pallial cavity (DO).

Distance between ctenidium and anus (CA), measured as shortest distance between anterior end of ctenidium and left side of anus (Fig. 4F).

Shortest distance between anus and mantle edge (MA).

Characters of the stomach are:

Length (SL), taken as entire length of stomach, including style sac, for *Trochidrobia* and small species of *Fonscochlea,* and length of stomach excluding style sac portion for large species of *Fonscochlea*.

Length of style sac (SS).

Height of anterior stomach chamber (AS).

Height of posterior stomach chamber (PS).

Many characters of the genital system were measured.

Whereas small variations due to reproductive state could not be assessed in this analysis, all individuals for which genital characters were measured appeared to be sexually mature. Immature or parasitized specimens were rejected.

Characters of the male genitalia are:

Length and width of prostate gland (PR, PW).

Length of pallial portion of prostate gland (PP), that part protruding into pallial cavity.

Length of penis (PL).

Characters of the female genitalia are:

Length of glandular oviduct (GO).

Length of capsule gland (CG) and albumen gland (AG).

Length of genital opening (GP).

Length and width of bursa copulatrix (BC, WB).

Length of duct of bursa copulatrix (DB).

Length and width of "seminal receptacle" (SR, WR), only for *Fonscochlea*.

Length of duct of "seminal receptacle" (DR), only for *Fonscochlea.*

Length of coiled portion of oviduct (CV), length of coiled section posterior to "seminal receptacle" *(Fonscochlea)* or bursa copulatrix *(Trochidrobia).*

Maximal and minimal diameters of coiled portion of oviduct (DV, MO).

Length of oviduct between seminal receptacle and bursa copulatrix (BS); *Fonscochlea* only.

Length of free portion of ventral channel (VC), that portion anterior to duct of bursa copulatrix.

For species of *Fonscochlea,* the following groups of anatomical ratios were used: a) pallial ratios: LC/SH (SH is shell height), LO/SH, FC/SH, MM/SH, HC/SH, MA/SH, CA/SH, MW/MM, LO/LC, HC/WC, AC/WC, WC/LC, WO/LO; b) general ratios: BM/SH, BM/RS, LT/LS, LD/SH, LG/LD; c) stomach ratios: SS/SL (see comments above under SL), PS/AS; d) male genital ratios: PL/SH, PP/SH, PP/PR; e) female genital ratios: AG/SH, CG/SH, CG/AG, BC/AG, DB/AG, SR/BC, CV/GO, VC/CV, VC/AG, BS/OD (OD = CV + VC), OV/GO (OV = CV + VC + BS). For *Trochidrobia,* the pallial ratios, stomach and general ratios, and male genital ratios were precisely the same as those for *Fonscochlea,* except that shell width (SW), rather than shell height, was used for scaling. The female genital ratios generated for *Trochidrobia* were AG/SW, CG/SW, CG/AG, BC/AG, DB/AG, CV/GO, VC/CV, VC/AG, DV/MO, DB/BC, and DV/VC.

Anatomy

Two species are described in detail, *F. accepta* (form A), from Welcome Springs, and *T. punicea,* from Blanche Cup Spring and Finniss Springs. Some supplementary information is given for *F. zeidleri* from Blanche Cup Spring.

The specimens were dissected by the same methods used to obtain the anatomical measurements above). Specimens fixed in Bouin's solution were sectioned in paraffin at about 6 microns and stained with Mallory's Triple Stain.

Physiology

Materials: The following snail species (with localities) were used in the experiments: *Trochidrobia punicea* (Finniss Springs), *Fonscochlea conica* (Welcome Springs), *Fonscochlea variabilis* form A (Blanche Cup, Coward Springs Railway Bore), *Fonscochlea accepta* form B (Finniss Springs), *Fonscochlea accepta* form A (Welcome Springs), *Fonscochlea aquatica* form A (Blanche Cup) and cf. form A (Kewson Hill) and *Fonscochlea zeidleri* form A (Finniss Springs, Blanche Cup, Kewson Hill and Coward Springs Railway Bore). These species represent the majority of those found in the southern and middle groups of springs found between Marree and Oodnadatta.

The springs from which the material studied was collected were, for logistical reasons, all in the southern half of the spring system between Marree and Oodnadatta (see Appendix 1 for detailed maps and station details). These were, in east-west order:

Welcome Springs (Stn 756), a moderately large spring with a low mound. A small pool near the head is a few cm deep and there is a shallow (< 1cm), rather long outflow. The substrate is a mixture of calcareous rock, sand and mud. Sedges are moderately common and filamentous algae are abundant.

Finniss Springs (Stn 693), a small spring with a very low sand mound. The substrate is sand and mud. Sedges are common and filamentous algae are present.

Blanche Cup Spring (Stn 739), a conical calcareous mound with a pool at the top (Fig. 1a). The outflow is shallow and mainly broad and flows over calcareous rock but the pool contains mainly mud. Sedges line the pool edges and filamentous algae are abundant in the pool and in the outflow.

Coward Springs Railway Bore (Stn 743), a very large swamp issuing from a large pond with the bottom composed mainly of silt. The water depth is generally in excess of several cm where the specimens were collected, in the vicinity of the pond outflow. Large sedges and rushes line the edges of the pool and outflow. Filamentous algae are abundant. This is the only known case in which the mound spring snails have become established in a bore drain. It is also the only known locality at which *F. zeidleri* is aquatic as well as amphibious. *Fonscochlea aquatica* is not found here and *T. punicea* is uncommon.

Kewson Hill Springs (Stn 742), one of several small springs issuing from this hill. They trickle down the steep hillside in narrow outflows where they form a series of small terraces (Ponder, 1986), each containing water a few mm deep. There is no vegetation apart from some filamentous algae.

Methods: All experiments were conducted in a makeshift laboratory set up in a large tent (5 × 4 m) in the field between August 27 and September 9, 1983. Snails from given populations were collected and then held in water in aerated plastic containers (16 × 16 cm) for one to three days before being used in the experiments. When possible, water from the spring from which a given sample of animals was collected was used for holding both the animals and for the experiments (Blanche Cup, Welcome Spring, Coward Springs Railway Bore). In instances in which a large water sample could not be obtained owing to shallow water and/or low discharge, water from a nearby spring or bore was used. In the case of Finniss Springs, the water was taken from a bore about 7 km southwest of Hermit Hill and the water used for the experiments with *F. aquatica* from Kewson Hill was taken from the Blanche Cup Spring. Full analyses of the water from these localities is given in Kinhill-Stearns (1984). A running record of the laboratory environment (air temperature, humidity) was kept. To avoid introducing age-related differences, only adult snails, i.e. those possessing a complete and thickened peristome, were used for the experiments.

A major problem encountered in physiological experiments involving shelled gastropods is determining when individuals are dead. Retraction of the snail into its shell usually occurs before death in response to unacceptable conditions. For most of the experiments the activity of the snails was used as an indicator of their tolerance to the conditions being presented. Given the time constraints inherent in the project, the customary replicates of each experiment could not be done. We preferred to use the available time to run each experiment for all of the taxa. The detailed methods of each type of experiment are given below.

In the desiccation experiments animals from given populations were placed in a series of 9-cm Petri dishes. Ten specimens were placed in each dish. The dishes were of three types: those lined with dry filter paper and without a lid (hereafter referred to as dry); those lined with moist filter paper and with a lid (moist); and those half-filled with water and with a lid (wet). The moist and wet tests served as controls. A total of 21 dishes, seven sets of each of the three types, was set up for each population tested. A separate set of dishes was checked after periods of one, two, four, six, 12, 24, and 48 hours from the beginning of the experiment. As the moistened dishes tended to dry out, despite having lids, they were frequently examined and re-moistened whenever necessary. To check for survival of snails in a set of dishes, the dishes were first flooded, if dry or moist, with water. The number of animals in each dish that were active 10 minutes after flooding was noted. A similar check for active animals was made one hour after flooding. Animals inactive after one hour were considered dead. Death was confirmed for the snails by tests carried out in some of the early runs: shells were gently crushed to expose the animal, placed under a dissecting microscope, and the mantle was not seen to retract when prodded.

In the salinity experiments table salt was added to the appropriate spring water to obtain solutions of six, nine, 12, and 24 ‰. The salinities of these solutions were tested using an optical refractometer. Each of these solutions, as well as a normal sample of the spring water, for which a zero salinity reading was obtained using the refractometer, serving as a control was added to a glass jar of about 380 cc brimfull capacity, which was then capped with a plastic lid to exclude air from the jar as much as possible. Ten specimens were placed into each of these five jars. After intervals of one, two, three, six, 12, and 24 hours, each of the jars was examined, but not opened, and the number of active or clinging snails counted. Mortality was not tested. The salinities for each of the water sources used, calculated from the conductivities given by Kinhill-Stearns (1984), are shown in Table 12.

In the experiments with deoxygenated water, water from the appropriate spring was boiled for two to three minutes in a glass beaker and then poured very gently, to prevent reoxygenation, into each of five 25 cc test tubes. Rubber stoppers were then gently inserted into each of the tubes. The tubes were cooled and then 20 snails were placed into each of them, as well as into a sixth tube containing well-oxygenated spring water as a control. The tubes were then again firmly stoppered, with an effort made to exclude air bubbles. After intervals of one, two, four, six, and 20 hours, a tube with deoxygenated water was checked in the following manner. First the number of active specimens in the tube was counted. Then the specimens from the tube were placed into a dish with oxygenated water. The number of active specimens in the dish was counted after periods of ten minutes and one hour. Specimens inactive after one hour

were considered dead. At the end of each of the five time periods, the control tube was examined as well, but not opened, and the number of active individuals in the tube counted.

The purpose of the temperature experiment was to determine activity of animals at various temperatures. Twenty specimens were placed into each of two 275 cc jars, half-filled with water. One jar was slowly heated by placing it into a steam-heated, water-filled dish. The jar was periodically removed from the water bath, the temperature of the water in the jar noted, and the number of active individuals in the jar counted when the desired temperatures were reached. The process was continued until such a temperature was reached at which all specimens became inactive. A similar method was used to determine tolerance to low temperatures: the second jar was placed into a small freezer and periodically removed to check the temperature and count the active animals. Again, the experiment was terminated when all specimens became inactive. The jars were not aerated during the experiments. Mortality was not tested and no attempt to achieve acclimation was made.

In determinations of submergence tolerance a 380 cc jar was filled to the brim with water and 20 snails were added. The jar was then capped with a lid that had a small hole in it so that an aerator tube could pass through it into the jar. An aerator stone was attached to the end of the tube. At intervals of one, two, four, 15, 24, 48, and 72 hours, the jar was examined and the number of active snails counted. In experiments of submergence/non-submergence preference a plastic plate was used (diameter of 220 mm), with a flat circular bottom (diameter of 150 mm), steeply-sloping sides (approximately 60° width of 13 mm), and a slightly-sloping rim (approximately 10° width of 22 mm). The dish was filled with water to the lower edge of the rim. Fifty snails were placed in the dish and left for three hours. At the end of this time period the numbers of specimens found on the bottom of the dish, on the steep slope and on the broad rim (out of the water) were counted.

In determinations of response to light a 200 × 200 × 15 mm clear perspex box, with tightly-fitting lid, was constructed for use in this experiment. Three lines were drawn across the width of the box in order to divide the box lengthwise into four equal zones. One hundred snails were placed in the box together with water. The water level in the box was then topped off and the lid placed on top, with a smear of petroleum jelly added to the sides to provide a seal. Care was taken to exclude any air bubbles from the box. Half of the box, containing two entire zones, was covered with a dark plastic sheet and then an Olympus dissecting microscope lamp was placed 2 cm above the mid-line at the uncovered end of the box. The lamp was oriented so that its beam was perpendicular to the plane of the box. The lamp was then turned on, to level 6 on the transformer, and the entire apparatus, box and lamp, was covered with a black plastic sheet to exclude other light. After one hour both the dark sheet and the sheet covering one half of the box were removed, and the numbers of animals in each of the four zones were quickly counted. The numbers of snails found in the light and light-middle zones were combined, as were those found in the dark and dark-middle zones, in order to obtain sufficiently high frequencies for the statistical analysis of these results. For most of the populations tested, two separate runs were done. The box was thoroughly washed and all grease removed between runs of this experiment.

To test for differences in results between runs, populations or species, the following statistical tests were used (following Siegel, 1956): Fisher's Exact Test, when the experiments involved fewer than 20 animals or when expected frequencies in cells were fewer than five; and The Chi-Square Test of Independence, with continuity correction, when the experiments involved 20 or more animals with expected frequencies in the cells exceeding five. Null hypotheses were rejected when the significance level was less than or equal to 0.05.

RESULTS

Taxonomy

The hydrobiids occurring in the Lake Eyre Supergroup are formally described in this section. Two new genera, *Fonscochlea* with six species and *Trochidrobia* with four species, are erected, with a new subgenus, *Wolfgangia,* of *Fonscochlea,* containing one species. Geographic forms are recognised in four of the species of *Fonscochlea,* these being formally described but not named.

A summary of measurement details is given in Appendix 2, Tables 18–21.

TABLE 2. Tests for sexual dimorphism in shell height (SH) and shell width (SW). The asterisk indicates a significant difference, at the level indicated, between males and females for all pooled measurements for the taxon.

	SH		SW	
Species	.05	.001	.05	.001
F. accepta form A	*	*	*	*
F. accepta form B	*	*	*	*
F. accepta form C				
F. aquatica form A	*	*	*	*
F. aquatica form B	*	*		
F. variabilis form A	*	*	*	*
F. variabilis form B	*	*	*	*
F. variabilis form C	*	*	*	*
F. billakalina			*	
F. conica	*	*	*	*
F. zeidleri form A			*	*
F. zeidleri form B	*	*		
T. punicea	*	*	*	*
T. smithi				
T. minuta			*	*
T. inflata				

Type species: *Fonscochlea accepta* n.sp.

Distribution: Artesian springs between Marree and Oodnadatta, northern South Australia.

Diagnosis: Shells (Figs. 5–7, 14, 19, 22, 23, 25) of known species small to large for family (1.3 mm long), non-umbilicate, ovate-conic to ovate, smooth or with weak axial rugae formed from enlarged growthlines. Protoconch (Fig. 9) of about one and one-half whorls, minutely pitted, the pits sometimes arranged into spiral rows (subgenus *Wolfgangia)*. Aperture rather large relative to shell length (AH/SH >0.4), oval, thickened when mature, without external varix; outer lip slightly prosocline to slightly opisthocline. Periostracum thin, sometimes developing weak ridges that coincide with the growthlines and, sometimes, spiral scratches.

Operculum (Fig. 8) corneous, oval, flat, of few whorls, nucleus eccentric, inner surface with small calcareous smear and/or calcareous pegs.

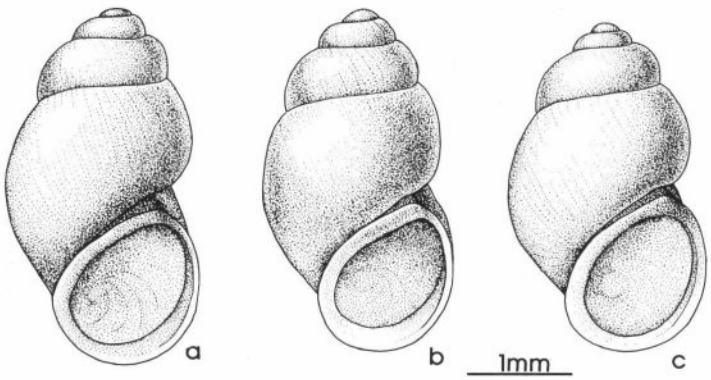


FIG. 5. Shells of *Fonscochlea accepta*.
a. *Fonscochlea accepta* form A, holotype. Welcome Springs (003).
b. *Fonscochlea accepta* form B. Old Finniss Springs (694) (SAM, D. 17918).
c. *Fonscochlea accepta* form C. Emerald Springs (703) (SAM, D. 17919).

Those species shown to be sexually dimorphic in size (at $P<0.01$) are listed in Table 2. Because most of the species showed evidence of dimorphism the morphometric data for each sex were treated separately. Some additional data are provided below.

Family Hydrobiidae

GENUS *FONSCOCHLEA* n. gen.

Derivation: *Fons* (Latin), a spring; *cochlea* (Latin), a snail (fem.).

Radula (Fig. 10) with rectangular central teeth, cusp formula $\frac{2-3+1+2-3}{1-2\ 1-2}$, lateral teeth 2−4+1+2−4. Inner marginal teeth with 8–15 cusps, outer marginal teeth with 17–25 cusps.

Head-foot (Figs. 11, 24a–g,i) typical of family. Cephalic tentacles slightly tapering to parallel-sided; weakly and inconspicuously ciliated on ventral surfaces. Snout well developed, slightly shorter to slightly longer than tentacles. Pigmentation heavy to light,

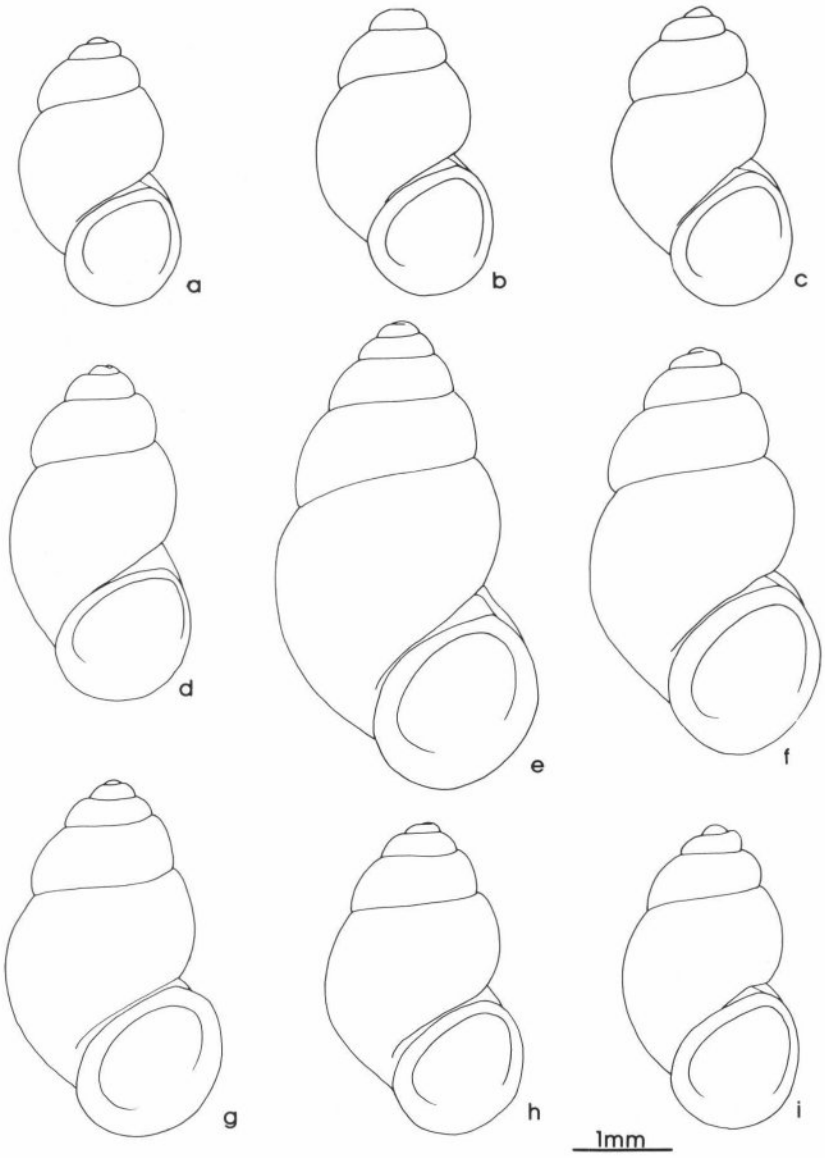


FIG. 6. Shells of species of *Fonscochlea*. a–d,i. *Fonscochlea accepta* form B. a. Finniss Swamp West (690)(AMS, C.152978). b. Sulphuric Springs (735) (AMS, C.152979). c. Hermit Hill Springs (711) (AMS, C.152980). d. Old Woman Spring (733) (AMS, C.152981). i. Old Finniss Springs (710) (AMS, C.152982). e–h. *Fonscochlea zeidleri* form A. e. Elizabeth Springs (024) (AMS, C.152975). f–h. Blanche Cup Spring (008) (AMS, C.152977).

pigment granules black and white. No accessory tentacles.

Pallial cavity (Fig. 4F) with well-developed ctenidium, osphradium oval, about three to four times as long as broad; its posterior extremity situated near posterior end of ctenidium. Ctenidium about 3–4.5 times length of osphradium.

Alimentary canal typical of family. Stomach (Figs. 43a, 44b, 45) with anterior and posterior chambers, single digestive gland opening and no caecal appendage.

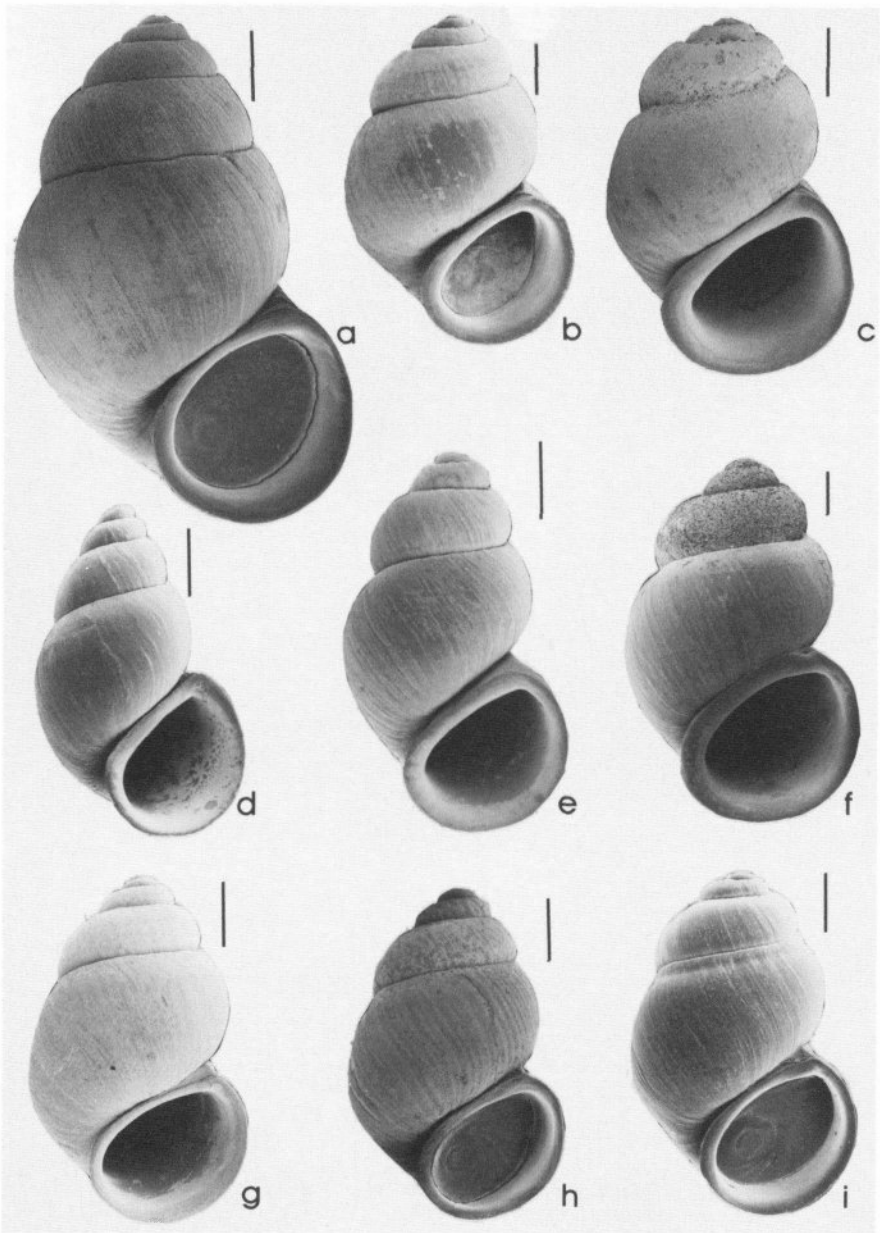


FIG. 7. Shells of species of *Fonscochlea*.
a. *Fonscochlea zeidleri* form A, Strangways Springs (030) (AMS, C.152992).
b. *Fonscochlea zeidleri* form B, Big Cadnaowie Spring (661) (AMS, C.152993).
c. *Fonscochlea aquatica* cf. form A, very squat variety, Kewson Hill Springs (742) (AMS, C.152994).
d. *Fonscochlea billakalina*, paratype, Old Billa Kalina Spring (026) (AMS, C.152995).
e. *Fonscochlea variabilis* form B, The Fountain Spring (032) (AMS, C.152996).
f. *Fonscochlea aquatica* form B, Freeling Springs (665) (AMS, C.152997).
g. *Fonscochlea accepta* form A, Welcome Springs (003) (AMS, C.152998).
h. *Fonscochlea accepta* form B. Old Finniss Springs (694B) (AMS, C.152999).
i. *Fonscochlea accepta* form C, Emerald Springs (703) (AMS, C.153000).
Scale: 0.5mm.

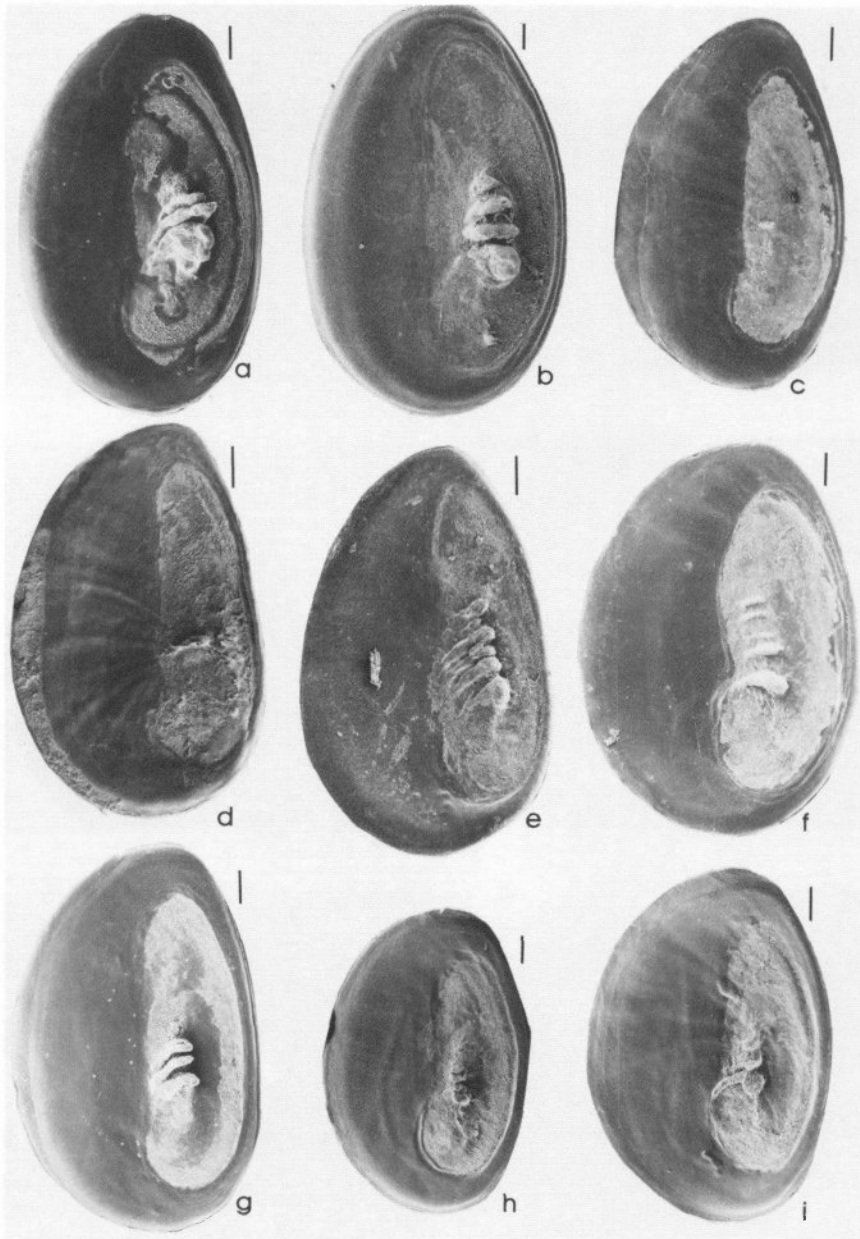


FIG. 8. Opercula of species of *Fonscochlea*.
a. *Fonscochlea zeidleri* form B, Big Cadnaowie Spring (661).
b. *Fonscochlea zeidleri* form A, Coward Springs Railway Bore (018).
c. *Fonscochlea aquatica* cf. form A, Kewson Hill Springs (742).
d. *Fonscochlea billakalina*, Old Billa Kalina Spring (026).
e. *Fonscochlea variabilis* form B, The Fountain Spring (032).
f. *Fonscochlea aquatica* form B, Freeling Springs (665).
g. *Fonscochlea accepta* form B, Old Finniss Springs (694B).
h,i. *Fonscochlea accepta* form A, Welcome Springs (003).
Scale: 0.1mm.

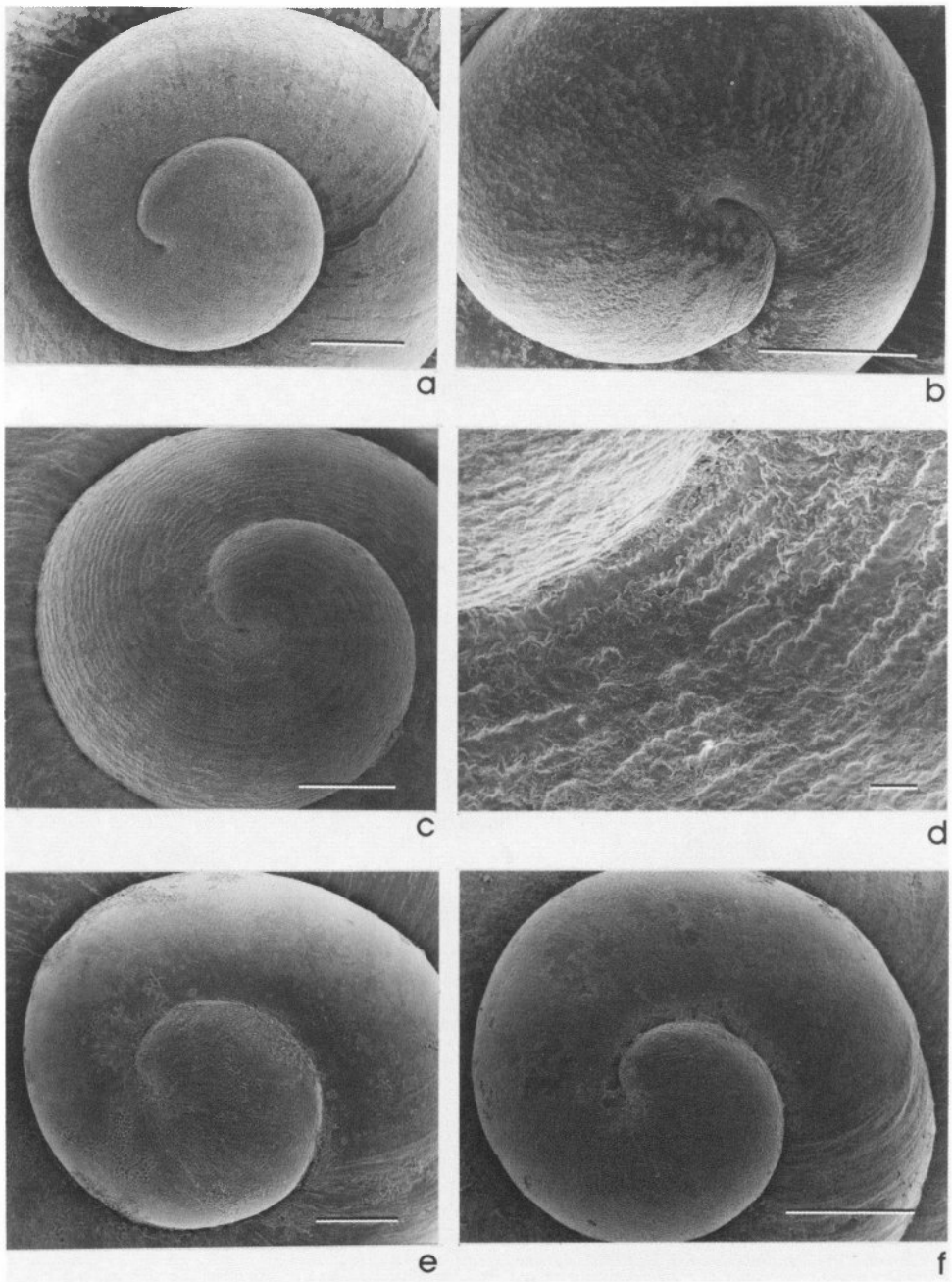


FIG. 9. Protoconchs of species of *Fonscochlea*.
a. *Fonscochlea accepta* form A, Welcome Springs (003).
b. *Fonscochlea accepta* form C, Emerald Springs (703).
c–d. *Fonscochlea zeidleri* form A, Strangways Springs (030).
e. *Fonscochlea aquatica* form A, Outside Springs (039).
f. *Fonscochlea conica*, Welcome Springs (003).
Scale: d = 0.01mm; all others = 0.1mm.

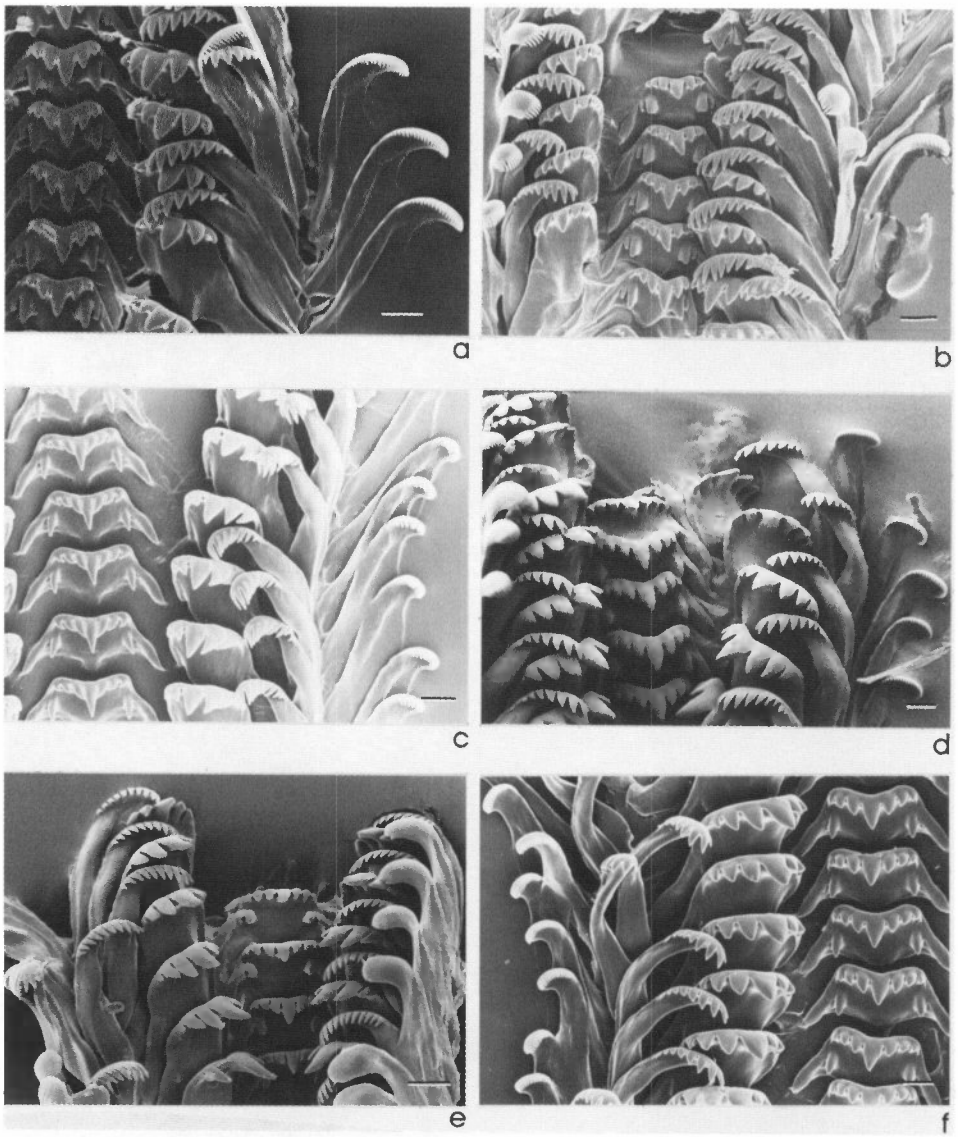


FIG. 10. Radulae of *Fonscochlea*.
a. *Fonscochlea zeidleri* form B, Big Cadnaowie Spring (661).
b. *Fonscochlea zeidleri* form A, Coward Springs Railway Bore (018).
c. *Fonscochlea accepta* form B, Old Finniss Springs (694B).
d. *Fonscochlea accepta* form C, Emerald Springs (703).
e. *Fonscochlea variabilis* form B, The Fountain Spring (032).
f. *Fonscochlea aquatica* form B, Freeling Springs (665).
Scale: 0.01mm.

Female reproductive system (Figs. 12, 27, 47) with two sperm sacs, i.e. anterior bursa copulatrix and posterior "seminal receptacle", and coiled oviduct lying on inner (left) side of albumen gland, sperm sacs and major oviduct folds being opposite posterior part of gland or partly extending behind it. Coiled oviduct an unpigmented, coiled or undulating

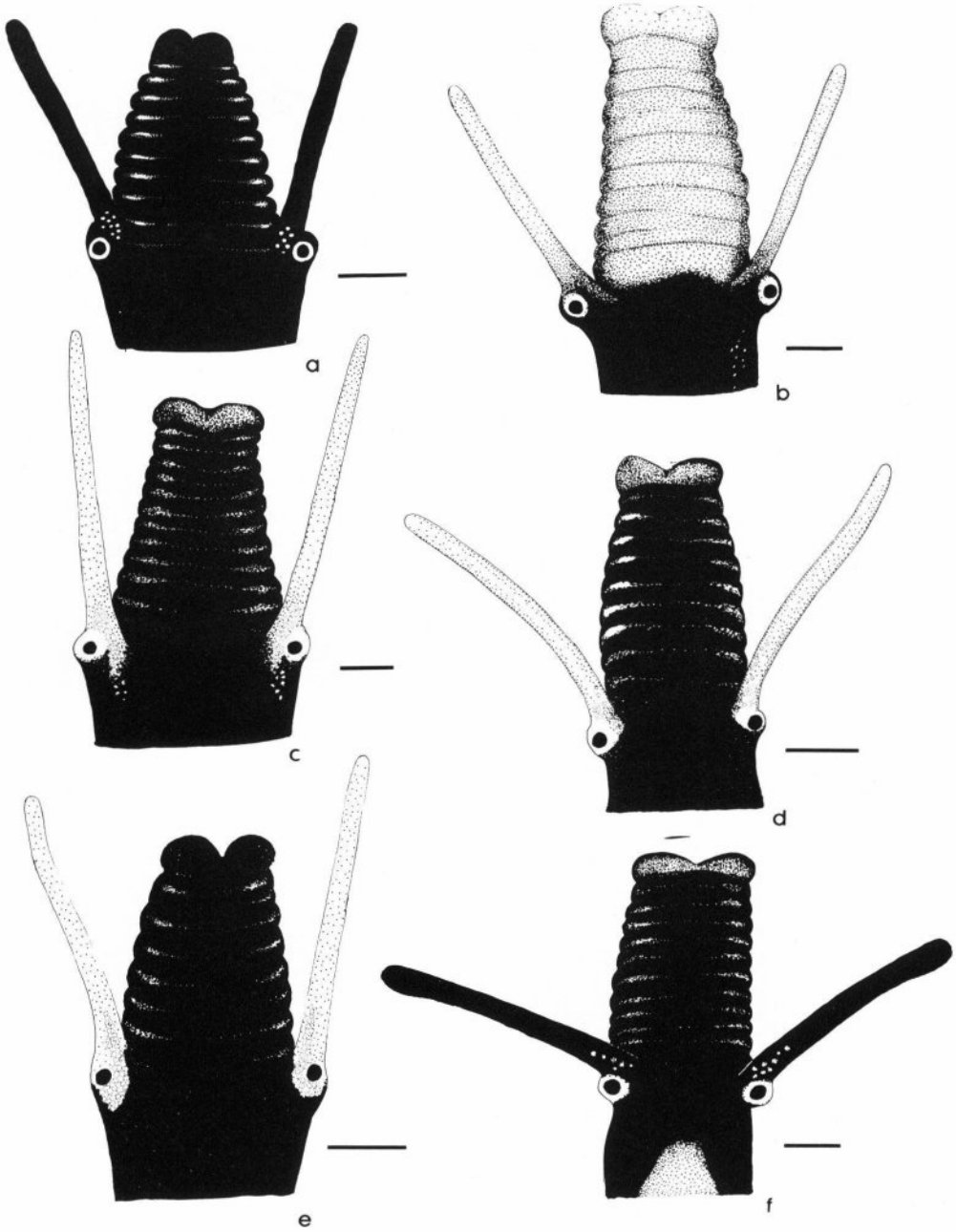


FIG. 11. Dorsal views of heads of large species of *Fonscochlea;* all from living material.
a. *Fonscochlea zeidleri* form A, Kewson Hill Springs.
b. *Fonscochlea zeidleri* form A, Welcome Springs.
c. *Fonscochlea aquatica* form A, Blanche Cup Spring.
d. *Fonscochlea accepta* form A, Welcome Springs.
e. Fonscochlea aquatica cf. form A, Kewson Hill Springs.
f. *Fonscochlea accepta* form B, Old Finniss Springs.
Scale: 0.25mm.

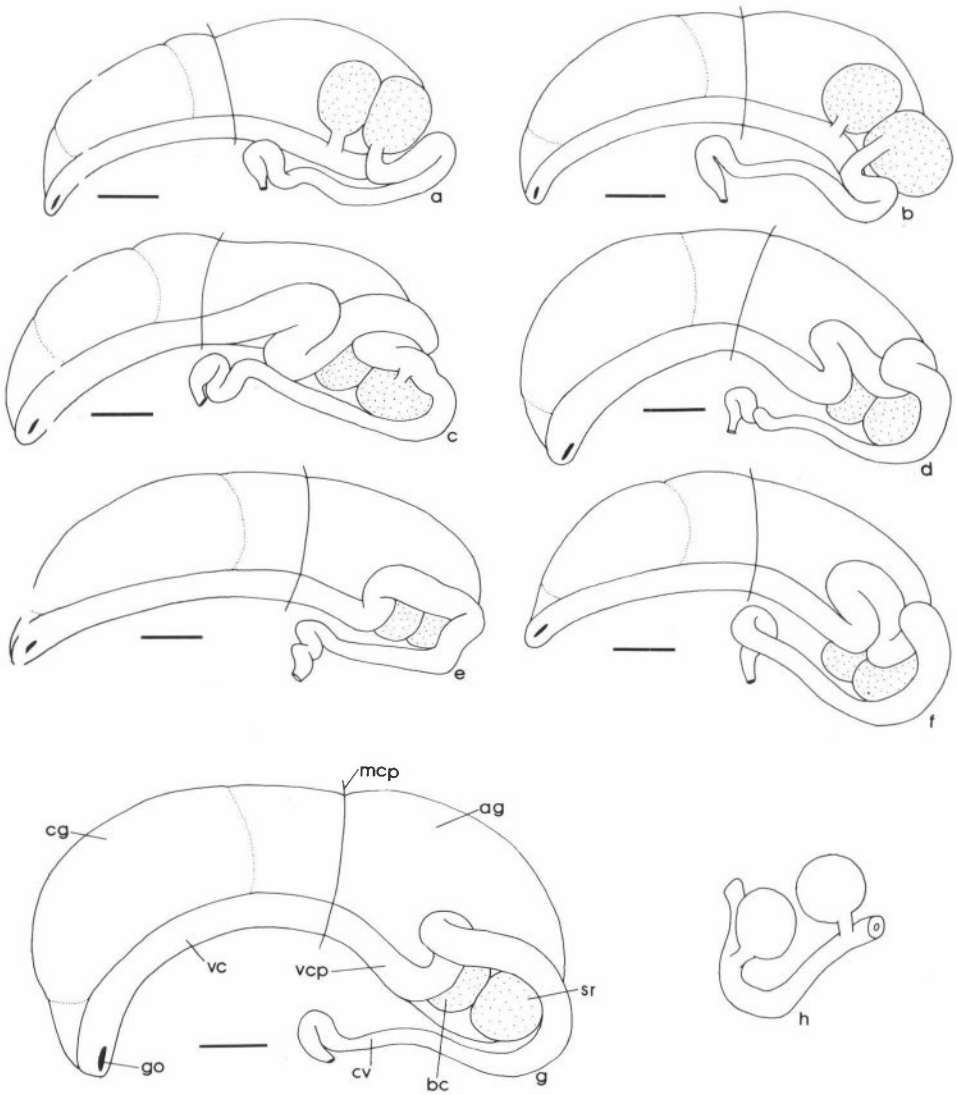


FIG. 12. Female genitalia of species of *Fonscochlea*.
a. *Fonscochlea zeidleri* form B, Big Cadnaowie Spring.
b. *Fonscochlea zeidleri* form A, Old Finniss Spring.
c. *Fonscochlea aquatica* form A, Blanche Cup Spring.
d. *Fonscochlea accepta* form A, Welcome Springs.
e. *Fonscochlea accepta* form C, Emerald Springs.
f. *Fonscochlea accepta* form B, Old Finniss Springs.
g,h. *Fonscochlea accepta* form A, Davenport Springs; detail of sperm sacs and their ducts shown in h.
ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; cv, coiled oviduct; go, oviduct opening; mcp, posterior limit of pallial cavity; sr, seminal receptacle; vc, ventral channel; vcp, posterior extension of ventral channel.
Scale: 0.25mm.

muscular tube extending from immediately behind posterior pallial wall, where its initial section forms U-shaped, glandular loop, to loop posteriorly around sperm sacs at, or just behind, albumen gland. Gonopericardial duct represented by tissue strands only.

Oviduct between sperm sacs very short to moderately long, forming U-shaped loop. Anterior to bursal duct, which opens to oviduct opposite posterior part of albumen gland, muscular oviduct either runs straight to ventral channel or thrown into loop. Bursa copulatrix and "seminal receptacle" approximately equal in size and with ducts markedly shorter than length of sacs. Both sperm sacs similar histologically and rather thick-walled. Capsule gland approximately equal in size to albumen gland or slightly smaller or larger. Ventral channel well defined, with conspicuous ciliated lateral fold. Genital opening subterminal.

Male reproductive system with vas deferens complexly coiled beneath anterior part of testis. Pallial and visceral vas deferens enter and leave prostate gland in middle section. Prostate gland extends into pallial wall, as slight bulge in some species to about half its length in others. Pallial vas deferens narrow, tubular, and lying beneath epithelium of right side of pallial floor, undulating as it passes across neck and enters base of penis. Penis (Fig. 46) with swollen, unpigmented base bearing prominent concentric creases; distal two thirds smooth and tapering to point, often pigmented and muscular. Penial duct similar to pallial vas deferens, i.e. very narrow, ciliated and with only very thin muscle layer; straight in distal part of penis, undulating in proximal part. Penial pore simple.

Egg capsules hemispherical, attached to substrate.

Nervous system (Fig. 43b) with typical hydrobiid pattern: cerebral ganglia separated by short commissure, left pleural ganglion attached to suboesophogeal ganglion and right pleural ganglion separated from supraoesophageal ganglion by long connective.

See anatomical section below for further details of anatomy.

Remarks: The distinctive features of this genus include the equal-sized sperm sacs, the short ducts connecting these sacs to the oviduct and the position at which they enter the oviduct. In most hydrobiids the bursal duct opens to the oviduct opposite the anterior end of the albumen gland, not the posterior end as in *Fonscochlea*. The pegged operculum, and the shell of some of the smaller species, resemble states seen in the Australian species of *Hemistomia sensu lato* (Ponder, 1982). This genus, and the related genus *Tatea* T. Woods, 1879, can be distinguished from *Fonscochlea* in having a more "typical" hydrobiid reproductive system (Ponder, 1982). In these genera the seminal receptacle is thin-walled and much smaller than the bursa copulatrix, and the bursal duct opens to the oviduct in the region near the anterior end of the albumen gland. In most other respects these three genera are similar.

Subgenus *Fonscochlea s.s.*

Diagnosis: Shell (Figs. 5, 6a–d, i, 7c–i, 14b, d, 19, 22, 23, 25) thin to moderately thick, aperture with thin to slightly thickened peristome. Protoconch microsculpture (Fig. 9a,b,e,f) of irregular, shallow pits.

Operculum (Fig. 8c–i) with prominent pegs, weak pegs or pegs absent.

Radula (Fig. 10c–f) as for genus. (Table 3)

Head-foot (Figs. 11c–f, 20a–g, i) with cephalic tentacles slightly longer than snout.

Female genital system (Figs. 12c–h, 27) as for genus except that the oviduct between the ventral channel and the bursal duct is always bent or folded and the sperm sacs lie behind (to the right of) the coiled oviduct and their ducts emerge from their dorsal sides.

Male system as for genus.

Remarks: The typical subgenus includes five of the six known taxa of *Fonscochlea*. It encompasses two radiations, one of small species and the other of large species, all of which are aquatic.

Group 1: the large aquatic species.

Fonscochlea accepta n.sp.

Derivation: *accepta* (Latin), welcome, a reference to the type locality.

Diagnosis: Shell about 2.4 to 3.8 mm long, with about 2.5–3.6 convex (convexity ratio 0.08–0.25) teleoconch whorls. Aperture with thin peristome, outer lip slightly prosocline. Inner lip narrow, loosely attached to parietal wall. Operculum with strong pegs.

Shell (Figs. 5, 6a–d,i, 7g–i; 9a,b), see diagnosis. Colour dark brown.

Operculum (Fig. 8g,i) with several, usually 3–4, strong pegs.

Radula (Fig. 10c,d) as for genus (see Table 3 for details).

Head-foot (Fig. 11d,f), see under descriptions of the forms of this species below.

Anatomy typical of subgenus. Described in more detail in the anatomical section below.

The typical form of this species is described

TABLE 3. Cusp counts from radular teeth of species of *Fonscochlea* and *Trochidrobia*. Missing counts from the outer marginal teeth are the result of not being able to make accurate counts from the available preparations.

Species	Central tooth		Lateral tooth		Inner marginal tooth	Outer marginal tooth
	No. of lateral cusps	No. of basal cusps	No. of inner cusps	No. of outer cusps	No. of cusps	No. of cusps
F. accepta form A	3–4	1	3–4	3–4	9–10	24–25
F. accepta form B	3	1–2	2–3	3–4	9–12	—
F. accepta form C	4	1–2	3	3–4	10–13	—
F. aquatica form A	3–4	1	2–3	2–4	7–10	—
F. aquatica form B	2–3	1	3	3	8–9	21–25
F. variabilis form A	4–6	1–2	2–3	2–4	12–15	—
F. variabilis form B	3–4	1–2	2–3	2–3	9–12	—
F. variabilis form C	2–4	1–2	2	2–3	9–11	—
F. billakalina	3–4	1–2	2–3	2–4	10–12	—
F. conica	4–6	1–2	3	3–4	14–18	—
F. zeidleri form A	2–3	2	2–3	3	9–13	17–21
F. zeidleri form B	2–3	2	2–3	3	9–10	20–21
T. punicea	5–8	1–2	3–6	4–6	24–31	—
T. smithi	6–7	1	4–5	5–6	23–25	—
T. minuta	4–7	1–2	4–6	6–7	22–24	—
T. inflata	6–8	1	5–6	5–7	18–23	—

below as "form A" where a holotype is designated for the species.

Localities: Southern Springs: Welcome, Davenport, Hermit Hill and Emerald Springs (Fig. 13).

Remarks: Three geographically separated forms are recognised. Discriminate analysis did not convincingly separate two of these using shell and opercular characters but reasonable discrimination was achieved using pallial data. The forms are primarily distinguished by differences in their ctenidia and unquantified differences, including tentacle shape and pigmentation and habitat preference.

This species has a range of about 80 km with the typical form occupying about a 25 km range, separated from the Hermit Hill populations (form B) by about 12 km and those in turn separated from Emerald Spring, the locality of the third form, by about 40 km.

This species is the "large aquatic" species of the Southern Springs. It is generally abundant in the pool at the head of the springs and in their outflows. It can sometimes be seen clustering on the sides of the outflows but it is not amphibious and, if emergent, is covered by a film of water.

Fonscochlea accepta form A.

(Figs. 5a, 7g, shell; 9a, protoconch; 8h,i, operculum; 11d, head-foot; 43a, 44b, stomach; 43b, nervous system; 46a, penis; 12d,g,h, female genitalia.

Diagnosis: Tends to have longer and more numerous ctenidial filaments (Table 18B) than *F. accepta* form B and shorter filaments than *F. accepta* form C. Radular sac longer, and ratio of buccal mass to radular sac (BM/RS) smaller, than in both other forms. Also differs from *F. accepta* form B in pigmentation and morphology of cephalic tentacles.

Shell (Figs. 5a, 7g; 9b, protoconch) as for species, but not so broad relative to length as *F. accepta* form C. See Table 18A for measurement data.

Operculum (Fig. 8h) as for species. See Table 18A for measurement data.

Radula as for species. See Table 3 for data.

Head-foot (Fig. 11d) black on sides of foot and on neck and snout. Tentacles parallel-sided or taper slightly distally and lightly to darkly pigmented, except for pale median stripe most obvious in individuals with darker tentacles. An indistinct red-brown patch on outer dorsal side of tentacles just in front of eyes present and few dense white pigment cells lie above eyes.

Anatomy (Figs. 12d,g,h, female genitalia; 43a, 44b, stomach; 43b, nervous system; 46a, penis) as for species. See Tables 18B–E for measurement data.

Type material: holotype (Fig. 5a) (SAM, D.17917, stn 003); and paratypes (003, AMS,

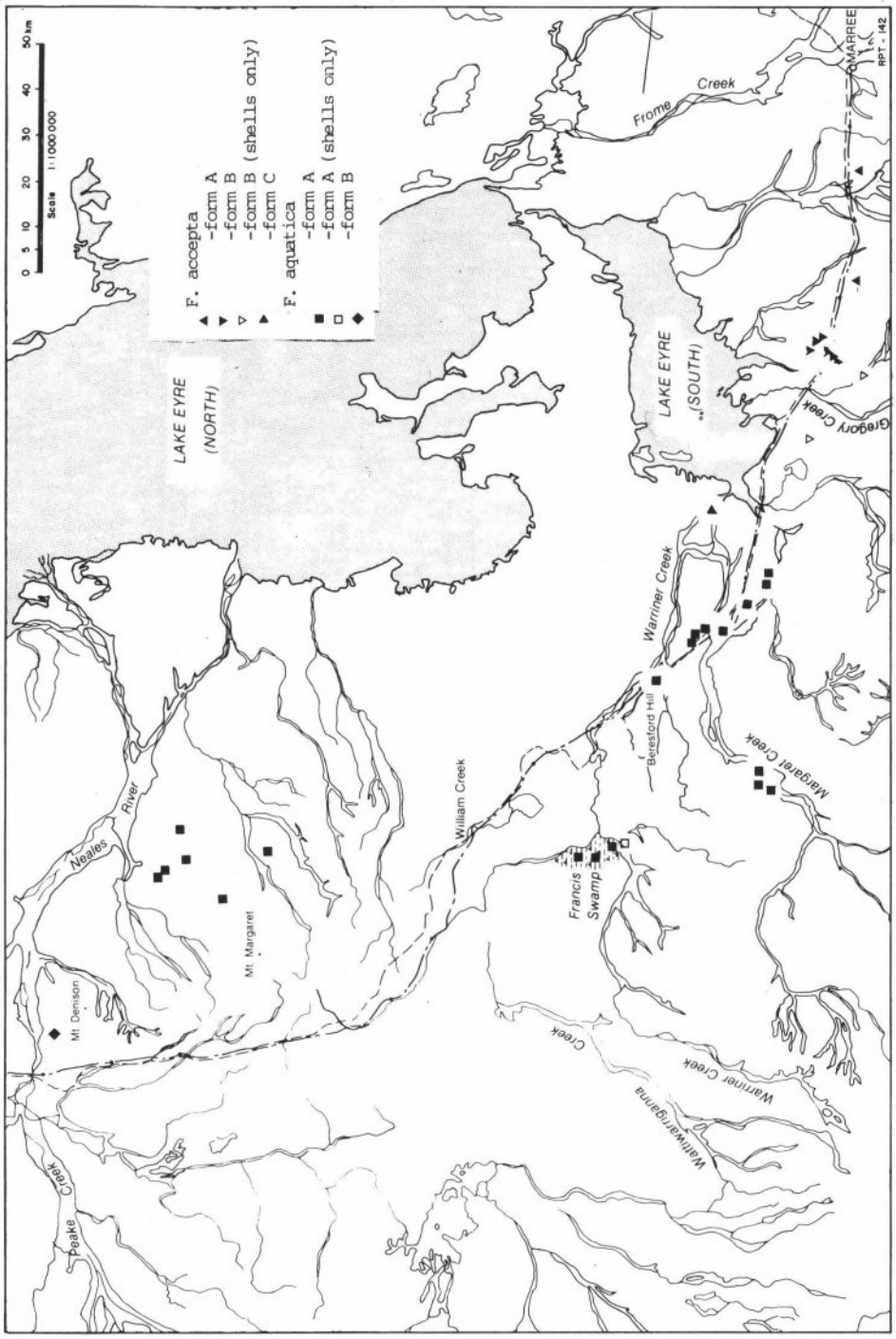


FIG. 13. Distribution of large aquatic species, *Fonscochlea accepta*, *F. aquatica*.

C.152848, many, C.152998, 1, figured; 756A, AMS, C.152849, many; 756B, AMS, C.152850, many; 756C, AMS, C.152851, many).

Dimensions of holotype: length 3.26 mm, width 1.83 mm, length of aperture 1.43 mm.

Localities: Welcome Springs (002, 003, 754A–D, 755A–D, 756A–C); Davenport Springs (004, 005, 752A,C, 753A,B (Fig. 13).

Remarks: The populations at Welcome and Davenport Springs do not seem to show any significant differences in any of the non-genital characters measured but there are some differences in measurements in the female genitalia. In particular BS/OD, CV/GO and OV/GO are significantly different. It is possible, on more detailed analysis, that these populations, which are more than 20 km apart, will be shown to be separable.

Fonscochlea accepta form B.

Figs. 5b, 6a–d,i, 7h, shell; 11f, head-foot; 12f, female genitalia; 8g, operculum; 10c, radula

Diagnosis: Ctenidial filaments fewer and shorter than in other two forms, and ctenidium tends to be shorter, although these differences not consistently significantly different for all populations. Radular sac shorter, and ratio of buccal mass to radular sac (BM/RS) larger, than in both other forms of *F. accepta*. Cephalic tentacles with reduced or absent median stripe and not tapered.

Shell (Figs. 5b, 6a–d,i, 7h) generally similar to form A but some individuals approach *F. accepta* form C in shape. See Table 18A for measurement data.

Operculum (Fig. 8g) as for species. See Table 18A for measurement data.

Radula (Fig. 10c) as for species. See Table 3 for data.

Head-foot (Fig. 11f) similar to that of *F. accepta* form A but median stripe on tentacles reduced or absent and tentacles usually slightly swollen distally, or if not, parallel-sided (i.e. not tapered).

Anatomy (Fig. 12f) as for species. See Tables 18B–E for measurement data.

Voucher material: primary voucher specimen (Fig. 5b) (SAM, D.17918, stn 694B); additional material from same station (694B, AMS, C.152852, many, C.152999, 1, figured; 693A, AMS, C.152853, 36; 693B, AMS, C.152854, 50; 693C, AMS, C.152855, 10; 694A, AMS, C.152856, 10; 694C, AMS, C.152857, 16).

Dimensions of primary voucher specimen: length 3.17 mm, width 1.86 mm, length of aperture 1.38 mm.

Localities: Hermit Hill Complex: Hermit Hill Springs (711A–D, 712); Old Finniss Springs (693A–C, 694A–C, 710); Old Woman Springs (733A–E); Finniss Swamp West (690A–C, 691A–D, 730); Dead Boy Spring (689); Sulphuric Springs (735); Bopeechee Springs (692A,B). Shells, possibly referable to this form, are known from Priscilla (686) and Venable (687) Springs (Fig. 13).

Remarks: This form is distinguished from *F. accepta* form A in ctenidal characters, a shorter radular sac, and tentacle shape. The smaller gill seen in *F. accepta* form B might have evolved in response to the generally small springs found in the Hermit Hill area. This form also differs behaviourly from form A, preferring the shallow water in the outflows to the deeper water in pools, whereas *F. accepta* form A is found in pools in large numbers.

Using discriminate analysis on a subset of shell measurements and opercular measurements, populations of this form did not separate well from *F. accepta* form A, although partial separation is achieved (Figs. 15, 16; Table 4). Pallial measurements, however, produced a clear separation from form A and the next form (Figs. 17, 18; Table 4).

Fonscochlea accepta form C.

(Figs. 5c, 7i, shell; 9b, protoconch; 10d, radula; Fig. 12e, female genitalia)

Diagnosis: Shell with relatively shorter spire than many other populations, but this not consistent. Gill filaments longer, typically twice as long, and more numerous than those of *F. accepta* form B. Similar, but less pronounced, differences between this form and *F. accepta* form A, with ratios of ctenidial length/shell length (LC/SH) and length of ctenidial filaments to shell length (HC/SH) larger than in both other forms. Distance between anus and ctenidium (CA) and ratio of this distance over shell length (CA/SH) larger than in other two forms. Radular sac intermediate in length between other two forms. Head-foot (not observed in living material) similar to *F. accepta* form A in having well-developed, unpigmented dorsal stripe on tentacles.

Shell (Figs. 5c, 7i; 9b, protoconch) as for species except for a relatively larger aperture (mean of AH 1.52, males; 1.51, females; compared with 1.31–1.46 mm for the other two forms). AH/BW is larger in most individuals than in the other two forms (mean 0.62, com-

TABLE 4. Summary of results of discriminate analysis of the forms of the large aquatic species of *Fonscochlea*. The numbers are the Euclidean (taxonomic) distances between the groups.

	*F.ac.*A	*F.ac.*B	*F.ac.*C	*F.aq.*A	*F.aq.*A(r)	*F.aq.*cf.A	*F.aq.*B	
F. accepta form A	X	0.460	0.598	1.611	1.477	2.519	1.010	Right side: Female, shell & operculum
		0.470	0.131	1.472	1.274	2.693	1.042	Male, shell & operculum
F. accepta form B	0.459	X	0.503	1.762	1.742	2.418	1.302	
	0.198		0.442	1.570	1.521	2.517	1.229	
F. accepta form C	0.375	0.370	X	1.286	1.328	1.964	0.950	
	2.722	2.889		1.484	1.298	2.685	1.063	
F. aquatica form A	1.550	1.667	1.326	X	—	—	0.771	
(combined)	—	—	—		—	—	0.521	
F. aquatica form A	1.384	1.630	1.272	—	X	1.842	0.507	
(restricted)	9.365	9.533	6.756	—		2.119	0.372	
F. aquatica cf. form A	2.606	2.463	2.261	—	1.972	X	2.029	
	0.396	0.539	2.402	—	—		2.020	
F. aquatica form B	1.025	1.253	0.901	0.637	0.420	2.004	X	
	3.630	3.797	1.169	—	5.737	3.271		

Left top—shell + operculum combined sexes
Left bottom—pallial combined sexes

pared with 0.57–0.58). See Table 18A for measurement data.

Operculum as for species. See Table 18A for measurement data.

Radula (Fig. 10d) as for species. See Table 3 for data.

Head-foot similar to that of *F. accepta* form A as far as can be judged from preserved material.

Anatomy (Fig. 12e, female genitalia) as for species. See Tables 16B–E for measurement data.

Voucher material: primary voucher specimen (Fig. 5c) (SAM, D.17919, stn 703A); additional material from same station (703A, AMS, C.152858, many, C.153000, 1, figured; 703B, AMS, C.152859, 60).

Dimensions of primary voucher specimen: length 3.10 mm, width 1.90 mm, length of aperture 1.40 mm.

Locality: Emerald Springs (703A,B).

Remarks: This population is recognised as a separate form because it differs from the other two forms, particularly *F. accepta* form B, in gill characters, as described above. It appears to have head-foot characters similar to those of *F. accepta* form A, but differs from *F. accepta* form B in this respect, and also differs in the distance of the anus from the mantle edge from both of the other forms. Discriminate analysis on pallial measurement data readily separates this form (Figs. 17, 18; Table 4).

This form lives in the upper outflow of a large, isolated spring in swiftly flowing water that reaches a depth of as much as several centimeters. It is common in the roots of dense vegetation around the fenced spring head at the uppermost part of the outflow but relatively rare on the downstream side of the fence where it appears to require shelter beneath debris such as wood. This suggests that, unlike the other two forms, which are commonly seen in the open, this form is strongly photonegative.

Emerald Springs is unusual in containing only one species of hydrobiid. This locality is widely separated, by about 40 km, from other populations of *F. accepta,* the nearest being those in the vicinity of Hermit Hill (*F. accepta* form B).

Fonscochlea aquatica n.sp.

Derivation: a reference to the aquatic habit of this species, in contrast to *F. zeidleri.*

Diagnosis: Shell large for genus (2.6 to 4.8 mm long), with 2.1–3.7 teleoconch whorls. Aperture with thin peristome and orthocline to opisthocline outer lip. Inner lip broad and firmly attached to parietal wall. Operculum with weak or absent pegs.

Shell (Figs. 7c,f; 14b,d; 53c,e; 9e, protoconch) as for diagnosis. Colour yellowish-brown to chocolate or reddish-brown.

Operculum (Fig. 8c,f) with pegs weak to moderately strong, or absent altogether.

Radula (Fig. 10f) as for genus. See Table 3 for details.

Head-foot (Figs. 11c,e) with pale, tapering cephalic tentacles and the darkly-pigmented head and snout.

Anatomy (Fig. 12c, female genitalia) typical of subgenus. Similar to *F. accepta*, differences being mainly size-related.

The typical form of this species is described below as "form A" where a holotype is designated for the species.

Localities: Middle, South Western, Northern and Freeling Springs (Fig. 13).

Remarks: This species can be divided into two geographic forms, possibly subspecies, which are separated on shell and opercular characters. It differs from *F. accepta* in its larger size (SH) and most other shell measurements are significantly different in nearly all populations and, consequently, many other size-related characters. They also differ in apertural details and in the relatively weaker to absent pegs on the operculum; PH/OL, PC/OL and PN/OL are all significantly different in most populations. The ratio AH/BW (aperture height/body whorl) is significantly larger in *F. aquatica* than in *F. accepta* in nearly all populations. This species separated well from *F. accepta* in discriminate analysis using shell and opercular measurements (Figs. 15, 16; Table 4).

Fonscochlea aquatica form A.

(Figs. 7c, 14d, 53c,e, shell; 9e, protoconch; 8c, operculum; 11c,e, head-foot; 12c, female genitalia)

Diagnosis: Shell with 2.10–3.63 (mean 3.24, males; 3.26, females) weakly to moderately convex teleoconch whorls (convexity ratio 0.16–0.24; mean 0.17, males; 0.18, females). Aperture oval with inner lip attached to parietal wall over most of length. Colour yellowish to chocolate brown. Operculum with calcareous smear 0–0.4 mm long (mean 0.22 mm, males; 0.21, females).

Shell (Figs. 7c, 14d, 53c,e; 9e, protoconch) as for diagnosis. See Table 18A for measurement data.

Operculum (Fig. 8c) with 1–4 (mean 2.80, males; 2.57, females) pegs, 0.02–0.29 mm (mean 0.10 mm, males; 0.11 mm, females) high. See Table 18A for measurements.

Radula as for species. See Table 3 for data.

Head-foot (Fig. 11c,e) as for species; dorsal cephalic tentacles uniformly lightly to darkly pigmented, sometimes with narrow, short unpigmented stripe bordered with dark lines.

Anatomy (Fig. 12c, female genitalia) as for species. See Tables 18B–E for dimensions.

Type material: holotype (Fig. 14d) (SAM, D.17920, 009); and paratypes (008, AMS, C.152860, 2; 685, AMS, C.152861, many; 739, AMS, C.152862, many).

Dimensions of holotype: length 4.27 mm, width 2.45 mm, length of aperture 1.86 mm.

Localities: Middle Springs: Horse Springs East (747A,B, 748A–C), Horse Springs West (746A,B), Mt. Hamilton Homestead (006), Strangways Spring (745A), Blanche Cup Spring (008, 685,739), Little Bubbler Spring (744A–C), Bubbler Spring (013), unnamed springs, Blanche Cup Group (786, 787), Coward Springs (019, 764A–C), Kewson Hill Springs (740, 741, 742A,B, 765), Elizabeth Springs (766A–F, 767A,B, 771A–C), Julie Springs (772A–D, 773A,B), Jersey Springs (683A,B, 769A,B, 770A), Warburton Spring (681A–C, 682), Beresford Spring (028).

South Western Springs: Billa Kalina Springs (026, 723A–D, 759A, 761A–C, 762A,B, 763A,B), Francis Swamp (717B,C, 720A,B, 721A–C), Strangways Springs (007, 029–030, 678A,B, 679A–C). Shells only from Margaret Spring (722).

Northern Springs: Brinkley Springs (677), Hawker Springs (670B,C, 671, 672A–D, 673), Fountain Spring (031–033), Twelve Mile Spring (036,037), Big Perry Spring (034), Outside Springs (038–040, 041) (Fig. 13).

Remarks: This form is the large aquatic species living in the Middle, South Western and Northern Springs, replacing *F. accepta,* which occurs in the Southern Springs.

Specimens from the Kewson Hill Springs and, to a lesser extent Elizabeth, Jersey and Julie Springs, tend to have stunted shells (Figs. 7c, 53c) and smaller gills with fewer filaments than have other populations of this form. The only important characters consistently separating these populations are peg height (PH) and the length of the calcareous smear (PC) and these, together with the values of PH/OL and PC/OL, are significantly different from those of all other populations of *F. aquatica*. Peg number also tends to be less, but not consistently so. The non-opercular dif-

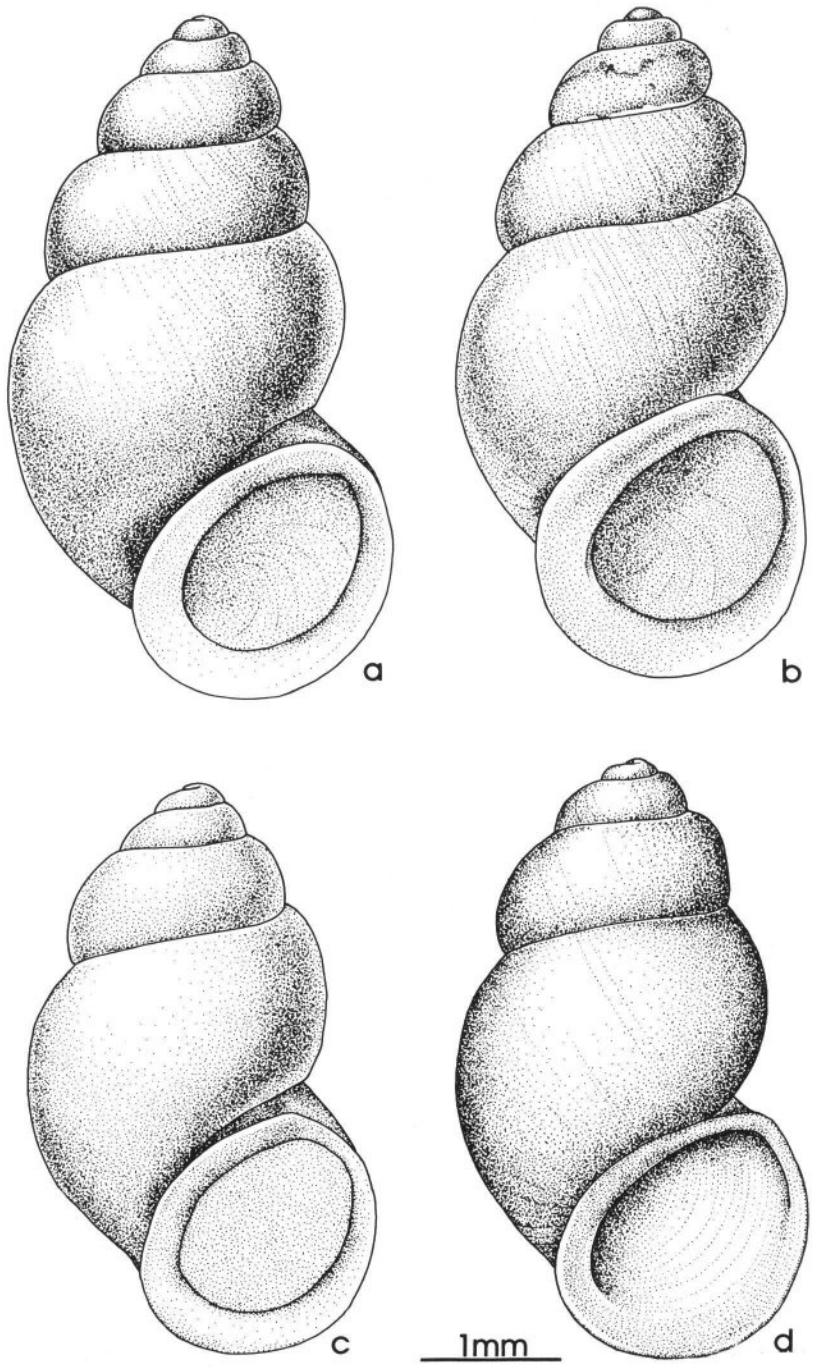


FIG. 14. Shells of species of *Fonscochlea*.
a. *Fonscochlea zeidleri* form A, holotype. Coward Springs (764).
b. *Fonscochlea aquatica* form B. Freeling Springs (665) (SAM, D.17921).
c. *Fonscochlea zeidleri* form B. Big Cadnaowie Spring (661) (SAM, D.17916).
d. *Fonscochlea aquatica* form A, holotype. Blanche Cup Spring (009).

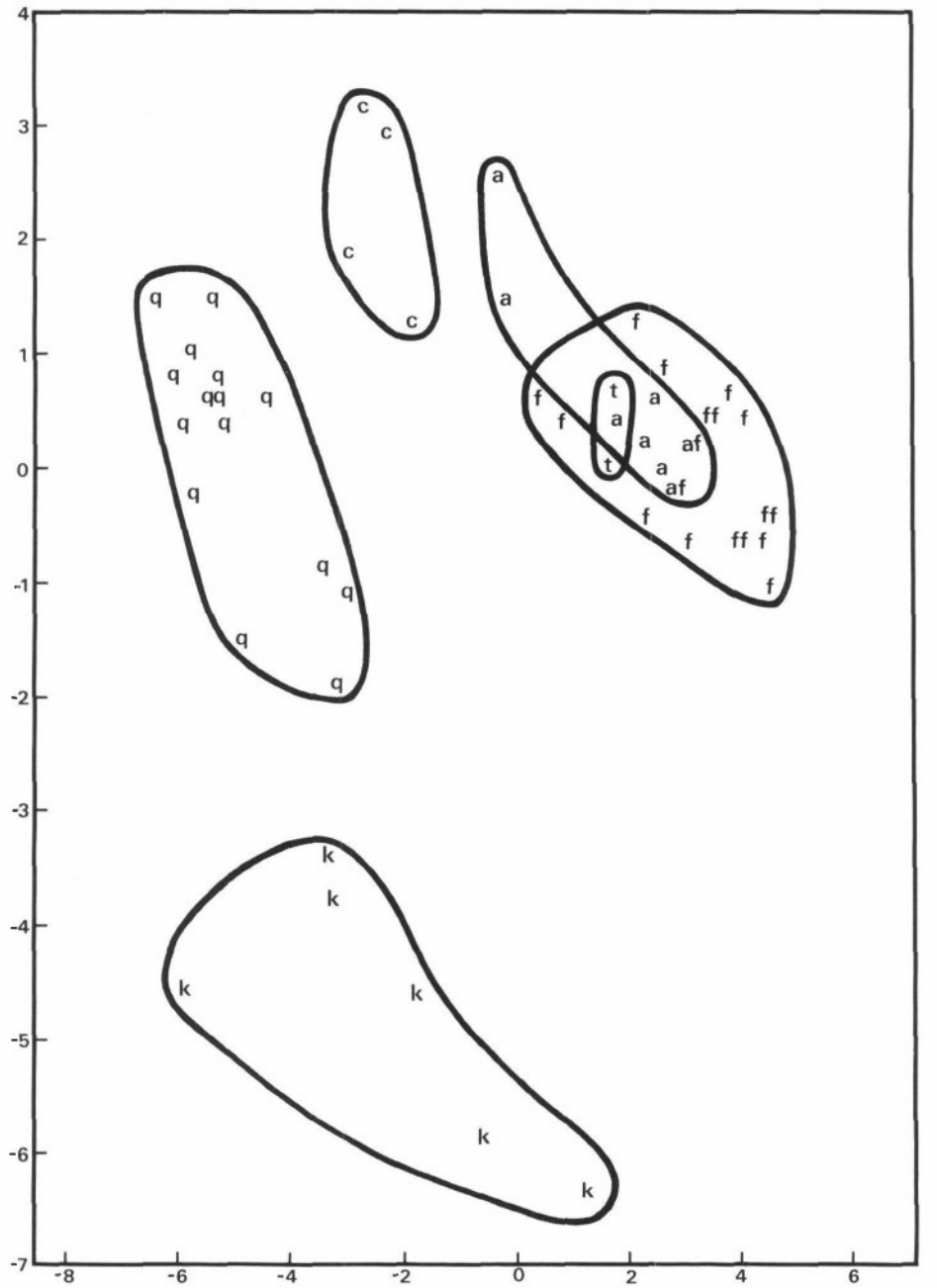


FIG. 15. Plot of group centroids, using the first two canonical axes, obtained from discriminate analysis of populations of large aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct populations. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: SH, 50.15%; SW, 41.40%; AH, 74.33%; TW, 53.49%; OL, 91.57%; PH, 78.06%; PC, 35.01%; PN, 38.94%. Second (vertical) axis: SH, 0.18%; SW, 19.15%; AH, 6.39%; TW, 2.14%; OL, 4.03%; PH, 13.72%; PC, 47.09%; PN, 0.06%. a, *F. accepta* form A; c, *F. aquatica* form B; f, *F. accepta* form B; *k, F. aquatica* cf. form A; q, *F. aquatica* form A, typical; t, *F. accepta* form C.

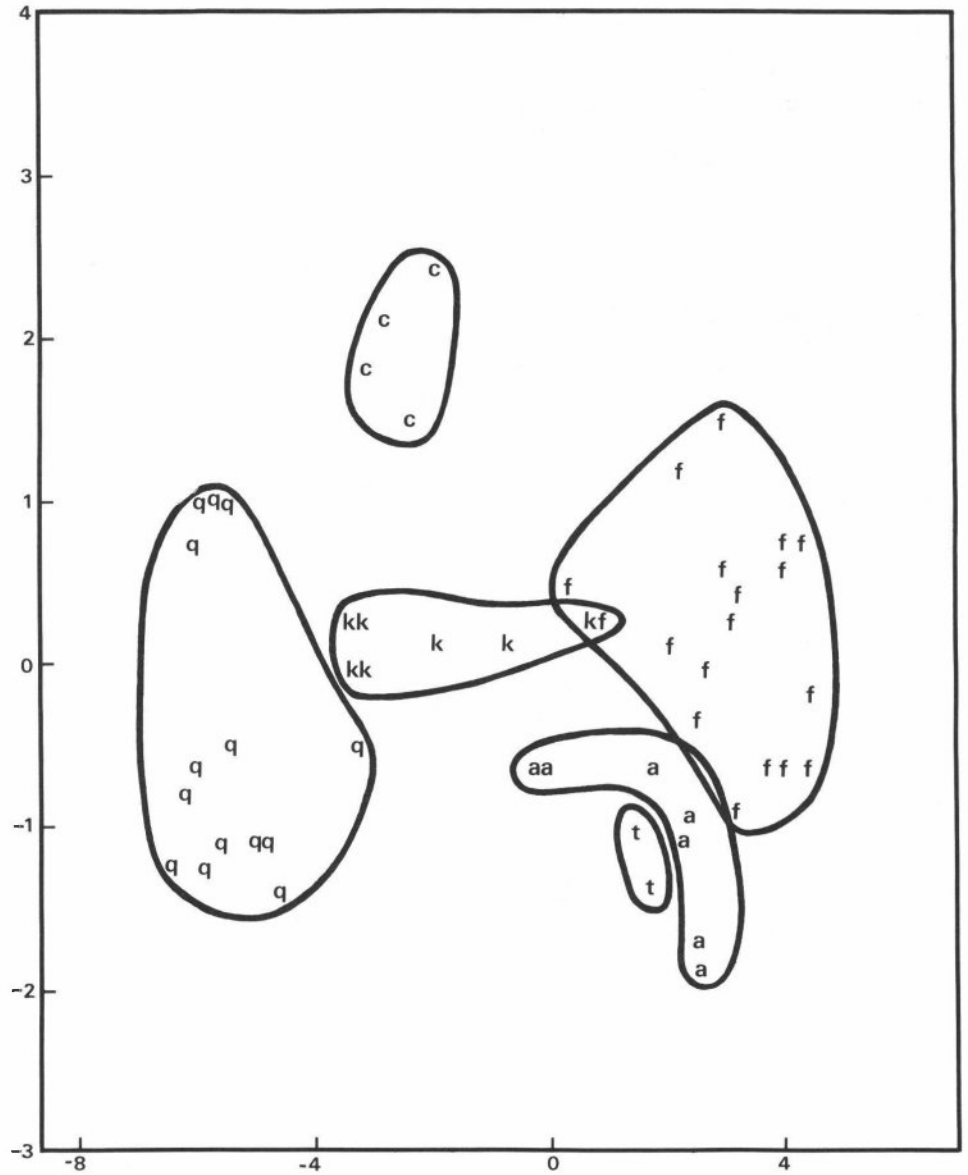


FIG.16. Plot of group centroids, using first and third canonical axes, obtained from discriminate analysis of populations of large aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purpose of this analysis, treated as distinct populations. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: SH, 50.15%; SW, 41.40%; AH, 74.33%; TW, 53.49%; OL, 91.57%; PH, 78.06%; PC, 35.01%; PN, 38.94%. Third (vertical) axis: SH, 0.42%; SW, 0.04%; AH, 0.32%; TW, 0.13%; OL, 0.52%; PH, 5.62%; PC, 7.36%; PN, 10.35%. a, *F. accepta* form A; c, *F. aquatica* form B; f, *F. accepta* form B; k, *F. aquatica* cf. form A; q, *F. aquatica* form A, typical; t, *F. accepta* form C.

ferences are not consistent within the geographic area in which the form occurs. The opercular and pallial differences are important but we do not judge them to be of sufficient magnitude to regard this form as a species, given the degree of overlap with typical *F.*

aquatica form A. These differences are as great as or greater than those between some groups of populations recognised here as distinct geographic forms but because these populations do not occupy a geographic area clearly separate from that of *F. aquatica* form A, it is not formally differentiated. These populations are recognised in the discussion below as *F. aquatica* cf. form A but are included in the diagnosis of form A above. They form a separate group when opercular and shell data are lumped together using discriminate analysis (Figs. 15,16). The Kewson Hill population (stn 741) in particular, has most shell measurements significantly different from all other populations of this species (including 683 and 767) and also differs from all populations (except stn 679) in the ratio BW/WH, but not in other shell ratios. Discriminate analysis using pallial measurements also separates the Jersey-Elizabeth-Kewson Hill populations from typical *F. aquatica* form A (Figs. 17, 18).

Somewhat surprisingly, there do not appear to be any consistent differences between the populations in the Northern and Blanche Cup Springs; despite their considerable separation, these group very closely in all the analyses. It is suggested below that the presence of *F. aquatica* form A in springs of the Middle Springs might be due to a relatively recent introduction to some of those springs, but that the form in the springs between Jersey Springs and Kewson Hill might be an earlier stock that differentiated at an infraspecific level. Biochemical evidence is required to determine the status of these populations.

Fonscochlea aquatica form B.

(Figs. 7f, 14b, shell; 8f, operculum; 10f, radula)

Diagnosis: Shell with 3.0 to 3.7 (mean 3.30, males; 3.33, females) teleoconch whorls, with more convex (convexity ratio 0.18–0.25; mean 0.21, males; 0.23, females) teleoconch whorls than is usual in typical form. Aperture more nearly circular than in typical form, with inner lip attached to parietal wall over shorter distance. Colour reddish to orange-brown. Operculum with calcareous smear (0.26–0.60 mm; mean 0.39 mm, males; 0.37 females) longer than in typical form.

Shell (Figs. 7f, 14b), see diagnosis. See Table 18A for measurements.

Operculum (Fig. 8f) as for species. Calcareous smear longer than in typical form. See Table 18A for measurements.

Radula (Fig. 10f) as for species. See Table 3 for data.

Head-foot as for species (preserved material only examined) except for distinct, dark, black to dark grey, dorsal stripe on tentacles of most individuals; rarely with short white stripe.

Anatomy as for species. See Tables 18B–E for measurement data.

Voucher material: primary voucher specimen (Fig. 14b) (SAM, D.17921, 665A); additional material from this station (665A, AMS, C.152863, many, C.152997,1, figured; 665B, AMS, C.152864, many; 665C, AMS, C.152865, many); 664A, AMS, C.152866, many; 664B, AMS, C.152867, many; 664C, AMS, C.152868, 32; 045, AMS, C.152869, 25; 046, AMS, C.152870, many.

Dimensions of primary voucher specimen: length 4.59 mm, width 2.47 mm, length of aperture 1.98 mm.

Localities: Freeling Springs (042–044, 045–046, 663, 664B,C, 665A–C).

Remarks: The Freeling Springs form of *F. aquatica* is consistently and readily distinguishable at sight from specimens in the springs farther southeast, the more convex teleoconch whorls and reddish colour in particular, being distinctive features. The circular aperture is probably correlated with the more convex whorls and the shorter area of attachment of the inner lip of the aperture to the parietal wall.

This form separates well from related taxa by discriminate analysis using shell and opercular measurements (Figs. 15, 16) and is also separated from *F. aquatica* form A using pallial measurements (Figs. 17, 18).

Discrimination of the large aquatic taxa of *Fonscochlea* and their forms was tested using discriminate analysis on shell and opercular measurements and pallial measurements. The results showed that all groups could be discriminated using these data, with 85% of all measured individuals (n = 625) being classified correctly with the shell + opercular data and 78% of the specimens (n = 103) using the pallial measurements. The Euclidian (taxonomic) distances between the groups are given in Table 4. With shell and opercular data the greatest distance score when sexes were treated as separate populations was 2.69 between *F. aquatica* cf. form A and *F. accepta* form A. All of the pairwise comparisons between *F. aquatica* and *F. accepta*

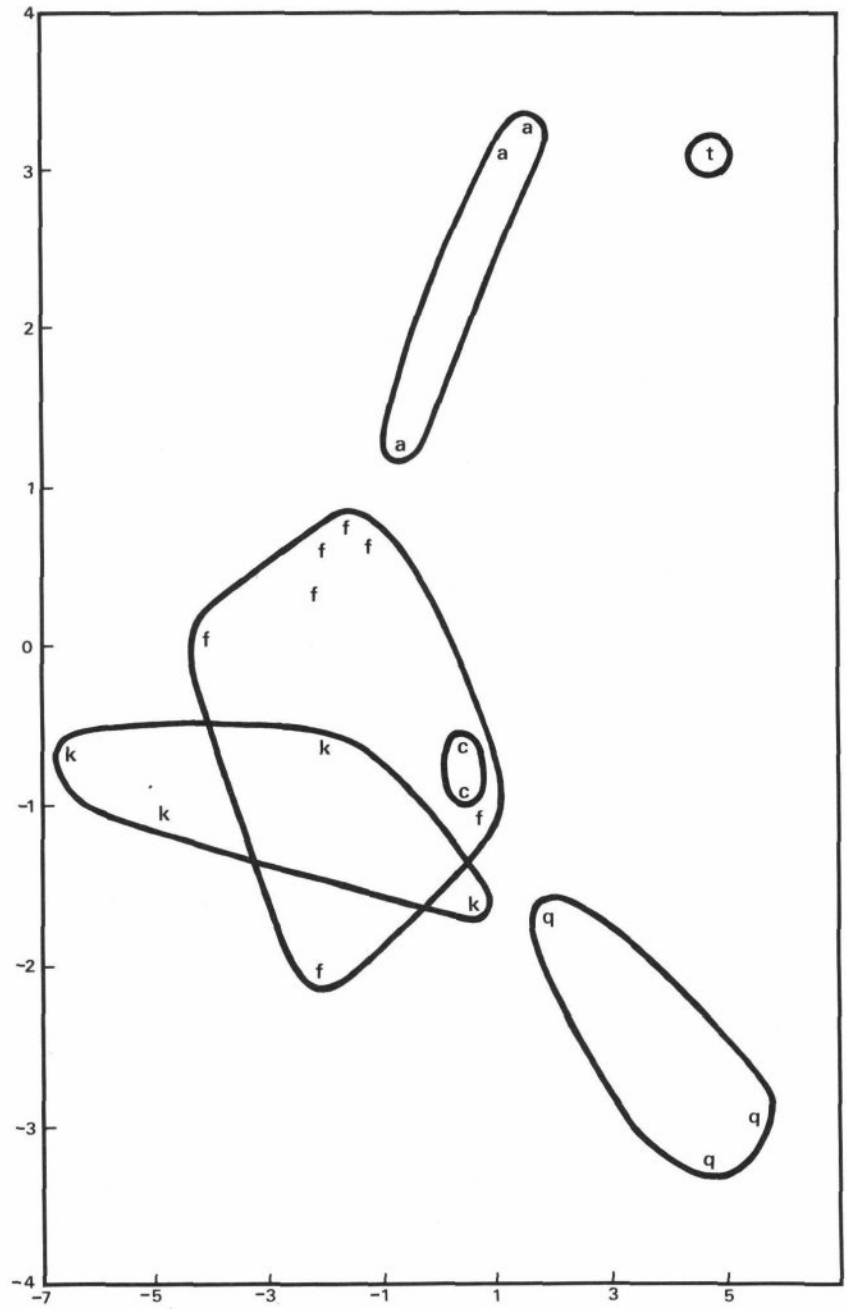


FIG. 17. Plot of group centroids, using first two canonical axes, obtained from discriminate analysis of populations, sexes combined, of large aquatic species and forms of *Fonscochlea* using pallial measurements. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: LC, 16.32%; WC, 77.51%; FC, 52.54%; AC, 78.58%; HC, 59.24%; LO, 46.76%; WO, 29.30%; DO, 1.12%, CO, 37.69%. Second (vertical) axis: LC, 19.95%; WC, 5.70%; FC, 30.44%; AC, 1.57%; HC, 33.13%; LO, 0.04%; WO, 6.27%; DO, 47.12%, CO, 8.90%. a, *F. accepta* form A; c, *F. aquatica* form B; f, *F. accepta* form B; k, *F. aquatica* cf. form A; q, *F. aquatica* form A, typical; t, *F. accepta* form C.

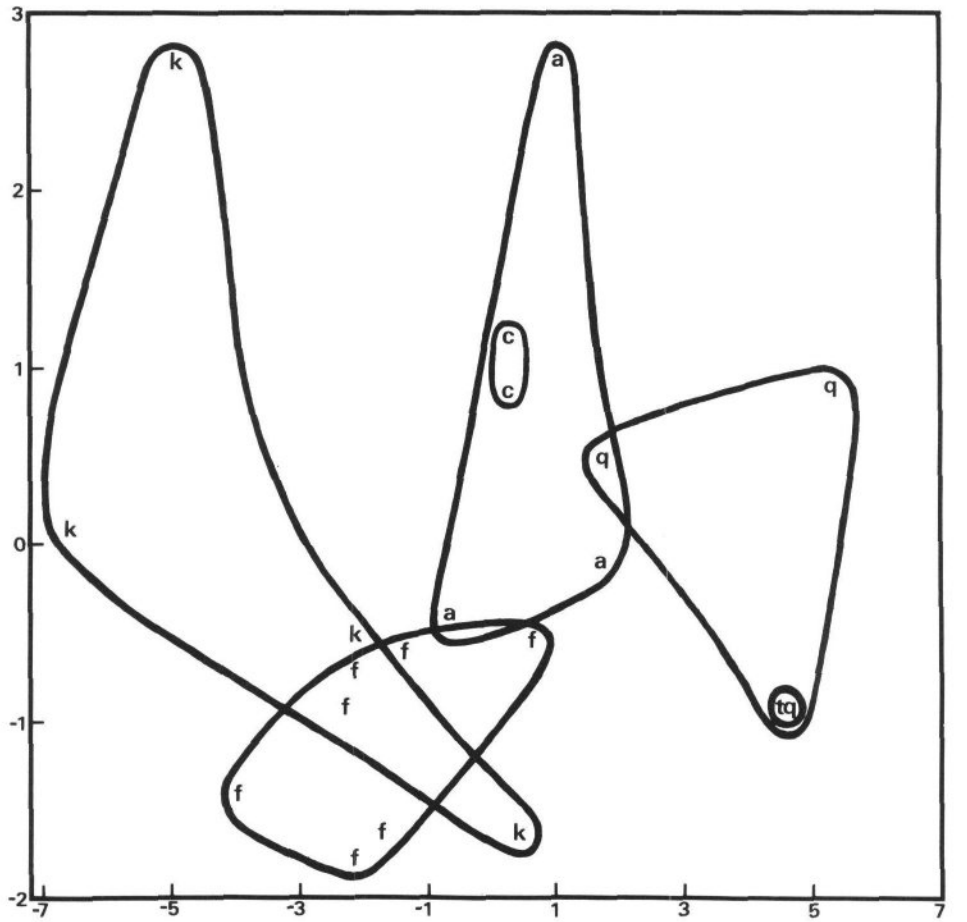


FIG. 18. Plot of group centroids, using first and third canonical axes, obtained from discriminate analysis of populations, sexes combined, of large aquatic species and forms of *Fonscochlea* using pallial measurements. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: LC, 16.32%; WC, 77.51%; FC, 52.54%; AC, 78.58%; HC, 59.24%; LO, 46.76%; WO, 29.30%; DO, 1.12%, CO, 37.69%. Third (vertical) axis: LC, 6.38%; WC, 0.62%; FC, 0.01%; AC, 12.12%; HC, 2.07%; LO, 4.27%; WO, 36.13%; DO, 10.62%, CO, 0.30%. a, *F. accepta* form A; c, *F. aquatica* form B; f, *F. accepta* form B; k, *F. aquatica* cf. form A; q, *F. aquatica* form A, typical; t, *F. accepta* form C.

scored >0.95 (all but one >1.0, the lowest distance score between females of *F. aquatica* form B and *F. accepta* form C). All of the pairwise comparisons between the groups within *A. aquatica* scored >0.37 (all but one >0.5, the lowest distance score between males of *F. aquatica* forms A and B). Within *F. accepta* all groups scored >0.13 (all but one >0.44, the lowest distance score between males of *F. accepta* forms A and C). Using pallial data the distance scores between *F. aquatica* and *F. accepta* were >0.39 (all but two >1.0, the lowest scores between *F. aquatica* cf. form A and *F. accepta* forms A and B, reflecting the reduced gill in this form of *F. aquatica*). The greatest scores (>9.3) were between *F. aquatica* form A and *F. accepta* forms A and B. Within *F. accepta* the forms had distance scores >0.19, this score being between forms A and B, form C having a score of >2.7 when contrasted with the other two forms. The groups within *F. aquatica* separated with scores >3.2, that between form A and cf. A being 5.7.

SNK tests (5% level) using pooled data,

combined and separate sexes, for each variable used in the discriminate analyses gave these results.

Shell and opercular characters:

SH—Combined sexes: significantly different for both species and all forms except *F. accepta* form C and *F. accepta* form A. Separate sexes: the same result except for *F. aquatica* form A, *F. aquatica* cf. form A and *F. aquatica* form B overlapping. The means for this character were not significantly different between males and females except for the two forms of *F. aquatica* (females larger).

SW—Combined sexes: means significantly different for *F. accepta* form B and *F. accepta* form A + *F. accepta* form C. Separate sexes: *F. accepta* form B, *F. accepta* form A + *F. accepta* form C + *F. aquatica* cf. form A and *F. aquatica* form A + *F. aquatica* form B are significantly different subsets. Only *F. aquatica* form A shows significant sexual dimorphism for this character.

AH—Combined sexes: significantly different for all forms of both species. Separate sexes: five subsets are discriminated; *F. accepta* form B, *F. accepta* form A + *F. accepta* form C, *F. aquatica* cf. form A + *F. aquatica* form B, *F. aquatica* form A male and female. Sexual dimorphism is apparent in only *F. aquatica* form A.

TW—Combined sexes: significantly different for the two forms of *F. aquatica,* the forms of *F. accepta* overlapping but, together, being significantly different from *F. aquatica.* Separate sexes: two groups of overlapping subsets are discriminated; one with *F. accepta* (all forms) + *F. aquatica* cf. form A, the other with *F. aquatica* form A + *F. aquatica* form B. This character does not significantly differ between males and females.

OL—Sexes combined: same result as for SH. Separate sexes: two groups of overlapping subsets are discriminated that correspond to the same groups as for the last variable (TW). There was no significantly different sexual dimorphism.

PH—Combined sexes: significantly different for *F. aquatica* form A, *F. aquatica* form B + *F. accepta* form B and *F. accepta* form A + *F. accepta* form C. Separate sexes: all form overlapping subsets except *F. aquatica* cf. form A. None show significant differences between sexes in this character.

PC—Combined sexes: means significantly different for the two forms of *F. aquatica* and these both separate from *F. accepta,* the forms of that species not being discriminated.

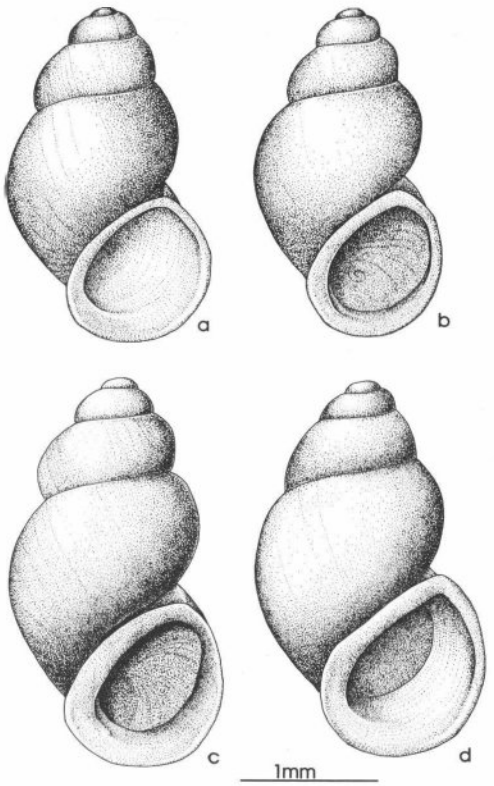


FIG. 19. Shells of species of *Fonscochlea.*
a. *Fonscochlea variabilis* form A, holotype. Blanche Cup Spring (009).
b. *Fonscochlea variabilis* form A, Bubbler Spring (013) (AMS, C.153001).
c. *Fonscochlea variabilis* form C, Freeling Springs (045) (AMS, C.152882).
d. *Fonscochlea billakalina,* holotype. Old Billa Kalina Spring (027).

Separate sexes: three groups are discriminated, *F. aquatica* cf. form A, *F. aquatica* form B and, the third (intermediate) group with the rest. There is no sexual dimorphism in this character.

PN—Combined sexes: all overlap except *F. aquatica* form A. Separate sexes: all overlap except *F. aquatica* cf. form A. There is no significant sexual dimorphism in this character.

It is clear from these results that the Jersey Springs-Kewson Hill form of *F. aquatica* is very distinct, as is also demonstrated with the pallial characters below.

Pallial characters (combined sexes only given here): LC—*F. accepta* form B + *F. aquatica* cf. form A + *F. accepta* form A are

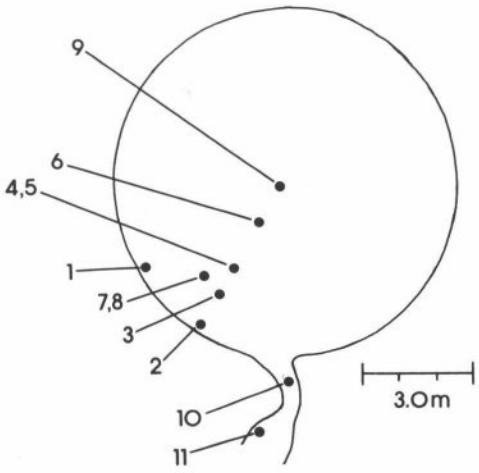


FIG. 20. Blanche Cup pool and upper outflow (Stn. 739), showing location of the 11 sampling sites for study of size-variation in *Fonscochlea variabilis*.

not separated but *F. aquatica* form B is significantly different from that subset and from a subset formed by *F. accepta* form C and *F. aquatica* form A.

WC—*F. aquatica* cf. form A is significantly different from all other forms, which form overlapping subsets.

FC—*F. aquatica* form A is significantly different from all others, which form overlapping subsets.

AC—There are no significant differences between any two forms.

HC—Three subsets are separated, one with *F. aquatica* cf. form A + *F. accepta* form B, another with *F. accepta* form C and the third (intermediate in size) with the three remaining forms.

LO—There are no significant differences between any two of the forms.

WO—All forms contained in overlapping subsets.

DO—Three different subsets are discriminated, one with the forms of *F. accepta,* the intermediate one with *F. aquatica* cf. form A + *F. aquatica* form B and the third with *F. aquatica* form A.

Group 2: the small aquatic species.

Fonscochlea variabilis n.sp.

Derivation: a reference to the variable shell of this species.

Diagnosis: Shell small (up to 3.5 mm long), conical, with 2–3.4 weakly to moderately convex (convexity ratio 0.05–0.30) teleoconch whorls. Aperture expanded in some populations, not in others. Inner lip narrow and loosely attached to parietal wall or separated from it. Colour pale to dark brown. Operculum with 1–7 strong pegs, peg height 0.06–0.2 mm.

Shell (Figs. 7e, 19a–c, 22a,c, 23d–f,h,i, 25b) see diagnosis.

Operculum (Fig. 8e) with strong pegs.

Radula (Fig. 10e) as for genus. Inner marginal with 9–15 cusps. See Table 3 for other details.

Head-foot (Fig. 24a,b,d,e) variably pigmented; cephalic tentacles with unpigmented narrow, dorsal stripe margined with pale grey to black lines. Cephalic tentacles and snout very pale grey to black, black around eyes or just behind eyes.

Anatomy (Fig. 27a,d, female genitalia) similar to other species in subgenus. No consistent significant anatomical differences between this species and *F. conica* noted, although data limited.

The typical form of this species is described below as "form A" where a holotype is designated for the species.

Localities: Middle, Northern and Freeling Springs.

Remarks: This species and two others, *F. conica* and *F. billakalina,* comprise the small aquatic group. They tend to prefer the upper outflow and spring head (Fig. 54) and to attach themselves to the undersides of hard objects (stones, wood, bones, etc.).

Some populations of this species show considerable variation, sometimes a dimorphism, in size that does not seem to be sexually based. See the remarks on form A of this taxon for a detailed analysis and discussion of one of these populations.

Apart from size-related differences, the three "small aquatic" species differ from *F. aquatica* and *F. accepta* in having the seminal receptacle displaced more posteriorly relative to the coiled oviduct (compare Figs. 12, 27).

Fonscochlea variabilis form A.

(Figs. 19a,b, 23d–f, shell; 24a,b,d,e, head-foot; 27a,d, female genitalia)

Shell 1.8–2.8 mm (mean 2.28, males; 2.42, females) in length, width/length ratio 0.58–0.65, with 2.00–3.38 moderately convex teleoconch whorls (convexity ratio 0.05–0.30,

TABLE 5. Descriptions of 11 stations in the Blanche Cup pool and upper outflow (Stn. 739) sampled for the study of shell variation in *Fonscochlea variabilis*.

Station	Distance from edge of pool	Water depth	Comments
1	2–5 cm	1–2 cm	30–60% covered by short sedge, sandy bottom.
2	20 cm	3 cm	mat of dead sedge on its side, mud bottom.
3	1.8 m	—	mat of filamentous algae lying between sedges.
4	2.8 m	15 cm	bottom sample, 5% algal cover, some dead sedge.
5	2.8 m	15 cm	sample from sedges (20–30% cover).
6	5 m	30 cm	beyond edge of dense sedge mats, bottom consisting of dead, algal-covered sedge and water weed.
7	2 m	10 cm	middle of sedge zone, sparse (30%) cover.
8	2 m	10 cm	as in (7), but in densely covered (60%) area.
9	4.5 m	1 m	fine sand bottom.
10	—	<2 cm	outflow, under stones.
11	—	<2 cm	outflow, filamentous algae.

mean 0.18) and aperture not markedly expanded. Operculum with strong pegs.

Shell (Figs. 19a,b, 23d–f), see diagnosis. See Table 19A for measurements.

Operculum with 1–5 (mean 2.96, males; 3.14, females) strong pegs 0.09–0.2 mm (mean 0.14 mm, males; 0.15 mm, females) in height, calcareous area 0.16–0.34 mm (mean 0.24 mm) long. See Table 19A for measurements.

Radula as for species. See Table 3 for details.

Head-foot (Fig. 24a,b,d,e) typically darkly pigmented with distinctive, triangular patch of black pigment behind eyes and patch of dense white granules anterior to, and on inner side of eyes. Small form of *F. variabilis* occurring at Blanche Cup Spring (see below) paler than large form (compare Fig. 24a,d), with pale grey snout and unpigmented tentacles.

Anatomy (Fig. 27a,d, female genitalia) as for species. See Tables 19B–C for measurements.

Type material: holotype (Fig. 19a) (SAM, D.16275, stn 009); and paratypes (008, SAM, D.3208, 74, AMS, C.152873, 1; 009, AMS, C.152871, many; 010, AMS, C.152874, 50; 011, AMS, C.152875, 30; 739, AMS, C.152931, 5).

Dimensions of holotype: length 2.45 mm, width 1.47 mm, length of aperture 1.07 mm.

Localities: Middle Springs: Blanche Cup Spring (008–012, 685, 739), Little Bubbler Spring (744A–C), Bubbler Spring (013–017), unnamed spring in Blanche Cup Group (786), Coward Springs Railway Bore (018, 684, 743) (Fig. 26).

Remarks: This form of *F. variabilis* and *F. conica* are found in the Blanche Cup Group although not in the same springs. *Fonscochlea variabilis* is found in the larger springs, whereas *F. conica* is restricted to the small springs. This is the only detected example of parapatry of any taxa in the two species groups of *Fonscochlea*.

Collections from Blanche Cup (Stn 739) contained not only typical *Fonscochlea variabilis* form A (SH, 2.0–2.7 mm), but also a smaller, adult (SH, <1.8 mm) "form," with a complete and thickened aperture. Possible explanations for the presence of these two phenotypes include sexual dimorphism, sympatry of congeners (the second species being *Fonscochlea conica* or another unnamed species), seasonal classes of *F. variabilis* form A that attained different sizes at maturity, and distinct ecomorphs of *F. v.variabilis*. In an effort to determine the significance and nature of this apparent size bimodality, the following data were gathered and analyzed.

Samples were taken from 11 stations in the pool and upper outflow of Blanche Cup (Fig. 20, Table 5), encompassing a range of microhabitats and including samples along a transect from the edge to the center of the pool. Stations 1–9 were sampled on 31/8/83 while Stations 10 and 11 were sampled on 27/11/83. A fine sieve having a mesh size of 1 mm was used to sample soft sediment and aquatic vegetation. At Station 10 snails were collected by washing them from the undersides of stones into a container. A maximum of five minutes of sampling was done at each station and the snails were preserved in formalin for later study. No snails were found at Stations 3, 6, and 9.

From each sample, 50 mature small aquatic *Fonscochlea* having a "mature" aper-

TABLE 6. Shell height statistics for *Fonscochlea variabilis* from 8 stations at Blanche Cup (Stn. 739).

	Shell Height (mm)					
	Males			Females		
Station	$\bar{X}$	SD	N	$\bar{X}$	SD	N
1	2.13	0.217	23	2.26	0.272	27
2	2.19	0.208	32	2.20	0.235	18
4	2.26	0.205	29	2.38	0.142	21
5	2.25	0.15	32	2.36	0.199	18
7	2.26	0.257	24	2.31	0.222	26
8	2.19	0.259	23	2.24	0.193	27
10	1.78	0.33	25	1.87	0.444	25
11	1.77	0.315	24	2.19	0.333	26

ture were selected at random and their shell heights were measured with the digitizing pad, for size-frequency analysis. The shells were then cracked and the snails sexed.

The small aquatic snails from a large sample obtained by general collecting at Blanche Cup on 29/8/83 were roughly sorted into typical *F. variabilis* form A and the small "form." Fifty-seven of the former and 55 of the latter were selected at random and all shell parameters were measured with the digitizing pad. The shells were then cracked, the snails sexed and the opercular data were obtained.

Size-frequency histograms, sexes separate, for the shells measured from the various stations are given in Fig. 21 and appropriate statistics are shown in Table 6. The small "form" was almost totally absent from the pool samples. Noteworthy is the lack of bimodality and paucity of snails of SH less than 1.87 mm in these samples (Fig. 21). The two samples from the outflow (10, 11) had large numbers of the small "form" (SH <1.69 mm) as well as typical *F. variabilis* form A. The results of a pairwise comparison, sexes separate, of shell height among all stations (SNK Test, null hypotheses of equality of shell height rejected at $P \leq 0.01$) are given in Table 7. There is little difference in shell height among the 6 stations in the pool, with only 4 of 30 possible comparisons having a significant difference. However, the two outflow samples (Stations 10, 11) do differ significantly in shell height for most pairwise comparisons with the pool samples: for Station 10, all possible comparisons (12 of 12) are significantly different; for Station 11, seven of 12 comparisons are significantly different. Note that shell height for females from Station 11 generally does not differ significantly from that of the pool samples.

While the histograms for the samples from the outflow suggest bimodality in size within sexes, the sample sizes are too small to provide statistically significant evidence of such bimodality. It is evident from the histograms that the apparent size bimodality is not due simply to sexual dimorphism: while females are generally larger than males, the outflow samples include both male and female snails assignable to the small "form", as well as normal-sized males and females.

Typical individuals of both sexes of *F. variabilis* form A and the small "form" were found to differ significantly (LSD Test, null hypotheses rejected at $P \leq 0.01$) in all shell and opercular parameters, excluding convexity, as well as the following ratios: PD/SH, SW/SH, AH/SH, and PC/OL. While these data suggest that two distinct phenotypes are indeed present in Blanche Cup, we do not have sufficient evidence at this point to separate them as species, or to determine whether they represent ecomorphs, seasonal classes, or different species. At this point, we consider them, tentatively, as forms of *F. variabilis* form A. The measurement data for the small form are not included in the summary of measurement data of *F. variabilis,* but are shown as separate data in Table 19. The small form is also treated individually in the discriminate analysis and it groups separately from typical *F. variabilis* form A and *F. conica* (Figs. 28–30; Table 8).

Using discriminate analysis on shell and opercular measurements this form, excluding the small Blanche Cup form, separated rather well from the other small aquatic taxa of *Fonscochlea* (Figs. 28–30; Table 8), although with a small amount of overlap with *F. conica.*

Fonscochlea variabilis form B.

(Figs. 7e, 22c, 23h,i, 25b, shell; 8e, operculum; 10e, radula)

Diagnosis: Shell 2.09–3.48 mm (mean

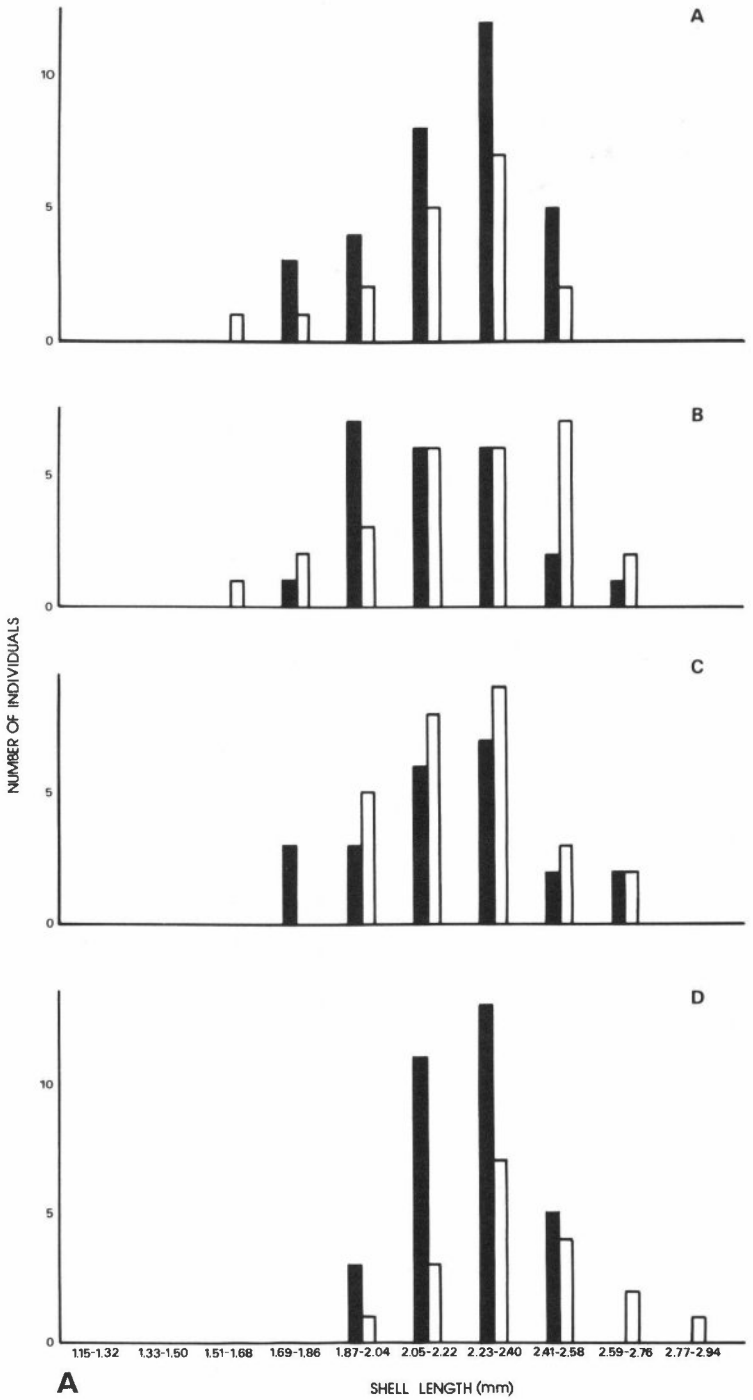
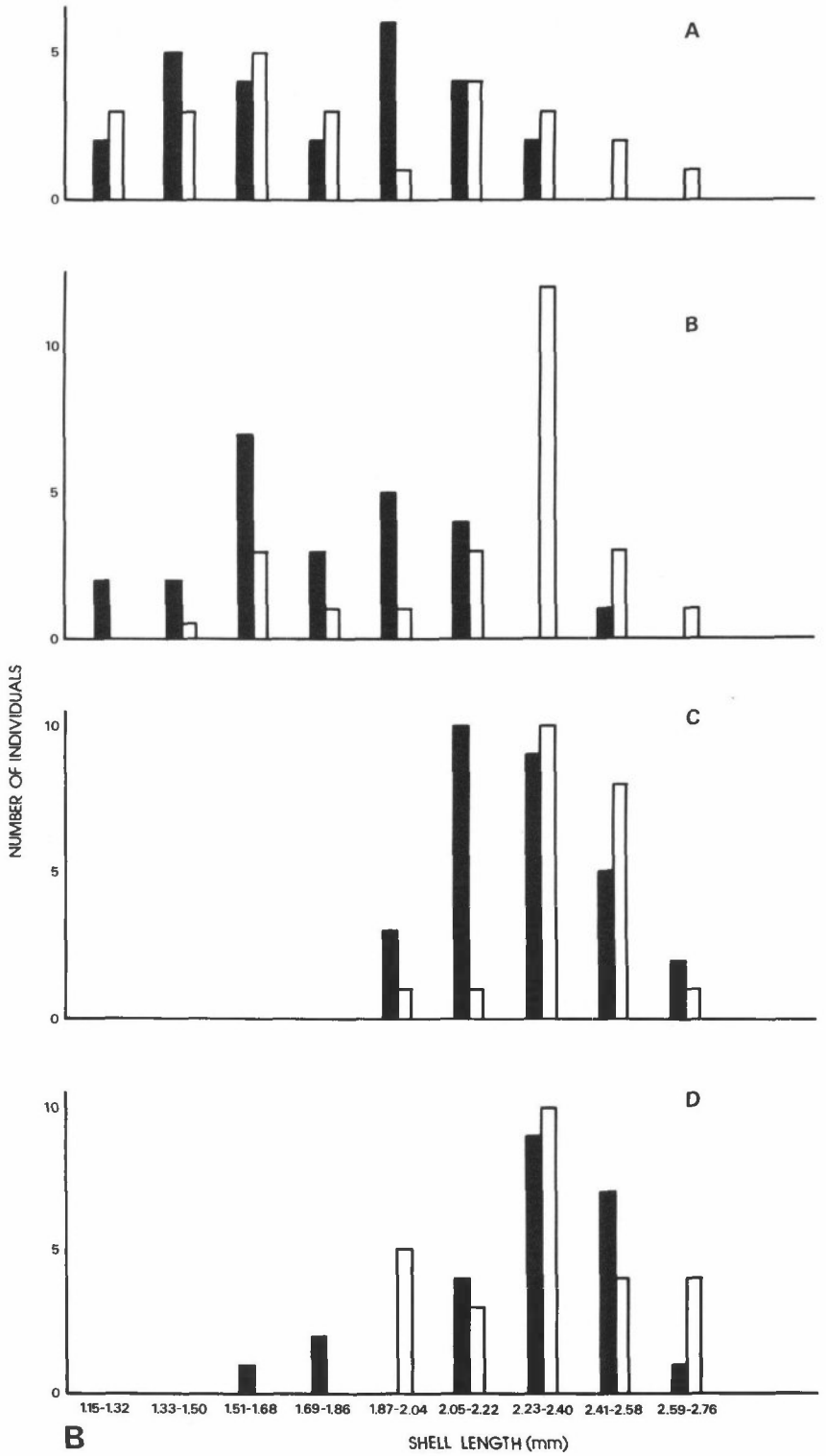


FIG. 21. Size-frequency histograms for *Fonscochlea variabilis* from eight stations at Blanche Cup (Stn. 739). Darkened columns, males; white columns, females.
A. Pool stations. A, stn 2; B, stn 1; C, stn 8; D, stn 5.
B. Pool and outflow stations. A, stn 11; B, stn 10; C, stn 4; D, stn 7.


A
B
C
D
NUMBER OF INDIVIDUALS
0
5
10
1.15-1.32
1.33-1.50
1.51-1.68
1.69-1.86
1.87-2.04
2.05-2.22
2.23-2.40
2.41-2.58
2.59-2.76
SHELL LENGTH (mm)

B

TABLE 7. Significant differences (SNK Test, $P \leq 0.01$) in shell height of *Fonscochlea variabilis* among stations at Blanche Cup (Stn. 739). Empty boxes indicate shell height for males or females does not differ significantly between that pair of stations.

	Station							
Station	1	2	4	5	7	8	10	11
1	—							
2		—						
4	F	F	—					
5	M			—				
7	M				—			
8						—		
10	M,F	M,F	M,F	M,F	M,F	M,F	—	
11	M	M	M,F	M	M	M	F	—

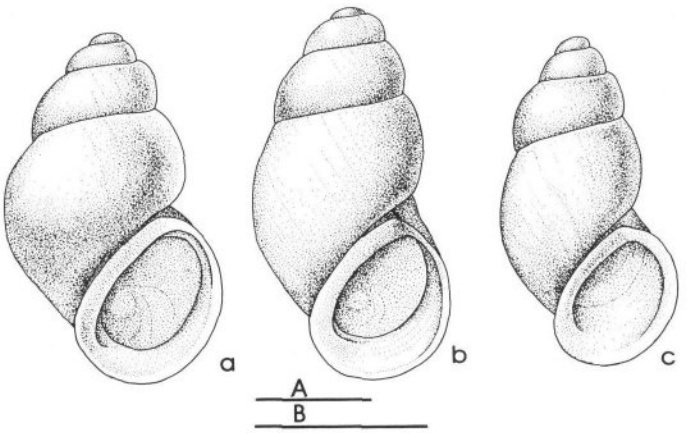


FIG. 22. Shells of species of *Fonscochlea*.
a. *Fonscochlea variabilis* form C. Freeling Springs (664) (SAM, D.17913).
b. *Fonscochlea conica*, holotype. Welcome Springs (003).
c. *Fonscochlea variabilis* form B. Twelve Mile Spring (036) (SAM, D.17912).
Scale: 1mm. Scale A: a,c,; scale B: b.

2.58 mm, males; 2.79 mm, females) in length with width/length ratio of 0.57–0.62, thus generally narrower than form A, but not consistently so. Teleoconch whorls 2.38–3.5 (mean 2.89, males; 2.98, females), convex (convexity ratio 0.10–0.25; mean 0.16, males; 0.19, females) and aperture noticeably expanded. Operculum with well-developed pegs.

Shell (Figs. 7e, 22c, 23h,i, 25b), see diagnosis. See Table 19A for measurements.

Operculum (Fig. 8e) with 2–7 (mean 3.88, males; 4.85, females) well-developed pegs 0.06–0.16 mm (mean 0.10 mm, males; 0.11 mm, females) long, calcareous area 0.16–0.47 mm (mean 0.28 mm, males; 0.31 mm, females) long. Calcareous area longer and PH/OL smaller than in most specimens of *F. variabilis* form A. See Table 19A for measurement details.

Radula (Fig. 10e) as for species. See Table 3 for data.

Head-foot not observed in living material but generally similar to form A except median dorsal unpigmented band on tentacles usually very narrow or absent but black lines usually present. Background pigmentation dark grey to black.

Anatomy as for species. See Tables 19B–C for measurements.

Voucher material: primary voucher specimen (Fig. 22c) (SAM, D.17912, stn 036); additional material from same station (SAM, D.2031, 9; 037, AMS, C.152876, many; 036, AMS, C.152877, many; 1003A, AMS,

TABLE 8. Summary of results of discriminate analysis of shell + opercular (right side) and pallial characters (left side) of small aquatic species of *Fonscochlea*. The numbers are the Euclidean (taxonomic) distances between the groups.

	F.va.A	*f.va*(small)	*F.va*.B	*F.va*.C	*F.conica*	*F.bill.*	
F. variabilis form A	X	2.268 1.792	1.780 1.003	1.444 1.478	0.724 0.697	1.584 1.613	Right side: Female Male
F. variabilis (small form)	3.421	X	3.953 2.727	3.662 3.139	1.577 1.127	1.684 1.714	
F. variabilis form B	1.480	3.382	X	0.446 0.502	2.440 1.661	3.283 2.492	
F. variabilis form C	1.506	3.421	0.162	X	2.139 2.978	2.899 2.978	
F. conica	0.660	1.376	2.073	2.115	X	1.283 1.395	
F. billakalina	1.524	1.683	2.906	2.908	1.311	X	

Left side: Combined sexes.

C.152878, many; 1003B, AMS, C.152879, many; 1003C, AMS, C.152880, many; 1003D, AMS, C.152881, 20; 037, AMS, C.152929, 3).

Dimensions of primary voucher specimen: length 2.95 mm, width 1.58 mm, length of aperture 1.21 mm.

Localities: Northern Springs: Hawker Springs (670A–C, 672A,B,D, 673), Fountain Spring (031–032), Twelve Mile Spring (035–037, 1003A–D), Big Perry Springs (034), Outside Springs (038, 040) (Fig. 26).

Remarks: This form is not readily separable from *F. variabilis* form A quantitatively on any single character. Shells are generally separable on the characters given in the diagnosis, although there is considerable overlap. Using discriminate analysis on a subset of shell measurements and opercular measurements, *F. variabilis* form B separated rather well from *F. variabilis* form A and *F. conica* (Figs. 28–30; Table 8).

Fonscochlea variabilis form C

(Figs. 19c, 22a, shell)

Diagnosis: Shell similar to *F. variabilis* form B but typically relatively broader than most populations of that form (width/length ratio 0.60–0.62), thicker (i.e. more solid) and sometimes larger (length 2.31–3.48 mm; mean 2.60 mm, males; 2.84, females). Operculum with well-developed pegs and long calcareous smear.

Shell (Figs. 19c, 22a) with 2.25–3.25 (mean 2.84, males; 2.96, females) teleoconch whorls, convexity ratio 0.16–0.25 (mean 0.23, males; 0.20, females), see diagnosis for other details. See Table 19A for measurements. Colour brown to reddish-brown.

Operculum with 3–6 (mean 4.36, males; 4.44, females) well-developed pegs 0.11–0.17 mm (mean 0.13 mm, males; 0.16 mm, females) in height, calcareous smear 0.31–0.50 mm (mean 0.37, males; 0.43, females), generally longer than in other forms of this species (but close to *F. variabilis* form B) and therefore PC/OL ratio significantly different. See Table 19A for measurement details.

Radula as for species. See Table 3 for data.

Head-foot as for species. Not examined in living material.

Anatomy as for species. See Tables 17B–C for measurements.

Voucher material: primary voucher specimen (Fig. 22a) (SAM, D.17913, stn 664B); additional material from same station (045, AMS, C.152882, 1, figured; 045, AMS, C.152883, many; 664A2, AMS, C.152884, many; 664A1, AMS, C.152889, 16; 664B, AMS, C.152885, many); 665A, AMS, C.152886, many; 665B, AMS, C.152887, many; 665C, AMS, C.152888, 50; 046, AMS, C.152890, 5.

Dimensions of primary voucher specimen: length 3.25 mm, width 2.00 mm, length of aperture 1.50 mm.

Localities: Freeling Springs (042–043, 045–046, 663, 664A,B, 665A–C) (Fig. 26).

Remarks: Specimens of this form are

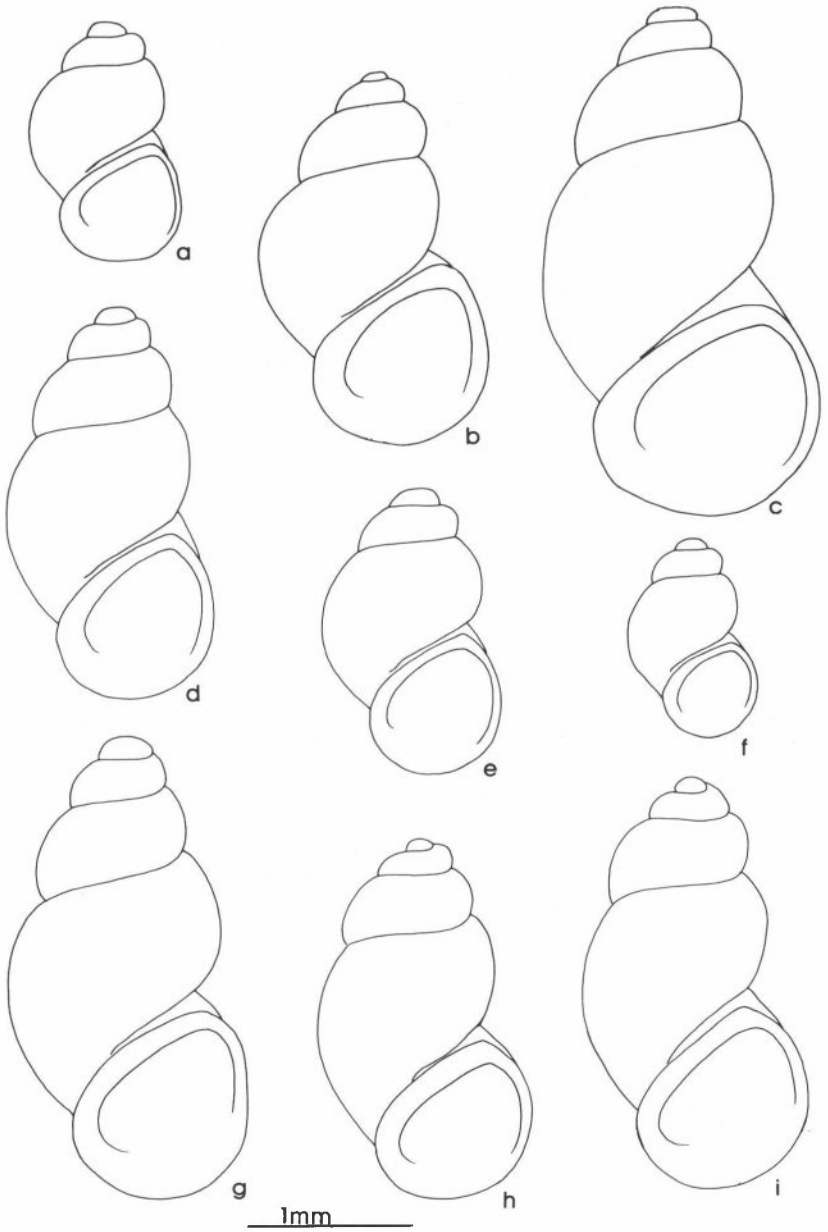


FIG. 23. Shells of *Fonscochlea billakalina* and *F. variabilis*.
a–c. *Fonscochlea billakalina*. Strangways Springs (679), showing size variation (AMS, C.152967).
d–e. *Fonscochlea variabilis* form A, Blanche Cup Spring (739), showing size variation (paratypes, AMS, C.152931).
f. *Fonscochlea variabilis*, small form from Blanche Cup Spring (739) (AMS, C.155863).
g. *Fonscochlea billakalina*, Strangways Springs (678) (AMS, C.152969).
h,i. *Fonscochlea variabilis* form B. Twelve Mile Spring (037), showing size variation (AMS, C.152967).

readily distinguished from other populations of *F. variabilis* on shell characters despite a small number of quantifiable differences. Discriminate analysis separated the single mea-

sured population of this form from the rest of the small aquatics (Figs. 28–30; Table 8). This is one of four "taxa" endemic to Freeling Springs.

Fonscochlea conica n.sp.

Derivation: a reference to the conical shape of the shell.
(Figs. 22b, 53b,f, shell; 9f, protoconch; 24f,g, head-foot; 27b, female genitalia).

Diagnosis: Shell small (1.41–2.83 mm long; mean 1.94 mm, males; 2.07 mm, females), conical, with 2.0–3.2 (mean 2.57, males; 2.67, females) weakly to moderately convex (convexity ratio 0.04–0.24; mean 0.13, males; 0.16, females) teleoconch whorls. Aperture not expanded; inner lip narrow, usually attached to parietal wall; outer lip slightly prosocline. Colour of shell ranges from yellowish brown to dark brown or orange-brown. Operculum with strong pegs. Head-foot lightly pigmented except for black triangle behind eyes.

Shell (Figs. 22b, 53b, f; 9f, protoconch), see diagnosis. Measurement data in Table 19A.

Operculum with 1–5 (mean 2.48, males; 2.64, females) strong pegs 0.05–0.17 mm (mean 0.10 mm, males; 0.11 mm, females) in height, calcareous area 0.08–0.29 mm (mean 0.17 mm, males; 0.18 mm, females) long. See Table 19A for measurement data.

Radula as for genus. Inner marginal teeth with 14–18 cusps. See Table 3 for other details.

Head-foot (Fig. 24f,g) is lightly pigmented with grey or pale grey, snout and cephalic tentacles very pale grey or unpigmented. Conspicuous black triangle behind eyes. Cephalic tentacles with inconspicuous pale dorsal line in posterior quarter to half.

Anatomy (Fig. 27b, female genitalia) very similar to that of *F. variabilis* except in size-related characters. See Tables 19B–E for measurement data.

Type material holotype (Fig. 22b) (SAM, D.17914, stn 003); and paratypes (003, AMS, C.152895, many; 756A, AMS, C.152896, 6; 756B, AMS, C.152897, many; 756C, AMS, C.152898, many).

Dimensions of holotype: length 2.15 mm, width 1.16 mm, length of aperture 0.90 mm.

Localities: Southern Springs: Welcome Springs (003, 755A,B,D, 756A–C), Davenport Springs (004, 005, 753A,B), Old Woman Spring (733B). Shells have been found at Finniss Swamp West (690), Venable Spring (687) and Priscilla Spring (686).

Middle Springs: Horse Springs East (747A,B, 748A–C), Horse Springs West (746), Strangways Spring (007, 745A), an unnamed spring in Blanche Cup Group (739, 785, 787), Coward Springs (019–022, 023, 764A–C), Kewson Hill (741, 742A, 765), Julie Springs (772A,B,D, 773A–C), Elizabeth Springs (024, 766A,C–E, 771A–C), Jersey Springs (025, 683A,B, 768A,B, 769A,B, 770A,B), Warburton Spring (681A–C, 682). Beresford Spring (028) (Fig. 26).

Remarks: The shells of the specimens assigned to this species are smaller, more compact and more solid than are those of most specimens of *F. variabilis*. These two species do not occupy the same spring groups, except in the Blanche Cup Group in which *F. conica* is found in small springs and *F. variabilis* form A in the larger springs.

The smaller, more conical shells and pale head-foot serve to distinguish this species from *F. variabilis* in the Blanche Cup Group and elsewhere. Because the protoconchs in both species have a similar diameter, the PD/SH ratio is significantly larger in nearly all populations of *F. conica* compared with *F. variabilis,* reflecting the generally larger shell of *F. variabilis*. The radulae also differ in the two species, *F. conica* having more cusps on the inner lateral teeth than do most specimens examined in the *F. variabilis* complex.

Discriminate analysis using shell and opercular measurements separated the populations of *F. conica* and *F. variabilis* well, although there is minor overlap with *F. variabilis* form A in the plot using the first and second axes. *F. variabilis* form B is well separated except in the plot using the second and third axes.

Despite the lack of any single character that consistently and significantly separates all individuals of *F. conica* from all individuals of *F. variabilis,* they are recognised as distinct species because of their virtually sympatric association in the Blanche Cup Group. The differences in radulae and in the pigmentation of the head-foot noted above reinforce the results of the discriminate analysis using the quantifiable shell and opercular differences. It is, however, freely admitted that the relationships of all of the small *Fonscochlea* are by no means clear and further analysis using electrophoretic methods is required to resolve the somewhat tentative arrangement proposed here.

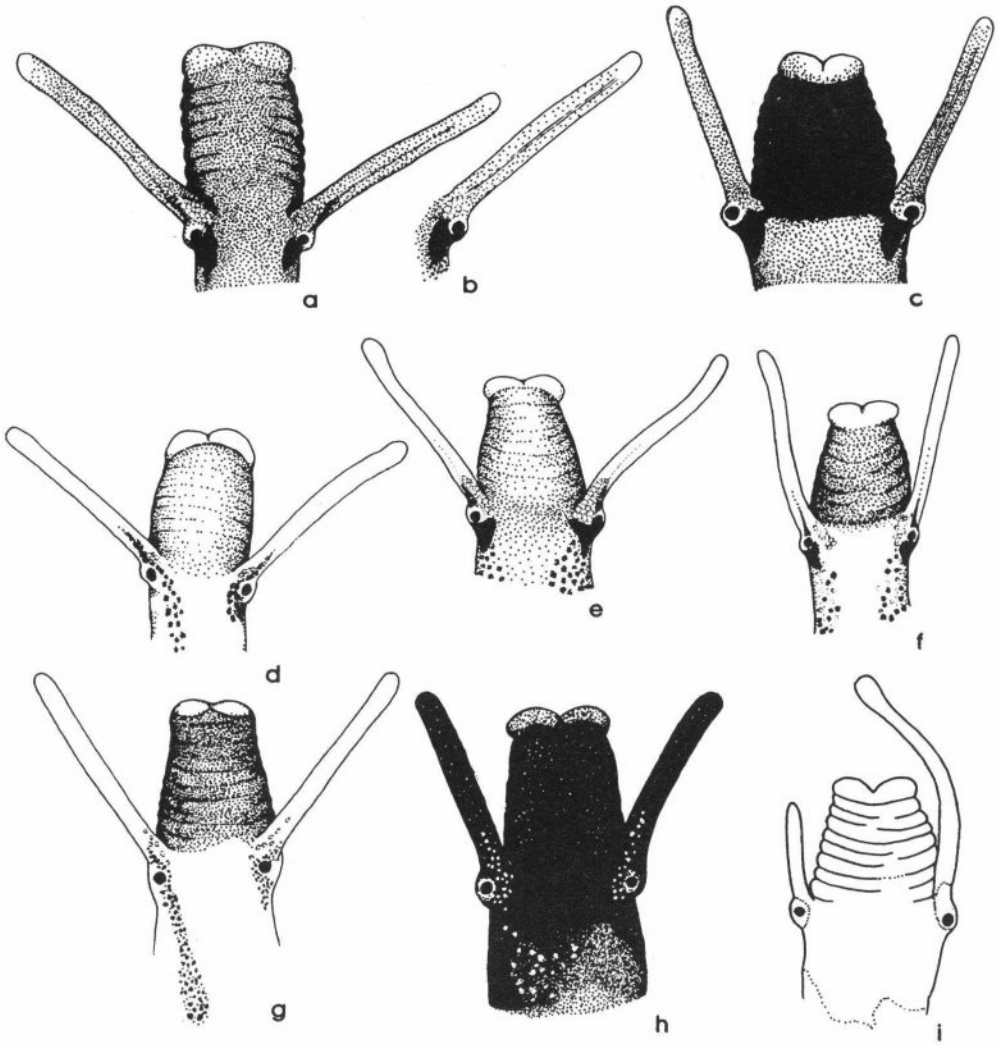


FIG. 24. Dorsal views of heads of species of *Fonscochlea* and *Trochidrobia punicea*. All figures except i from living material.
a, d. *Fonscochlea variabilis,* Blanche Cup Spring. a, form A, typical; d, small form.
b. *Fonscochlea variabilis* form A, Bubbler Spring, right tentacle only, showing the unpigmented stripe on the tentacle in this population. The remainder of the head is similar to that in a.
c. *Fonscochlea billakalina,* Old Billa Kalina Spring.
e. *Fonscochlea variabilis* form A, Coward Springs Railway Bore.
f,g. *Fonscochlea conica;* f, Welcome Springs; g, Elizabeth Springs.
h. *Trochidrobia punicea,* Blanche Cup Spring.
i. *Fonscochlea aquatica* cf. form A, Elizabeth Springs, showing abnormal tentacle development (from preserved specimen).
Scale: 0.2mm.

Fonscochlea billakalina n.sp.

Derivation: refers to Billakalina Station on which many of the springs containing this species are found.

(Figs. 7d, 19d, 23a–c,g, 25a,c–g, shell; 8d, operculum; 24c, head-foot; 27c, female genitalia).

Diagnosis: Shell similar to *F. variabilis* and *F. conica* but operculum differs markedly in having very weak to absent pegs.

Shell (Figs. 7d, 19d, 23a–c,g, 25a,c–g) with

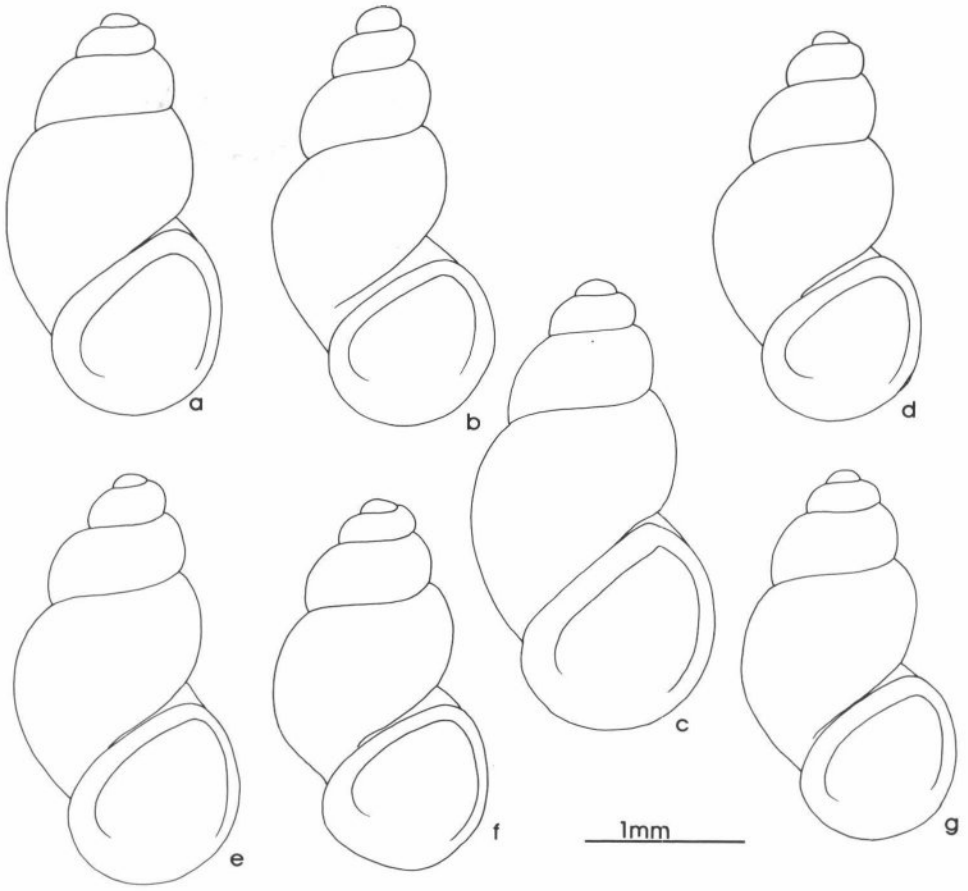


FIG. 25. Shells of *Fonscochlea billakalina* and *F. variabilis* form B.
Fonscochlea billakalina:
a,g. Billa Kalina springs, a, (759) (paratypes, AMS, C.152930); g, (763) (AMS, C.152964).
c. Old Billa Kalina Spring (027) (paratype, AMS, C.152963).
d,e. Francis Swamp, d, (721) (AMS, C.152966); e, (720) (AMS, C.152968).
f. Fenced Spring, Billa Kalina (723) (AMS, C.152965).
Fonscochlea variabilis form B:
b. Hawker Springs (673) (AMS, C.152970).

two forms present. One form (Figs. 23a–c,g, 25a,d,f,g) with shell similar to that of *F. variabilis* form B and 1.9–2.4mm in length; other form (Figs. 7d, 25c), restricted to spring at Old Billa Kalina Homestead ruin (027, 759), is similar to *F. variabilis* form A but is larger (2.8–3.2 mm long compared with 1.8–2.8 mm). Overall mean shell length 2.60 mm (males) and 2.64 mm (females). Teleoconch whorls 2.30–3.38 (mean 2.75, male; 2.77, female), convexity ratio 0.03–0.24 (mean 0.15, male; 0.14, females). Measurement data in Table 19A.

Operculum (Fig. 8d) with 0–5 (mean 1.40, males; 1.59, females) small pegs 0.02–0.14 mm (mean 0.07 mm) in height; calcareous area 0–0.33 mm (mean 0.13 mm) long. See Table 19A for measurement data.

Radula, see Table 3 for data.

Head-foot (Fig. 24c) as for species. Background pigmentation of snout and tentacles dark grey to black.

Anatomy (Fig. 27c, female genitalia) as for species. See Tables 19B–E for measurement data.

Type material: holotype (Fig. 19d) (SAM, D.17911, stn 027); and paratypes (SAM, D.2034, 30; SAM, D.2035, 32; 759B, AMS,

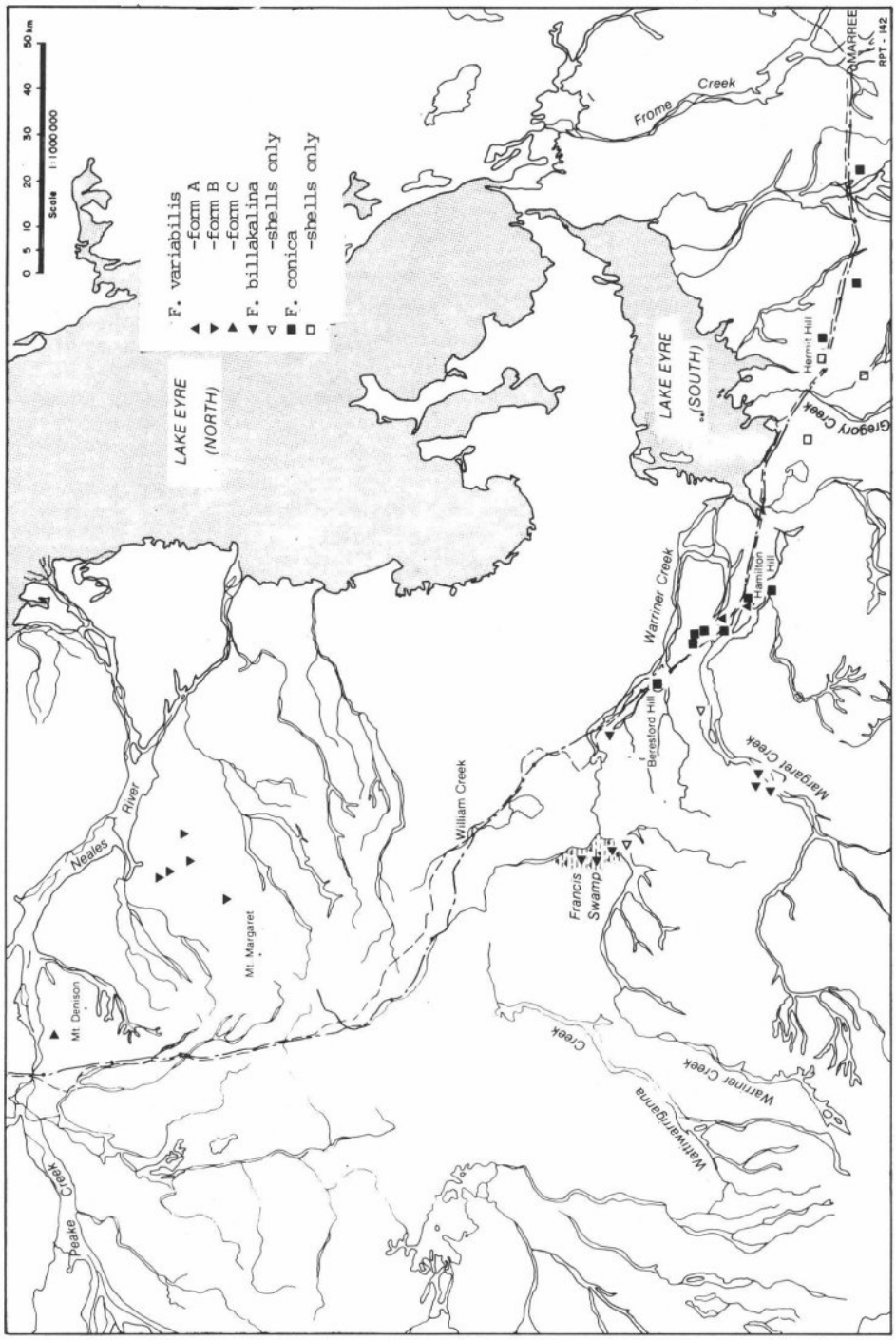


FIG. 26. Distribution of small aquatic species, *Fonscochlea variabilis*, *F. billakalina* and *F. conica*.

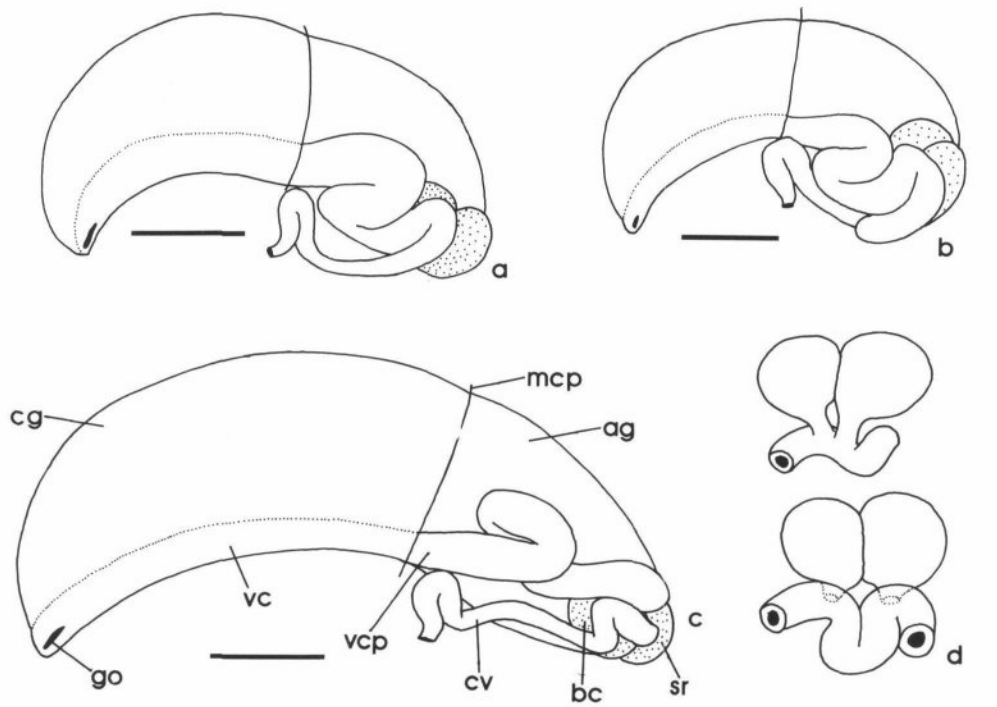


FIG. 27. Female genitalia of species of *Fonscochlea*.
a,d. *Fonscochlea variabilis* form A. The Bubbler Spring. d, detail of sperm sacs.
b. *Fonscochlea conica,* Horse Spring East.
c. *Fonscochlea billakalina,* Old Billa Kalina Spring.
ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; cv, coiled oviduct; go, oviduct opening; mcp, posterior limit of pallial cavity; sr, seminal receptacle; vc, ventral channel; vcp, posterior extension of ventral channel.
Scale: 0.25mm.

C.152891, 18; 759B, AMS, C.152892, many; 026, AMS, C.152893, many, C. 152995, 1, figured; 027, AMS, C.152894, many, C.152963, 1, figured; 759, AMS, C.152930, 1, figured).

Dimensions of holotype: length 2.78 mm, width 1.68 mm, length of aperture 1.33 mm.

Localities: South Western Springs: Billa Kalina Springs (026–027, 723A–D, 758C, 759A–C, 760, 761, 763A,B), Francis Swamp (717A,B, 720A–C, 721A–C), Strangways Springs (029, 030, 678A,B, 679A–C, 680). Shells from Welcome Bore/Spring (758) and Margaret Spring (722) might belong to this form (Fig. 26).

Remarks: The two shell forms seen in populations included in this taxon are, when extremes are examined, readily distinguished. Intermediate specimens, however, do occur in some populations.

The shell characters are virtually identical, in most populations, with those of *F. variabilis* form B but that taxon can be readily distinguished by its strong opercular pegs. With discriminate analysis, using shell and opercular measurements, this species is clearly differentiated from the other small aquatic taxa (Figs. 28, 29, 30; Table 8).

This taxon is recognised as a species because of the considerable differences between its operculum and those of the other small aquatic taxa. The lack of obvious correlated shell or anatomical characters is, in this case, judged to be outweighed by the strongly diagnostic opercular characters.

Discrimination of the small aquatic taxa (including the geographic forms) of *Fonscochlea* was tested using discriminate analysis on shell and opercular measurements. The results showed that all groups could be discriminated using these data, 87% of the measured specimens (n=617) being correctly classi-

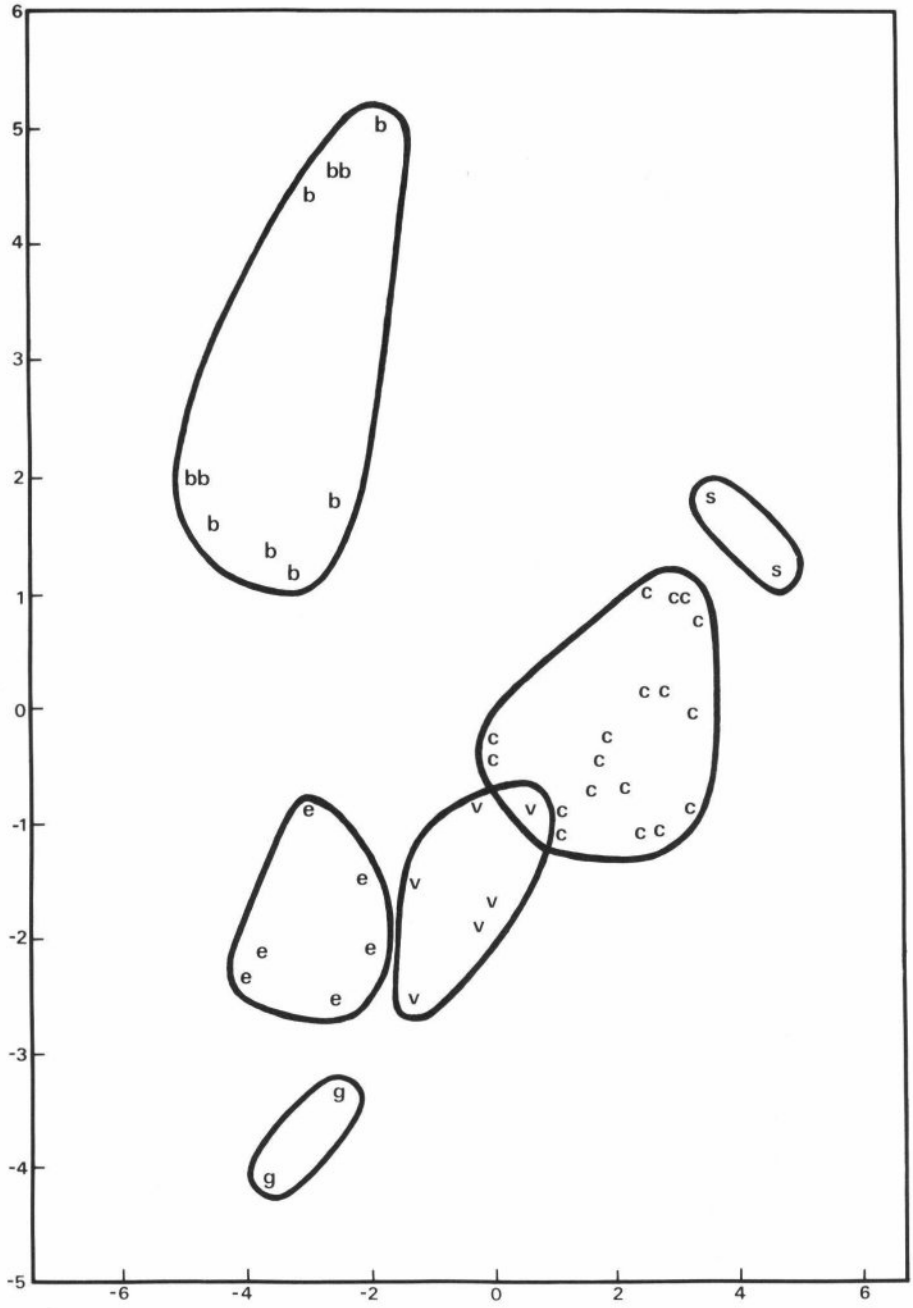


FIG. 28. Plot of group centroids, using first two canonical axes, obtained from discriminate analysis of populations of small aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct populations. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: SH, 27.96%; SW, 3.82%; AH, 59.38%; TW, 8.45%; OL, 75.41%; PH, 57.85%; PC, 5.26%; PN, 1.00%. Second (vertical) axis: SH, 18.18%; SW, 42.38%; AH, 5.27%; TW, 48.72%; OL, 14.38%; PH, 23.02%; PC, 72.13%; PN, 54.37%. b, *F. billakalina;* c, *F. conica;* e, *F. variabilis* form B; g, *F. variabilis* form C; v, *F. variabilis* form A; s, *F. variabilis,* small Blanche Cup form.

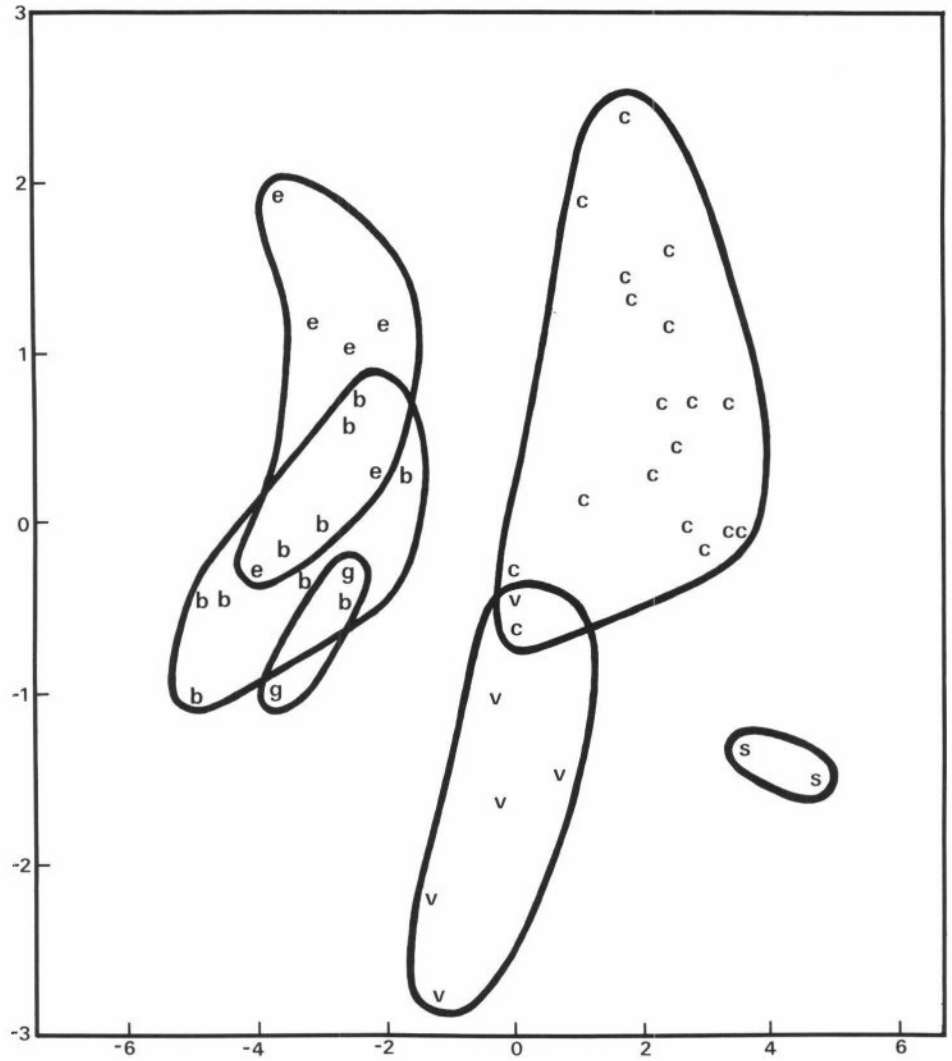


FIG. 29. Plot of group centroids, using first and third canonical axes, obtained from discriminate analysis of populations of small aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct populations. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: SH, 27.96%; SW, 3.82%; AH, 59.38%; TW, 8.45%; OL, 75.41%; PH, 57.85%; PC, 5.26%; PN, 1.00%. Third (vertical) axis: SH, 14.76%; SW, 3.03%; AH, 13.22%; TW, 5.61%; OL, 1.30%; PH, 9.07%; PC, 0.39%; PN, 1.98%. b, *F. billakalina;* c, *F. conica;* e, *F. variabilis* form B; g, *F. variabilis* form C; v, *F. variabilis* form A; s, *F. variabilis*, small Blanche Cup form.

fied. The Euclidian (taxonomic) distances between the groups are given in Table 8. The greatest distance score achieved between all pairwise comparisons was 3.95, between the small Blanche Cup form of *F. variabilis* and *F. variabilis* form B. Differences between the species was >1 in all cases except between *F. variabilis* form A and *F. conica* (score >0.69). *F. conica* separated from the other forms of *F. variabilis* with scores >1.1. *F. billakalina* had a distance score of > 1.58 when compared with all other groups. Within *F. vari-*

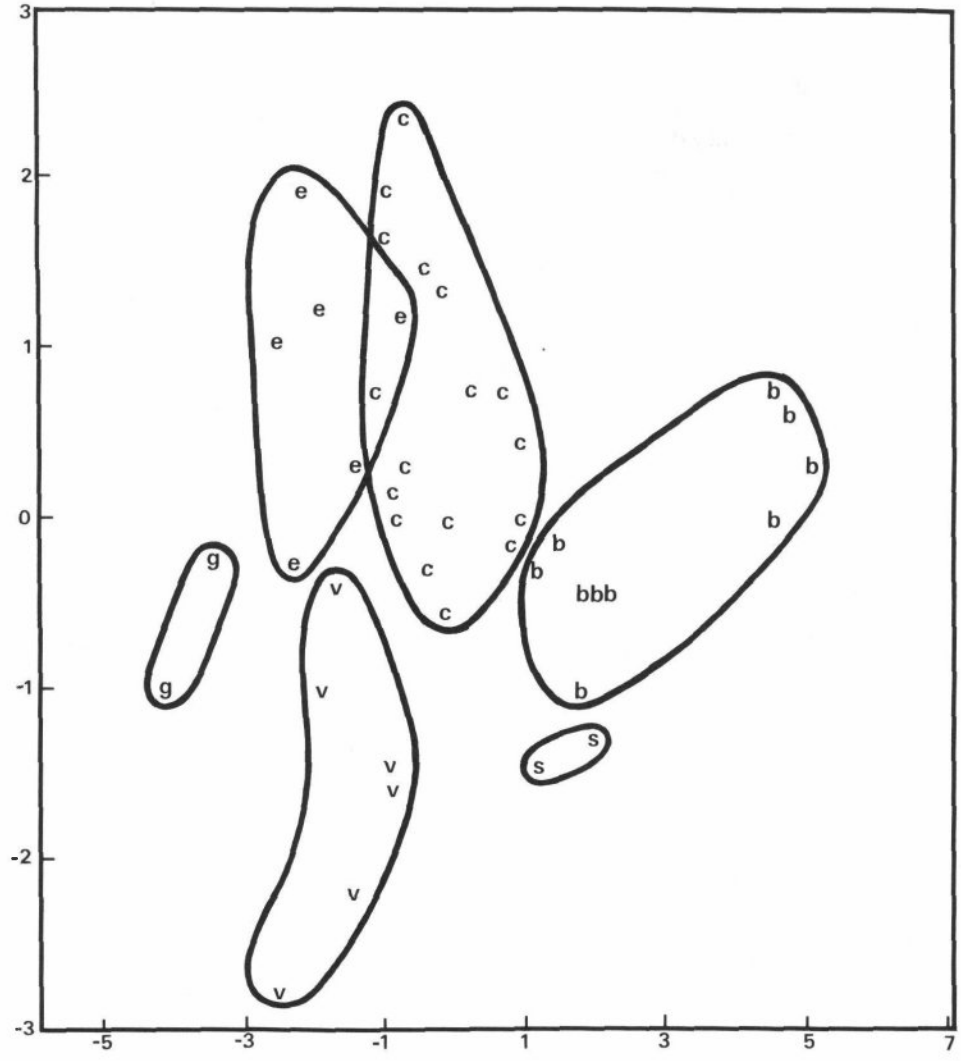


FIG. 30. Plot of group centroids, using second and third canonical axes, obtained from discriminate analysis of populations of small aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct populations. The axes contain the following percentages of the variance of the variables used: second (horizontal) axis: SH, 18.18%; SW, 42.38%; AH, 5.27%; TW, 48.72%; OL, 14.38%; PH, 23.02%; PC, 72.13%; PN, 54.37%. Third (vertical) axis: SH, 14.76%; SW, 3.03%; AH, 13.22%; TW, 5.61%; OL, 1.30%; PH, 9.07%; PC, 0.39%; PN, 1.98%. b, *F. billakalina;* c, *F. conica;* e, *F. variabilis* form B; g, *F. variabilis* form C; v, *F. variabilis* form A; s, *F. variabilis,* small Blanche Cup form.

abilis the scores separating the forms were >0.44, the lowest scores being achieved between forms B and C (0.44 females, 0.50 males), the comparisons between the other forms being > 1.

SNK tests (5% level) using pooled data, combined and separate sexes, for each variable used in the discriminate analyses gave the following results:

SH—Combined sexes: significantly differ-

ent for all except *F. variabilis* form C and *F. variabilis* form B. Separate sexes: only the small Blanche Cup form of *F. variabilis* and *F. conica* were clearly distinct, the others forming overlapping subsets. The means for this character were significantly different between males and females for all species and forms (females larger) except the small Blanche Cup form and *F. billakalina*.

SW—Combined sexes: all means significantly different. Separate sexes: the small Blanche Cup form, *F. conica* and *F. variabilis* form A all form separate subgroups but the others are included in overlapping subgroups. All except the small Blanche Cup form are sexually dimorphic (females larger), the means in all cases being significantly different.

AH—Combined sexes: significantly different for all species and forms except *F. variabilis* form B and *F. billakalina*. Separate sexes: same results as for SH.

TW—Combined sexes: significantly different for all except *F. variabilis* form A + *F. billakalina* and *F. variabilis* form C + *F. variabilis* form B. Separate sexes: the small Blanche Cup form is distinctly different but all other groups, except males of *F. conica,* form overlapping subsets. This character does not significantly differ between males and females except in *F. conica*.

OL—Sexes combined: same result as AH. Separate sexes: the small Blanche Cup form and *F. conica* formed distinct groups as did males of *F. variabilis* form A and females of *F. variabilis* form C. All other groups formed overlapping subsets. Differences between the sexes in this character were statistically significant in *F. conica, F. variabilis* form A, *F. variabilis* form C and *F. variabilis* form B.

PH—Combined sexes: significantly different for all except *F. conica* and *F. variabilis* form B, and *F. variabilis* form A and *F. variabilis* form C. Separate sexes: all form overlapping subsets except males of *F. variabilis* form C and *F. variabilis* form A which form their own group, as do the females of these two forms, these also being the only two groups to show significant sexual dimorphism in this character.

PC—Combined sexes: all means significantly different. Separate sexes: the small Blanche Cup form and *F. billakalina* are not significantly different but all others are. Sexual dimorphism is exhibited in *F. variabilis* form B and *F. variabilis* form C.

PN—Combined sexes: significantly different for all except the small Blanche Cup form and *F. billakalina*. Separate sexes: the same result but with *F. variabilis* form B and *F. variabilis* form C not discriminated. Only *F. variabilis* form B shows significant sexual dimorphism in this character.

Subgenus *Wolfgangia* n.subgen.

Derivation: named for Wolfgang Zeidler (Fem.).

Type species: *F. (W.) zeidleri* n.sp.

Diagnosis: Shell (Figs. 6e–h, 7a,b, 14a,c, 53a,d) as for genus; differs from *Fonscochlea s.s.* in being rather thick-shelled, aperture with thickened peristome and protoconch microsculpture consisting of spiral lines (Fig. 9c,d).

Operculum (Fig. 8a,b) with prominent pegs.

Radula (Fig. 10a,b) as for genus. Central teeth always with two pairs of basal cusps.

Head-foot (Fig. 11a,b) with cephalic tentacles about same length as snout or slightly shorter.

Anatomy: Female genital system (Figs. 12a,b, 47) as for genus except oviduct between capsule gland and bursal duct always straight and sperm sacs lie dorsal to muscular oviduct. Ducts of sperm sacs ventral to sacs. Male (Fig. 46b, penis) system as for genus.

Remarks: The species included in this subgenus can be divided into two morphologically similar forms, one of which is amphibious and the other aquatic. The amphibious form is the most widely distributed of the mound-spring snails; the other, one of the most restricted, is confined to a single spring.

The differences in the protoconch microsculpture, and in the female genital tract, together with the relatively larger snout and shorter tentacles possessed by *F. (W.) zeidleri,* are characters that separate this species from the remainder of those in the genus. This species does, however, possess several key features in common with species of *Fonscochlea s.s.,* the equal-sized sperm sacs being the most outstanding. For this reason, and because there do not appear to be any intergrading states represented in any of the known species, *F. (W.) zeidleri* is judged to be subgenerically separable from *Fonscochlea*.

This subgenus and its type species are named for Wolfgang Zeidler of the South Australian Museum, Adelaide, who first introduced the senior author to the mound springs and since then has assisted with this project in many ways.

Fonscochlea (Wolfgangia) zeidleri n.sp.

Diagnosis: As for subgenus description.

The typical form of this species is described below as "form A" where a holotype is designated for the species.

Localities: Oodnadatta Complex, Northern, Middle, Western and Southern Springs (Fig. 31).

Remarks: The characters separating the subgenus *Wolfgangia* from species of *Fonscochlea s.s.* also serve to separate this species. The shell of this species is similar to that of the two large aquatic species of *Fonscochlea, F. accepta* and *F. aquatica,* in size and shape but can be distinguished by its thicker peristome, with the inner lip separated from the parietal wall, and its more convex whorls. Two geographic forms are recognised and additional details are given under the descriptions of each of them.

Fonscochlea (Wolfgangia) zeidleri form A.

(Figs. 6e–h, 7a, 14a, 53a,d, shell; 9c,d, protoconch; 8b, operculum; 10b, radula; 11a,b, head-foot; 12b, 47, female genitalia; 46b, penis; 45, stomach)

Diagnosis: Shell large for genus, up to about 5.3 mm long, solid, width/length ratio 0.55–0.7 (usually 0.6–0.65) with 3–4.4 convex (convexity ratio 0.04–0.26; mean 0.16, males; 0.18, females) teleoconch whorls sculptured with distinct growth lines and, in some specimens, faint spiral scratches. Protoconch microsculpture (Fig. 9c,d) of fine, closely-spaced, irregular spiral lines. Aperture with thickened peristome, inner lip thickened and separated from parietal wall; outer lip orthocline to opisthocline, edge blunt. Colour yellowish brown to purplish brown. Operculum thick, with prominent pegs.

Shell (Figs. 6e–h, 7a, 14a, 53a,d; 9c,d, protoconch microsculpture), see diagnosis. See Table 20A for measurement data.

Operculum (Fig. 8b) thick, with 2–6 (mean 4.02) heavy opercular pegs. See Table 20A for measurement data.

Radula (Fig. 10b) as for subgenus. See Table 3 for data.

Head-foot (Fig. 11a,b) variable in degree of pigmentation; snout long and mobile, with well-developed concentric ridges. Cephalic tentacles tapering, about same length as snout or slightly shorter. Usually an unpigmented area around eyes; tentacles, in some populations, very pale and, in others, dark grey or black.

Anatomy (Fig. 12b, 47, female genitalia; 46b, penis; 45, stomach) as described for subgenus. See Tables 20B–E for measurements.

Type material: holotype (Fig. 14a) (SAM, D.17915, stn 764C); and paratypes (SAM, D.3206, 61; 764A, AMS, C.152889, 13; 764C, AMS, C.152900, many; 020, AMS, C.152901, 20; 021, AMS, C.152902, many; 022, AMS, C.152903, many; 023, AMS, C.152904, many; 019, AMS, C.152928, 6).

Dimensions of holotype: length 4.82 mm, width 2.87 mm, length of aperture 1.85 mm.

Localities: Southern Springs: Welcome Springs (754A, 755A,B,D; 756, shells only), Hermit Hill Springs (711A,B, 712), Old Finniss Springs (693A, 694B,C), Old Woman Springs (732, 733), Finniss Swamp West (690A,C). Shells have been collected from Priscilla Spring (686), Venable Spring (687) and an unnamed spring in Lake Eyre South (702).

Middle Springs: Horse Springs West (746A,B), Horse Springs East (748B,C), Mt. Hamilton Homestead ruins (006, 749), Strangways Spring (007, 745A), Blanche Cup Spring (008–012, 685), Bubbler Spring (013–017), Little Bubbler Spring (744), unnamed springs, Blanche Cup Group (785, 786, 787), Coward Springs (019–023, 764A–C), Coward Springs Railway Bore (018, 684, 743), Kewson Hill Springs (740A, 741, 742A), Julie Springs (772A–D, 773A–C), Elizabeth Springs (024, 766A–G, 767, 771A–C), Jersey Springs (025, 683A,B; 768, shells only; 769A,B, 770A–C), Warburton Springs (681A–C, 682), Beresford Spring (028). Fossil shells have been collected from the top of Hamilton Hill.

South Western Springs: Billa Kalina Springs (026, 027, 723A,C,D; 759, shells only; 760, 763A,B), Francis Swamp (717B, 720A,B, 721B,C), Strangways Springs (029–030, 678A,B, 679A–C, 680). Shells from Margaret Spring (722) and Welcome Bore (758).

Northern Springs: Brinkley Spring (677), Hawker Springs (670A–C, 671, 672C,D, 673), Big Perry Springs (034), Twelve Mile Spring (036, 037), Outside Springs (039). Shells from Spring Hill Springs (674).

Freeling Springs (043, 046, 664A–C, 665A–C).

Remarks: This form, the most widely distributed of the mound-spring snails, is of special interest because of its amphibious habit. It lives, in most springs, along the edges of

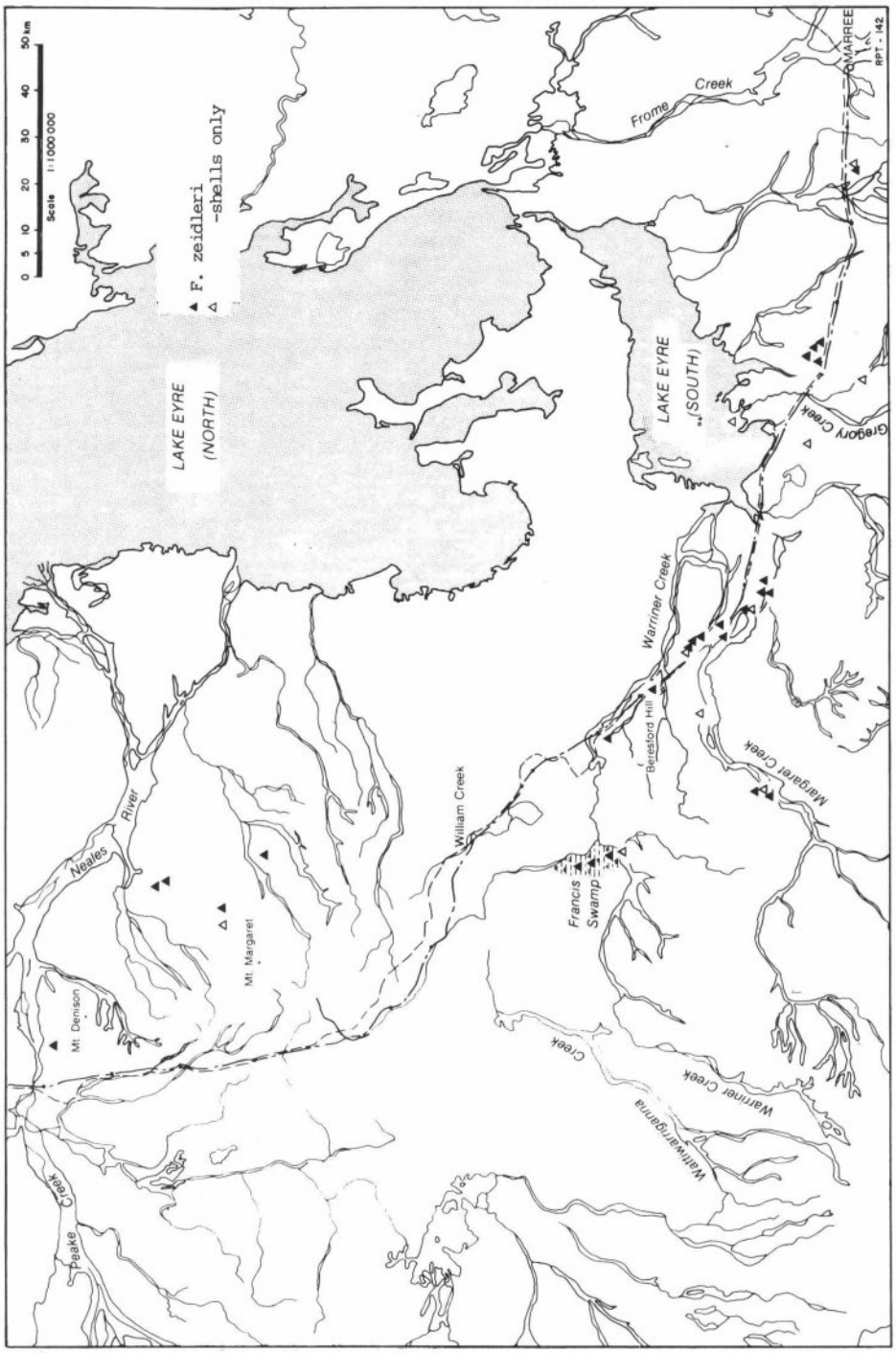


FIG. 31. Distribution of *Fonscochlea zeidleri* form A.

the outflows where it is either exposed, as on the hard substrates found on the calcareous mounds, or partly or completely buried in the sediment. The preference for burrowing in the substrate appears to differ between spring groups and might not be due entirely to substrate differences. For example the populations of this species at Hermit Hill are extremely cryptic, mainly because of this habit, whereas at Welcome Springs, with similar substrate available, they are much more conspicuous, large numbers being present on the surface.

Populations at Kewson Hill and Elizabeth Springs have two recognisable phenotypes. One is the typical shell form (Fig. 53d) indistinguishable from specimens found elsewhere. Another form (Fig. 53a) is shorter, darker, relatively broader, and with a relatively larger aperture than the typical form. These two forms have been found living together but usually occupying different microhabitats. The typical form is found along the edges of the outflow and around the head of the spring or seepage, the normal habitat for this species, whereas the squat form is invariably found in the outflows where it lives attached to any available emergent substrate, usually in very large numbers. Some individuals are found in the water but most are out of it. Some other populations (e.g., Blanche Cup and Horse Springs East) contain many intermediates between these two types (Fig. 6e–h).

Fonscochlea (Wolfgangia) zeidleri form B.

(Figs. 7b, 14c, shell; 8a, operculum; 10a, radula; 12a, female genitalia)

Diagnosis: Shell smaller than typical specimens of *F. (W.) zeidleri* form A (up to 4.06 mm long) and with relatively broader (shell width/shell length 0.63–0.65) than many populations of *F. (W.) zeidleri* form A. 2.9–3.5 convex (convexity ratio 0.14–0.22) teleoconch whorls. Aperture with orthocline outer lip. Value of aperture length/shell length significantly larger than in most populations of *F. (W.) zeidleri* form A. Colour dark brown.

Shell (Figs. 7b, 14c), see diagnosis. See Table 20A for measurement data.

Operculum (Fig. 8a) with 2–6 (mean 3.85, males; 3.4, females) prominent opercular pegs. See Table 20A for measurement data.

Radula (Fig. 10a) as for subgenus. See Table 3 for data.

Head-foot similar to that of *F. (W.) zeidleri* form A but, in most specimens, weakly pigmented except for large patch of black pigment behind eyes. Snout and cephalic tentacles lack pigment in some specimens but in a few are darkly pigmented.

Anatomy (Fig. 12a, female genitalia) as described for subgenus. See Tables 20B–E for measurements.

Voucher material: primary voucher specimen (Fig. 14c) (SAM, D.17916, stn 661); and material from the same population (661, SAM, D.17945, many; AMS, C.152905, many, C.152993, 1, figured).

Dimensions of primary voucher specimen: length 4.04 mm, width 2.56 mm, length of aperture 1.72 mm. This is one of the largest specimens of this form.

Locality: Oodnadatta Spring Complex: Big Cadnaowie Spring (661).

Remarks: This population is distinguished as a separate form, despite few morphological differences, because it is considerably geographically isolated, has a distinctive shell shape (although duplicated in a few examples of *F. (W.) zeidleri* form A) and its fully aquatic habit is a considerable departure from the amphibious habit of the typical form. The lack of significant morphological differentiation suggests that it is probably only recently derived from *F. (W.) zeidleri* form A.

The populations of *F. (W.) zeidleri* form A that develop squat shells with width/length ratios similar to those of *F. (W.) zeidleri* form B are virtually all associated with harsh environments, e.g., the Kewson Hill Springs (Fig. 53a). The conditions that appear to bring about the shortening of the shell in *F. (W.) zeidleri* form A, small, shallow outflows and hard substrate, are not those in which *F. (W.) zeidleri* form B is found. This form lives in a large, degraded spring in a few metres of sedges in a narrow, outflow with a significant flow of water. It is completely aquatic and very abundant in this part of the habitat. A very few individuals were found in the remainder of the spring, which has been severely damaged by livestock. This spring has since been fenced as part of the mound-spring fencing programme, mainly because of the reported existence of this unusual population (Ponder & Hershler, 1984).

Discrimination of the two forms of *Fonscochlea zeidleri* was tested using discriminate analysis on a subset of shell measurements.

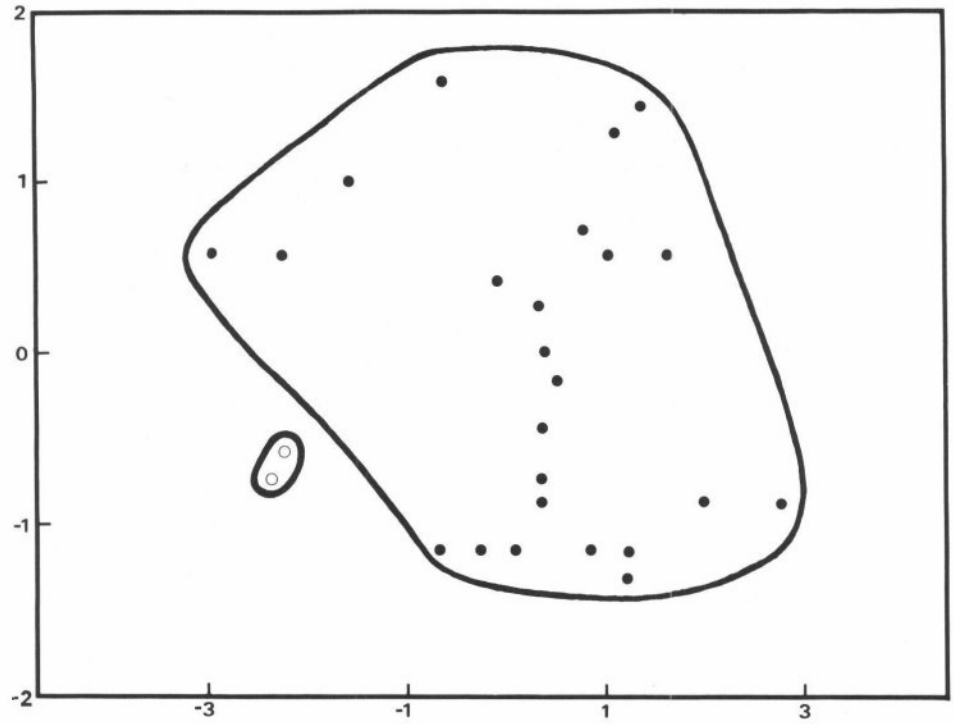


FIG. 32. Plot of group centroids, using first two canonical axes, obtained from discriminate analysis of populations of *Fonscochlea zeidleri* using shell measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct populations. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: SH, 82.65%; SW, 0.29%; AH, 69.38%; TW, 18.79%. Second (vertical) axis: SH, 2.19%; SW, 55.66%; AH, 21.12%; TW, 47.45%.
Closed circles, *F. zeidleri* form A; open circles, *F. zeidleri* form B.

The results (Fig. 32) showed that both groups could be discriminated using these data, 92% of the measured specimens (n = 284) being correctly classified.

SNK tests (5% level) using pooled data, combined and separate sexes, for each variable used in the discriminate analyses gave the following results:

SH, AH and TW were significantly different for combined sexes of both forms. No characters separated the two forms using separate male and female data. Sexual dimorphism was apparent only in TW for both forms.

Genus *Trochidrobia* n.gen.

Derivation: *Trochi* (Latin), a child's hoop, and used for a genus of gastropods *(Trochus),* pertaining to the shape of the shell; *drobia,* from *Hydrobia,* the type genus of Hydrobiidae (fem.).

Type species: *Trochidrobia punicea* n.sp.

Distribution: Artesian springs between Marree and Oodnadatta, northern South Australia.

Diagnosis: Shell (Figs. 33, 37) of known species small (as much as 2mm in diameter), trochiform to depressed-trochiform, umbilicate, smooth, with only sculpture weak axial growth lines. Protoconch (Fig. 34) of about one and one-half whorls, sculptured with irregular minute pits, or pits and spiral threads. Aperture oval, peristome thin, no external varix; outer lip simple, not expanded or flared, with thin edge. Periostracum smooth, thin.

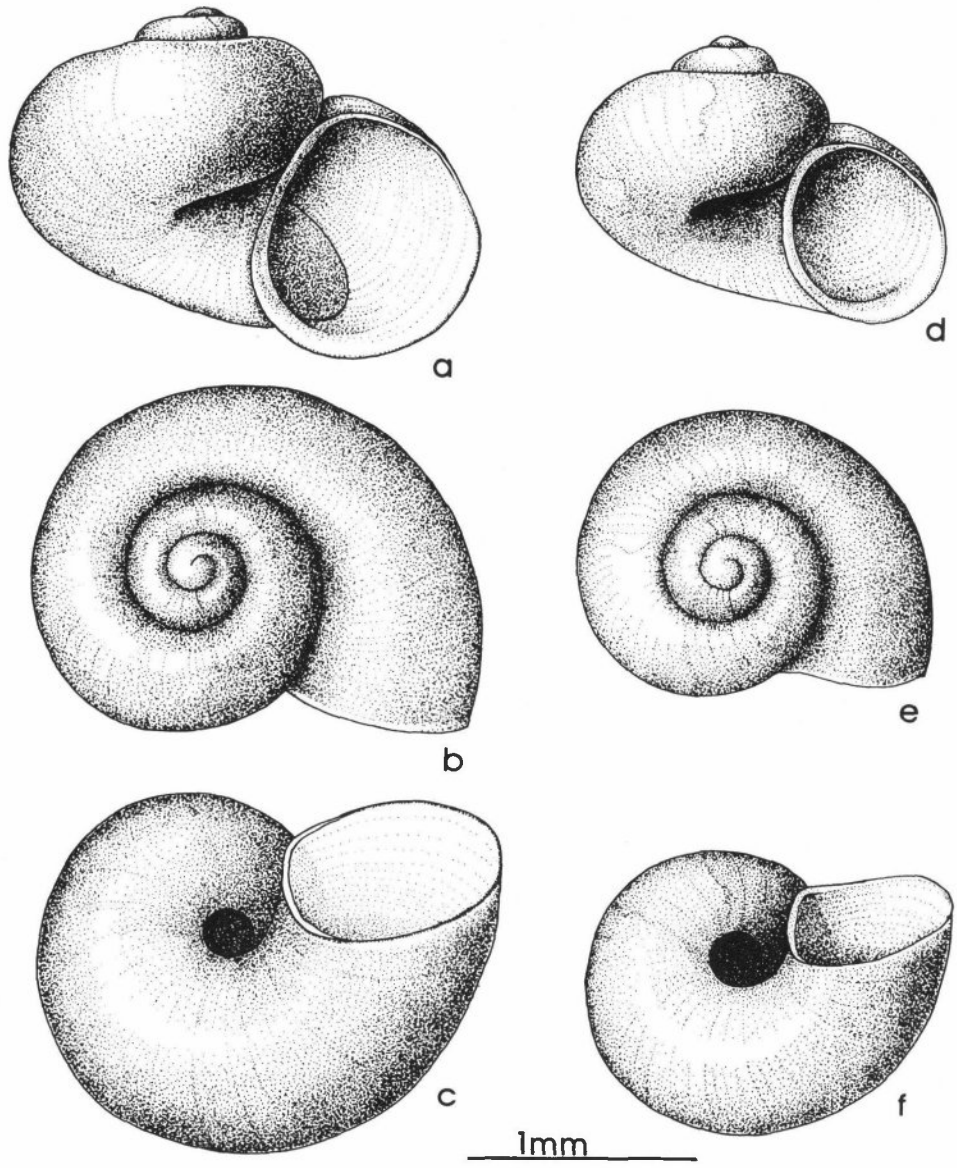


FIG. 33. Shells of *Trochidrobia*.
a–c. *Trochidrobia punicea*, holotype. Blanche Cup Spring (009).
d–f. *Trochidrobia smithi*, holotype. Twelve Mile Spring (036).

Operculum (Fig. 35a,c,e,f) corneous, oval, nucleus subcentral, thin, simple.

Radula (Fig. 35b,d) with central teeth formula $\frac{4-8+1+4-8}{1-2 \quad 1-2}$, lateral teeth 3–6+1+4–7, inner marginal teeth with 18–31 cusps, outer marginal teeth with many small cusps.

Head-foot (Fig. 24h) with cephalic tentacles longer than snout, parallel sided, inconspicuously ciliated ventrally. Pigmentation usually dense, pigment granules black

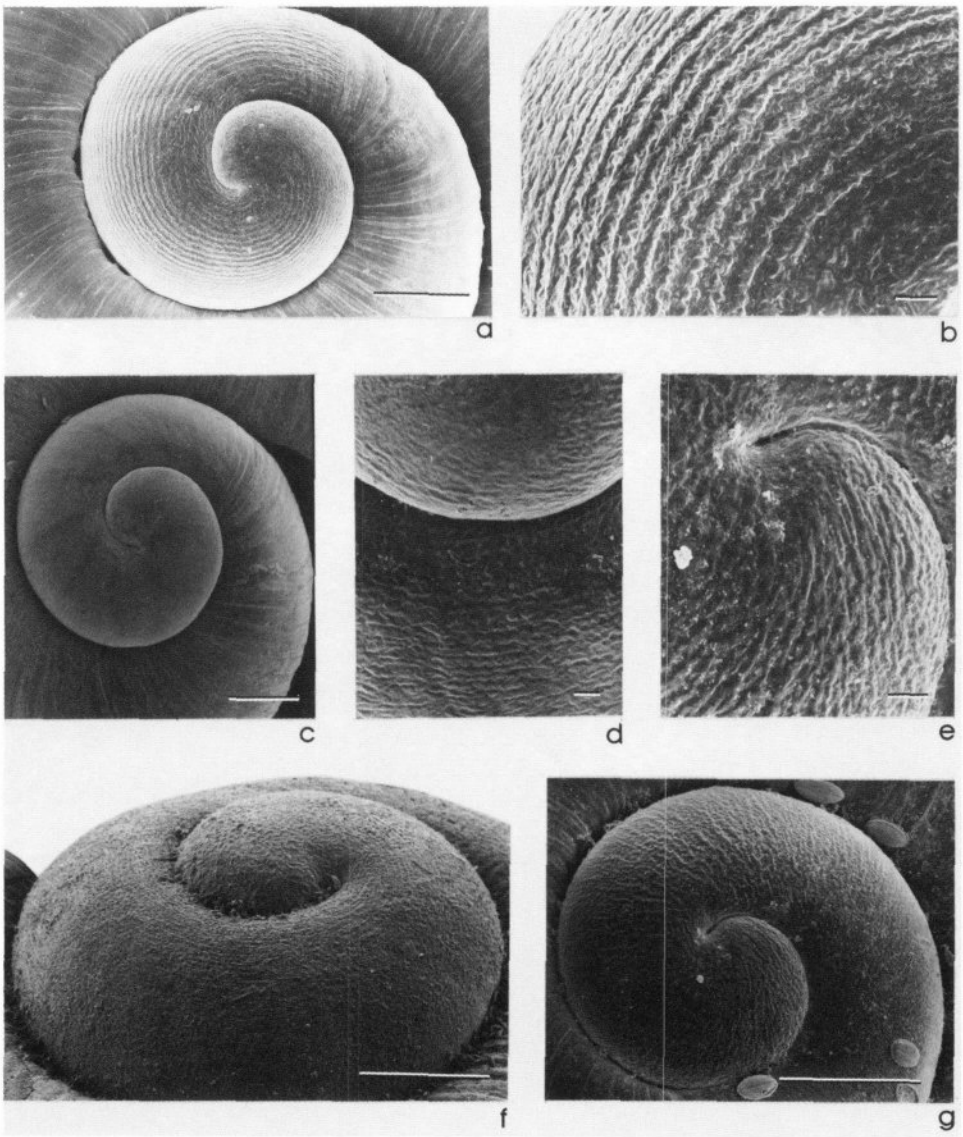


FIG. 34. Protoconchs of species of *Trochidrobia*.
a,b. *Trochidrobia punicea,* Coward Springs (020).
c,d. *Trochidrobia smithi,* The Fountain Spring (032).
e,g. *Trochidrobia minuta,* Freeling Springs (045).
f. *Trochidrobia inflata,* Freeling Springs (043).
Scale: a,c,f,g = 0.1mm; b,d,e = 0.01mm.

and white. General head-foot typical of family.

Anatomy: pallial cavity (Fig. 48) with well-developed ctenidium; osphradium oval, about 2–4 times as long as broad and about one-half to one-third length of ctenidium, its posterior extremity situated near posterior end of ctenidium.

Female reproductive system (Figs. 36, 38) with single sperm sac and coiled oviduct lying

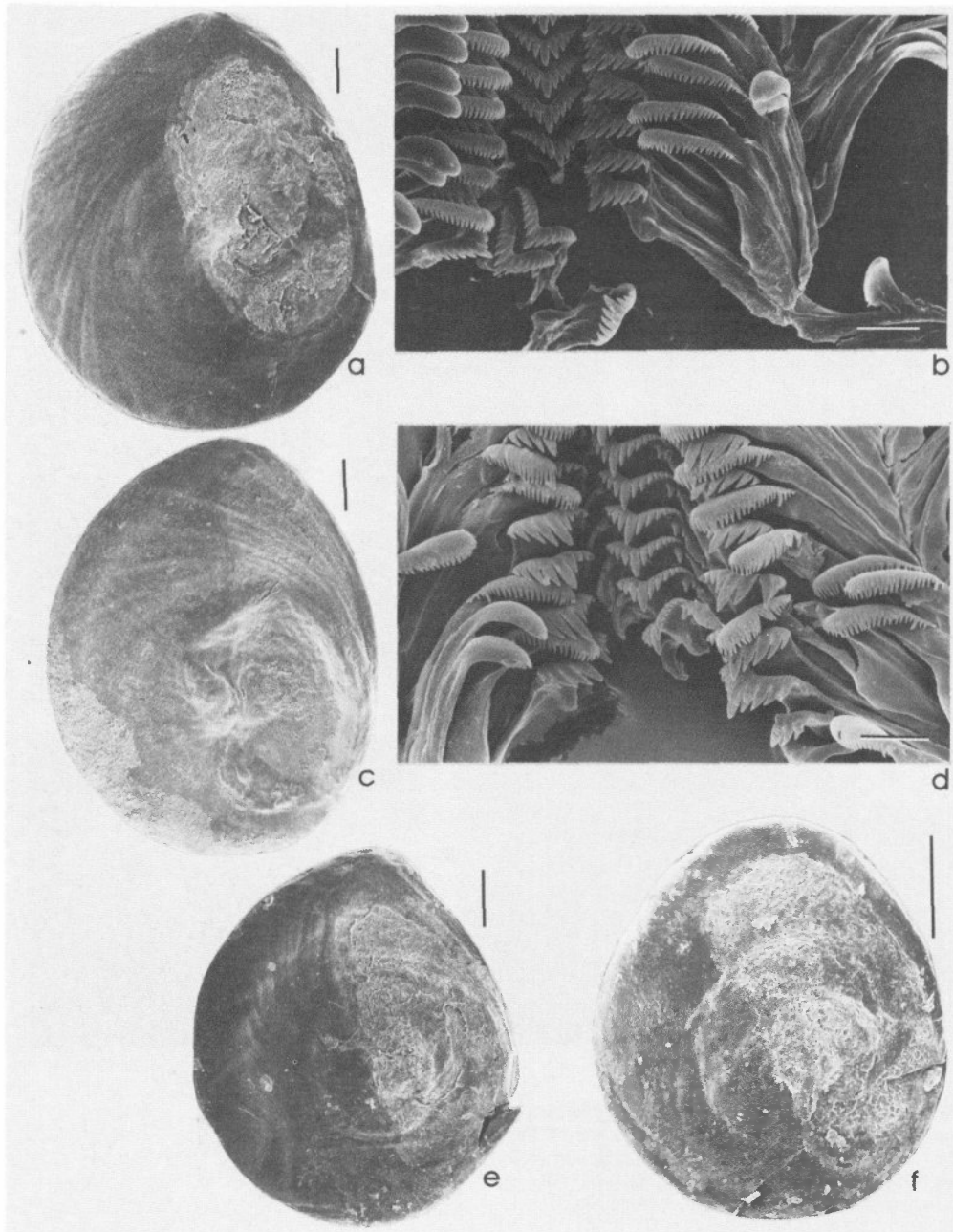


FIG. 35. Radulae and opercula of *Trochidrobia*.
a. Operculum of *Trochidrobia punicea*, Blanche Cup Spring (008).
b. Radula of *Trochidrobia punicea*, Welcome Springs (002).
c. Operculum of *Trochidrobia inflata*, Freeling Springs (043).
d. Radula of *Trochidrobia smithi*, Old Billa Kalina Spring (027).
e. Operculum of *Trochidrobia smithi*, Old Billa Kalina Spring (027).
f. Operculum of *Trochidrobia minuta*, Freeling Springs (045).
Scale: a,c,d,e = 0.1mm; b,d = 0.01mm.

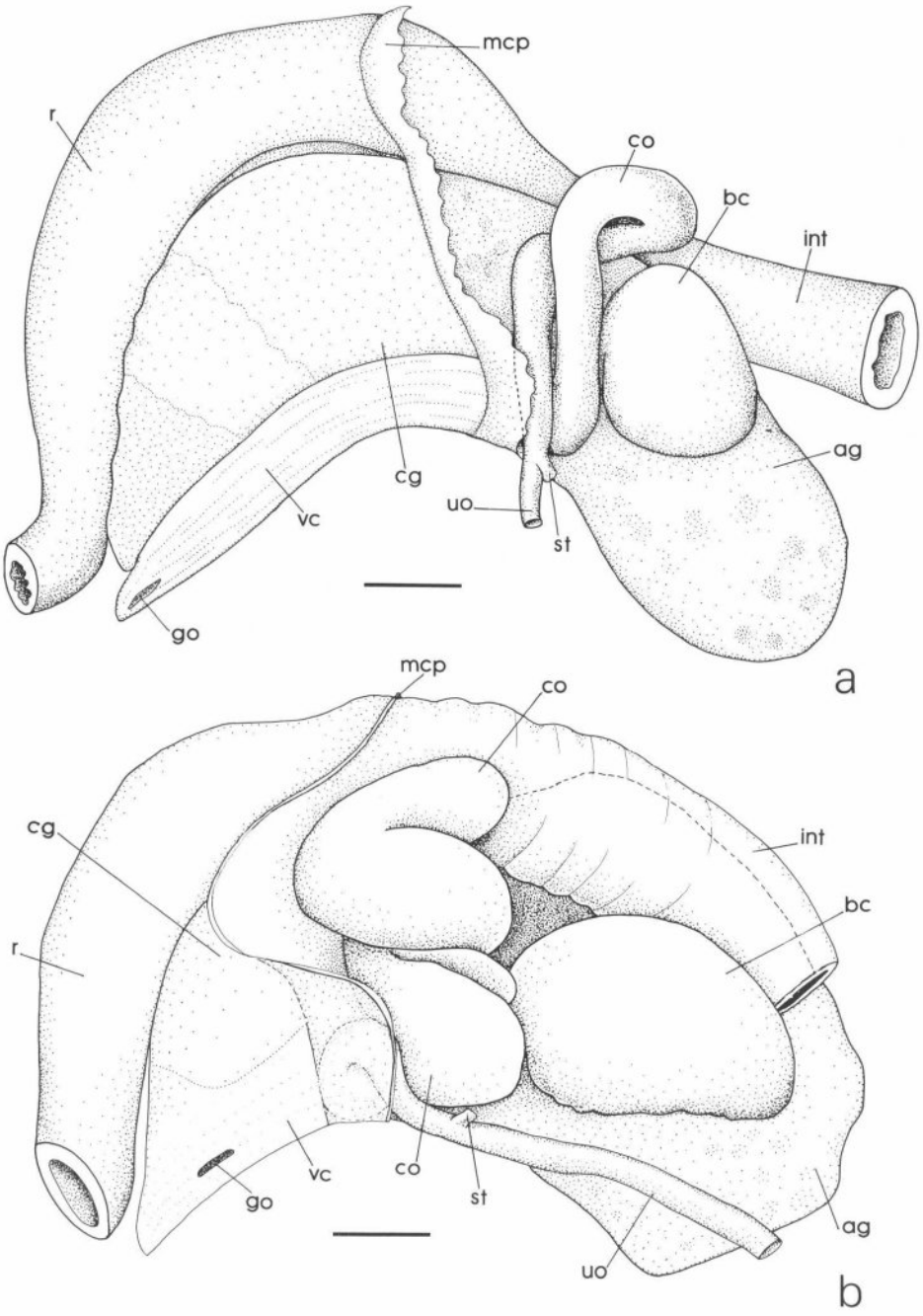


FIG. 36. Female genitalia of species of *Trochidrobia*.
a. *Trochidrobia smithi*. Outside Springs (039).
b. *Trochidrobia punicea*. Strangways Spring, E. of Blanche Cup (007).
ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; co, coiled part of oviduct; go, oviduct opening; int, intestine; mcp, posterior limit of pallial cavity; r, rectum; st, tissue connection between oviduct and pericardium; uo, upper oviduct; vc, ventral channel.
Scale: 0.1mm.

on inner (left) side of albumen gland or mainly situated behind this gland. Coiled part of oviduct an unpigmented tube lying largely in front of large bursa copulatrix. Bursa copulatrix about one-third to one-half of length of albumen gland, its narrow duct opens to oviduct in different locations depending on species. Gonopericardial duct absent but represented by strand of tissue. Oviduct straight anterior to point of opening of bursal duct. Accessory sperm storage occurs in swollen part of posterior ventral channel of capsule gland or in coiled oviduct. Capsule gland about same length as albumen gland to about half its length, with a well-developed ventral channel containing ciliated lateral fold. Genital pore terminal, subterminal or placed at about one-third of distance along capsule gland. Egg capsules spherical, cemented in umbilicus of shell with mucus (known only in *T. punicea*).

Male reproductive system with vas deferens complexly coiled beneath anterior part of testis. Pallial and visceral vas deferens enter and leave prostate gland in middle section. Prostate gland extends into pallial wall one-third to one-half of its length. Pallial vas deferens a narrow, straight, ciliated tube lying just beneath epithelium on right side of pallial floor but undulates as it passes up right side of neck to enter base of penis. Penis (Fig. 49) with swollen basal portion and tapering distal portion. Basal part unpigmented, concentrically creased and narrow penial duct undulates within it. Distal portion smooth, usually pigmented, coiled anti-clockwise when at rest, penial duct straight within it, emerging at pointed distal extremity.

Alimentary canal typical of family; buccal mass well developed with U-shaped radular sac protruding behind. Salivary glands simple, tubular. Stomach (Fig. 44a) with distinct anterior and posterior chambers, anterior one larger, lacks caecal appendage. Style sac contains crystalline style, comprises about one-third to one-half of total length of stomach. Single digestive gland opening immediately posterior to oesophageal opening. Digestive gland covers inside of right side of stomach to about halfway across anterior chamber. Intestine makes U-shaped fold on pallial roof in one species.

Nervous system with left pleural and suboesophageal ganglia abutting and right pleural and supra-oesophageal ganglion separated by long connective.

See anatomical account for further detail.

Remarks: The species contained in *Trochidrobia* are similar in shell and opercular characters to those in the European *Horatia-Pseudamnicola* complex but differ in several important character states. These include the lack of a seminal receptacle (not one or two); a longer, coiled oviduct; two pairs of basal cusps on the central teeth of the radula (not a single pair); a penis having a slender, simple distal portion longer than the basal part (not shorter than the base); and the left pleural and suboesophageal ganglia abutting (not separated by a connective) (see Radoman, 1966, 1983, for further detail regarding the European taxa).

Some species in the *Beddomeia* complex in Tasmania, particularly *Valvatasma tasmanica* (T. Woods, 1876), are similar to species of *Trochidrobia* in shell form. They differ, however, in having an operculum with an eccentric nucleus and a radula with a single pair of basal cusps. All of the species in the *Beddomeia* complex have a seminal receptacle. Another species similar to the *Beddomeia* group is *Jardaniella thaanumi* (Pilsbry, 1900), from north Queensland. This species has two pairs of basal cusps on the radula, an eccentric opercular nucleus and a seminal receptacle (all data on *Beddomeia* group from Ponder, unpublished).

Heterocyclus petiti (Crosse, 1872) from New Caledonia has a depressed, umbilicate shell but the outer lip is flared and the calcareous, multispiral operculum is of different construction (Starmülner, 1970). It is unlikely that this species is even remotely related.

The only other Australian genus of depressed shell form is *Posticobia,* which is related to *Hemistomia* (see Ponder, 1981). *Horatia nelsonensis* Climo, 1977, from Nelson, New Zealand, is known only from shells but it is probable that this species is a depressed form of *Opacinacola,* a New Zealand genus normally having higher-spired shells.

Trochidrobia punicea n.sp.

Derivation: *puniceus* (Latin) purple, red. A reference to the dark purple-red colour of the shell of living specimens.

(Figs. 33a–c, shell; 34a,b, protoconch; 35a, operculum; 35b, radula; 24h, head-foot; 48, pallial cavity; 44a, stomach; 36b, female genital system; 49a, penis)

Diagnosis: Shell up to 2.22 mm in diameter, depressed (width/height ratio 1.1–1.3), with 1.50–2.25 convex whorls and widely umbilicate. Protoconch microsculpture (Fig. 34a,b) of close spiral ridges with irregular surface pitting over the entire surface. Aperture sometimes separated from parietal wall. Colour yellowish brown to dark orange-brown. Female genitalia with very much thickened coiled oviduct, long bursal duct and simple ventral channel. Rectal arch absent in male (rectum lies alongside prostate gland).

Shell (Fig. 33a–c), see diagnosis. See Table 21A for measurement data.

Operculum (Fig. 35a) as for genus.

Radula (Fig. 35b) as for genus. See Table 3 for data.

Head-foot (Fig. 24h) variably pigmented, dark pigmentation common, usually with narrow dorsal unpigmented stripe on proximal half of tentacles continuous with unpigmented zone around eyes.

Anatomy (Figs. 48, pallial cavity; 44a, stomach; 36b, female genital system; 49a, penis), see anatomical section below for full description. See Tables 21B–C for measurement data.

Type material: holotype (Fig. 33a–c) (SAM, D.17922, stn 009); and paratypes (008, SAM, D.3208, 58; SAM, D.2030, 60; 739, AMS, C.152906, many; 009, AMS, C. 152907, many; 008, AMS, C.152908, many; 010, AMS, C.152909, many; 011, AMS, C.152910, 20; 012, AMS, C.152911, 10).

Dimensions of holotype: length 1.62 mm, width 2.08 mm, length of aperture 1.08 mm.

Localities: Southern Springs: Welcome Springs (002, 003, 754A–D, 755A–D, 756A–C), Davenport Springs (005, 752A–C, 753A,B), Hermit Hill Springs (712), Dead Boy Springs (689), Finniss Swamp West (690A–C, 691), Bopeechee Springs (692A,B), Old Finniss Springs (693A–C, 694A–C, 710), Old Woman Spring (733A–E), Sulphuric Springs (735, 737). Shells from Priscilla Spring (686), Venable Spring (687).

Middle Springs: Horse Springs East (747A,B, 748A–C), Horse Springs West (746A), Mt. Hamilton Homestead ruins (749), Strangways Springs (007,745A,B), Blanche Cup Spring (008–012, 739), Bubbler Spring (013–017), Little Bubbler Spring (744A–C), an unnamed spring, Blanche Cup Group (785, 786, 787), Coward Springs (019–022, 023, 764A–C), Kewson Hill Springs (741, 742B, 765), Julie Springs (772A–D, 773A–C), Jersey Springs (025, 768A, 769A,B, 770A,B), Elizabeth Springs (024, 766A–E, 767A,B, 771A,B) (Fig. 39).

Fossil shells similar to this species have been collected from travertine on the top of Hamilton Hill.

Remarks: The shell of this species is virtually identical to that of *T. smithi* described below, the only characters, apart from protoconch microsculpture (which has been examined in only a few specimens), distinguishing these two species being anatomical ones. See under *T. smithi* for details.

Both of these species are extremely abundant in most of the springs in which they occur. They live in a variety of microhabitats and appear to be particularly abundant in shallow, firm-bottomed outflows. They are positively phototropic, living fully exposed in the outflows. See physiology section below for more details.

Trochidrobia smithi n.sp.

Derivation: named for Dr. B.J. Smith.

(Figs. 33d–f, shell; 34c,d, protoconch; 35e, operculum; 35d, radula; 36a, female genitalia; 49b, penis)

Diagnosis: Shell and head-foot virtually identical to those of *T. punicea,* maximum width of shell 2.13 mm, with 1.63–2.13 (mean 1.92) teleoconch whorls. Protoconch microsculpture (Fig. 34d) of spirally arranged wrinkles, weaker than spiral sculpture of *T. punicea*. Female genitalia with narrow coiled oviduct and expanded posterior part of ventral channel (Fig. 36a). Rectal arch present in male (rectum separated from prostate gland).

Shell (Figs. 33d–f; 34c,d, protoconch, see diagnosis. See Table 21A for measurements.

Operculum (Fig. 35e) as for genus.

Radula (Fig. 35d) as for genus. See Table 3 for data.

Head-foot very similar to that of *T. punicea,* variably pigmented, uniformly dark pigmentation being common.

Anatomy (Figs. 36a, female genitalia; 49b, penis) very similar to that of *T. punicea;* see diagnosis for differentiating characters. See Tables 21B–C for measurements.

Type material: holotype (Fig. 33d–f) (SAM, D.17923, stn 036); and paratypes (SAM, D.2028, 5; 037, AMS, C.152912, many; 036, AMS, C.152913, many; 1003B, AMS, C.152915, many; 1003C, AMS, C.152916, many; 1003D, AMS, C.152917, many).

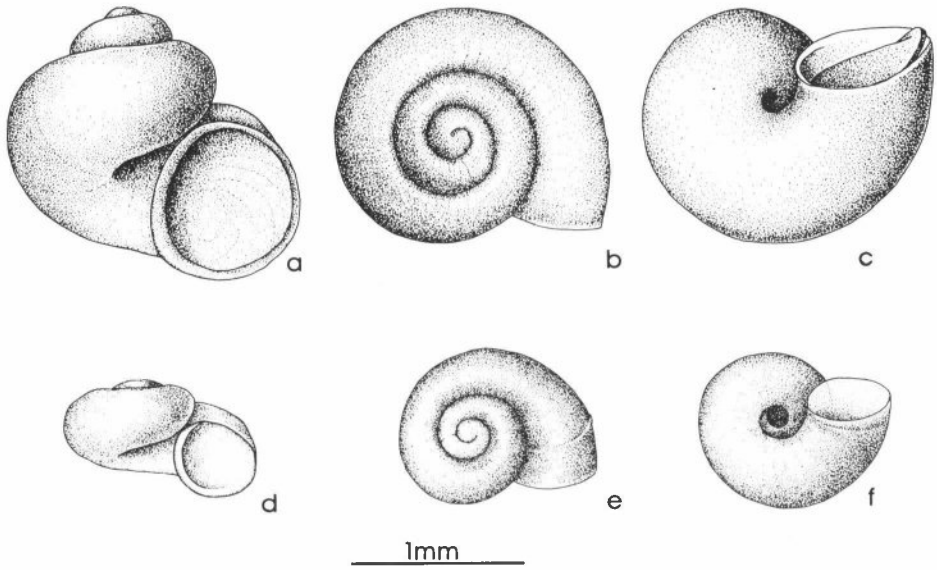


FIG. 37. Shells of species of *Trochidrobia*.
a–c. *Trochidrobia inflata*, holotype. Freeling Springs (042).
d–f. *Trochidrobia minuta*, holotype. Freeling Springs (046).

Dimensions of holotype: length 1.31 mm, width 1.66 mm, length of aperture 0.78 mm.

Localities: Middle Springs: Warburton Spring (681A–C, 682), Beresford Spring (028).

South Western Springs: Billa Kalina Springs (026–027, 723A–D, 758C, 759A; 760, shells only; 761B, 762A,B, 763A,B), Francis Swamp (717A–C, 720A–B, 721A–C), Margaret Spring (722, shells only), Strangways Springs (029–030, 678A,B, 679A–C).

Northern Springs: Brinkley Springs (677), Hawker Springs (670A–C, 671, 672A–D, 673), Fountain Spring (031–033), Twelve Mile Spring (035–037, 1003B–C) Outside Springs (038–040), Big Perry Spring (034) (Fig. 39).

Remarks: Although this species is virtually identical to *T. punicea* in shell characters, it can be immediately recognised on dissection, the female genitalia being readily distinguished from those of *T. punicea* in having a markedly narrower coiled oviduct and in the posterior part of the ventral channel being expanded and, in males, in having a prominent rectal arch. The ecology of this species appears to be very similar to that of *T. punicea*.

Discriminate analysis, using only shell measurements, achieved some separation of *T. punicea* and *T. smithi* (Figs. 40, 41; Table 9). A clear separation was achieved with female genital measurements (Fig. 42; Table 9).

This species is named for Dr. B. J. Smith, formerly of the Museum of Victoria, Melbourne, as a small mark of appreciation of his contributions to the study of Australian non-marine molluscs.

Trochidrobia minuta n.sp.

Derivation: a reference to the small size of this species.

(Figs. 37d–f, shell; 34e,g, protoconch; 35f, operculum; 38b, female genitalia)

Diagnosis: Shell very small (up to about 1.2 mm in diameter), very depressed (width/height ratio 1.5–1.6), with 1.25–1.5 (mean 1.47, males; 1.43, females) weakly convex whorls and widely umbilicate. Protoconch sculptured with irregular wrinkles and pits not arranged spirally (Fig. 34e,g). Colour yellowish white to pale brown. Head-foot darkly pig-

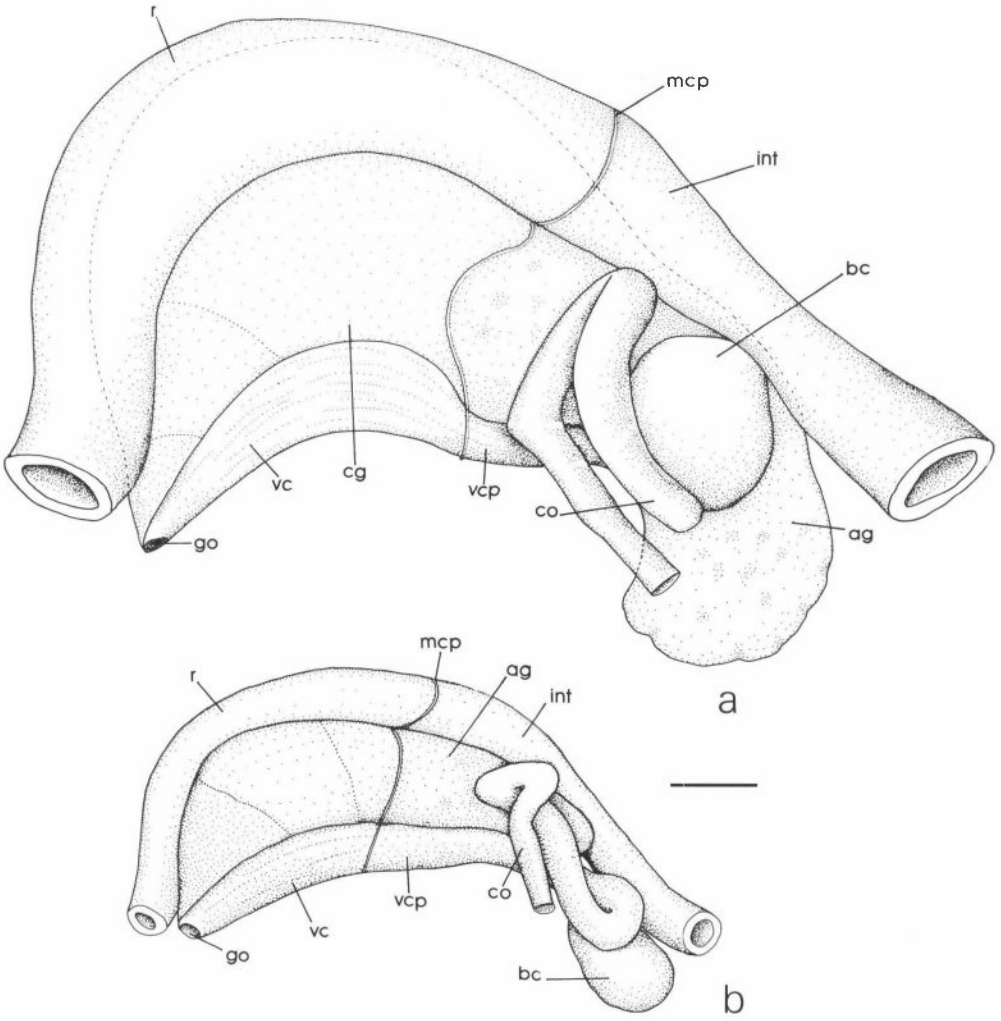


FIG. 38. Female genitalia of species of *Trochidrobia*.
a. *Trochidrobia inflata,* Freeling Springs.
b. *Trochidrobia minuta*, Freeling Springs.
ag, albumen gland; bc bursa copulatrix; cg, capsule gland; co, coiled part of oviduct; go, oviduct opening; int, intestine; mcp, posterior limit of pallial cavity; r, rectum; vc, ventral channel; vcp, posterior extension of ventral channel.
Scale: 0. 1mm

mented. Female genitalia with bursa copulatrix placed largely behind albumen gland (in other species it lies alongside albumen gland). Coiled oviduct narrow, short, and ventral channel simple.

Shell (Figs. 37d–f; 34e,g, protoconch), see diagnosis. See Table 21A for measurement data.

Operculum (Fig. 35f) as for genus.

Radula as for genus. See Table 3 for data.

Head-foot with darkly pigmented snout and grey triangular zone posterior to eyes. Very narrow unpigmented zone around eyes. Cephalic tentacles pale grey, unpigmented distally, without median line.

Anatomy (Fig. 38b, female genitalia), as for

genus. See diagnosis for differentiating characters. See Table 21B–C for measurement data.

Type material: holotype (Fig. 37d–f) (SAM, D.17924, stn 046); and paratypes (045, AMS, C.152918, many; 664A1, AMS, C.152919, 2; 664A2, AMS, C.152920, 29; 046, AMS, C.152921, many).

Dimensions of holotype: length 0.72 mm, width 1.11 mm, length of aperture 0.50 mm.

Localities (Fig. 39): Northern Springs: Fountain Spring (031–032, 1002), Big Perry Springs (034,1001), Outside Springs (1006), Twelve Mile Spring (1003).

Freeling Springs (043, 045, 046, 663, 664), unnamed spring north of Freeling Springs (666).

Remarks: This minute species is very distinctive and is readily separable on shell characters from *T. punicea* and *T. smithi,* although small individuals of those species approach it in size. Apart from most shell dimensions, the shell ratios PD/SH and SW/SH are significantly different in populations of *T. minuta* when compared with *T. smithi* and *T. punicea.* The flat spire and pale colour are particularly characteristic. Discriminate analysis (Figs. 40, 41, shell; 42, female genital anatomy; Table 9) readily distinguished this species from congeners.

This species is abundant in the upper and middle parts of the spring outflows at Freeling Springs, but appears to be less common in the Northern Springs. The occurrence of this species together with *T. smithi* in some of the Northern Springs is of interest because the size difference between these species is not so marked as it is between all other sympatric congeners in the mound springs. It would be of interest to compare the interactions between these two species with those between *T. minuta* and *T. inflata,* which show greater size differences.

Trochidrobia inflata n.sp.

Derivation: a reference to the inflated shell of this species.

(Figs. 37a–c, shell; 34f, protoconch; 35c, operculum; 38a, female genitalia)

Diagnosis: Shell up to 1.72 mm in diameter, with rather high spire (width/height ratio about 1), 1.38–2.13 (mean 1.94, males; 1.95, females) convex whorls, and narrowly umbilicate. Protoconch microsculpture (Fig. 34f) of spirally arranged pits and wrinkles. Colour brown. Female genitalia similar to those of *T. smithi* but lacking expansion of ventral channel.

Shell (Fig. 37a–c), see diagnosis. See Table 21A for measurement data.

Operculum (Fig. 35c) as for genus.

Radula as for genus. See Table 3 for data.

Head-foot darkly pigmented, dark grey to black, with rather narrow unpigmented zone around eyes and very narrow median unpigmented line on cephalic tentacles in some specimens, sometimes margined with black lines.

Anatomy (Fig. 38a, female genitalia) as for genus. See diagnosis for differentiating characters. See Table 21B–C for measurements.

Type material: holotype (Fig. 37a–c) (SAM, D.17925, stn 042); and paratypes (042, AMS, C.152922, many; 043, AMS, C.152923, many; 044, AMS, C.152924, many; 663, AMS, C.152925, 4).

Dimensions of holotype: length 1.58 mm, width 1.61 mm, length of aperture 0.88 mm.

Localities: Freeling Springs (042–046, 663, 664B,C, 665A–C) (Fig. 39).

Remarks: The small umbilicus and relatively high spire enable this species to be readily distinguished. It is particularly abundant in the lower parts of the spring outflows and is sympatric with *T. minuta.* These two species differ significantly in size and in the values of shell ratios PD/SH, SW/SH and AH/SH.

Discrimination of all of the taxa of *Trochidrobia* was tested using discriminate analysis of measurements of shell and female genitalia. With the shell measurements 76% of the measured individuals (n = 219) were correctly classified (combined sexes) (Figs. 40, 41). With female genital measurements (Fig. 42) 88% of all measured individuals (n = 26) were correctly classified. The generalized (taxonomic) distances between the groups are given in Table 9. Using shell measurements the greatest distance score achieved with pairwise comparisons between the species was 1.4 (the comparison between *T. minuta* and *T. smithi;* males 1.41, females 1.46), the lowest 0.12 (between females of *T. smithi* and *T. punicea*). With female genitalia the highest score (4.3) was achieved between *T. minuta* and *T. punicea,* with the comparison between *T. punicea* and *T. smithi* being 2.64. The lowest score (0.74) was between *T. smithi* and *T. inflata.*

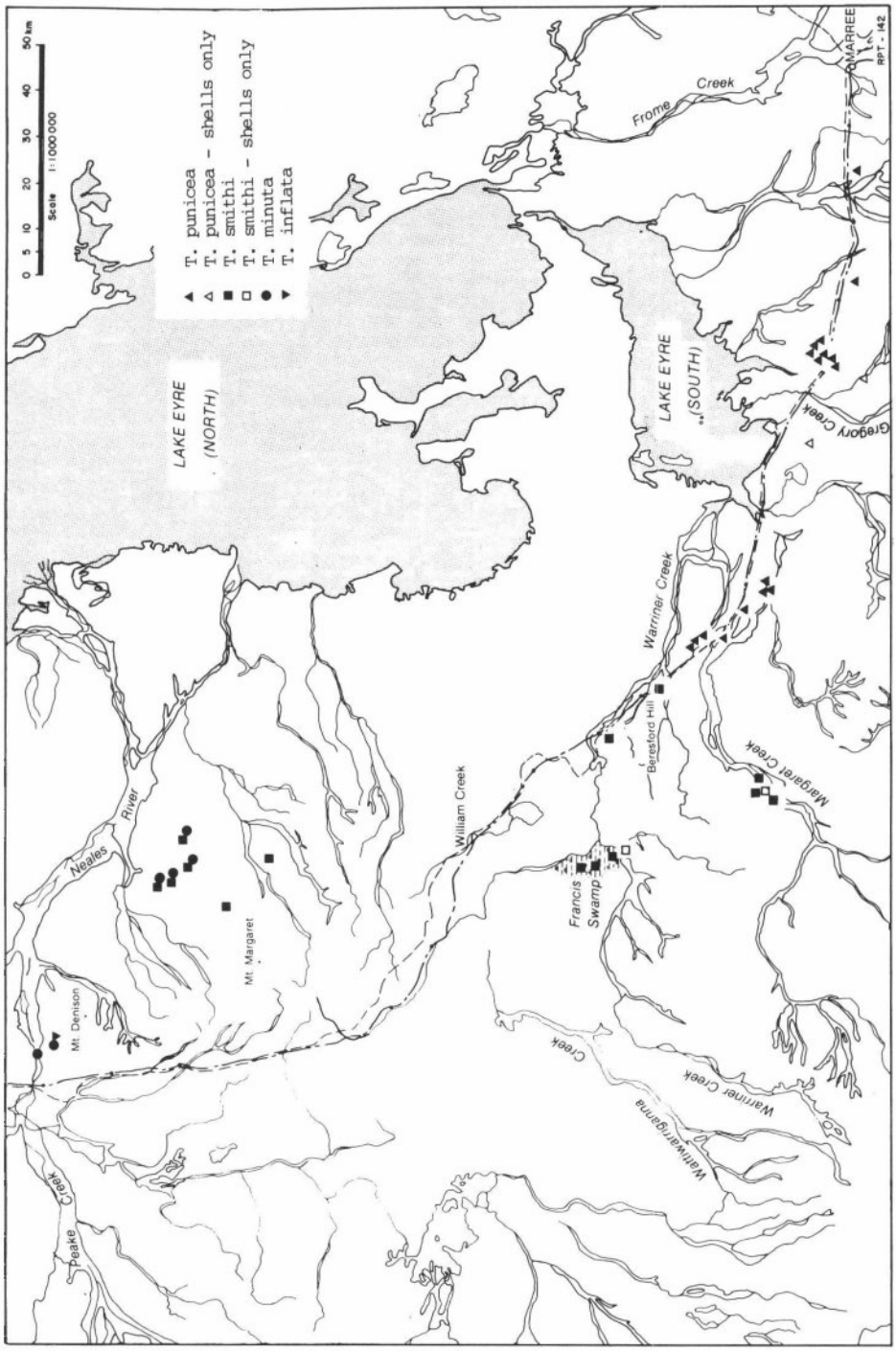


FIG. 39. Distribution of the species of *Trochidrobia*.

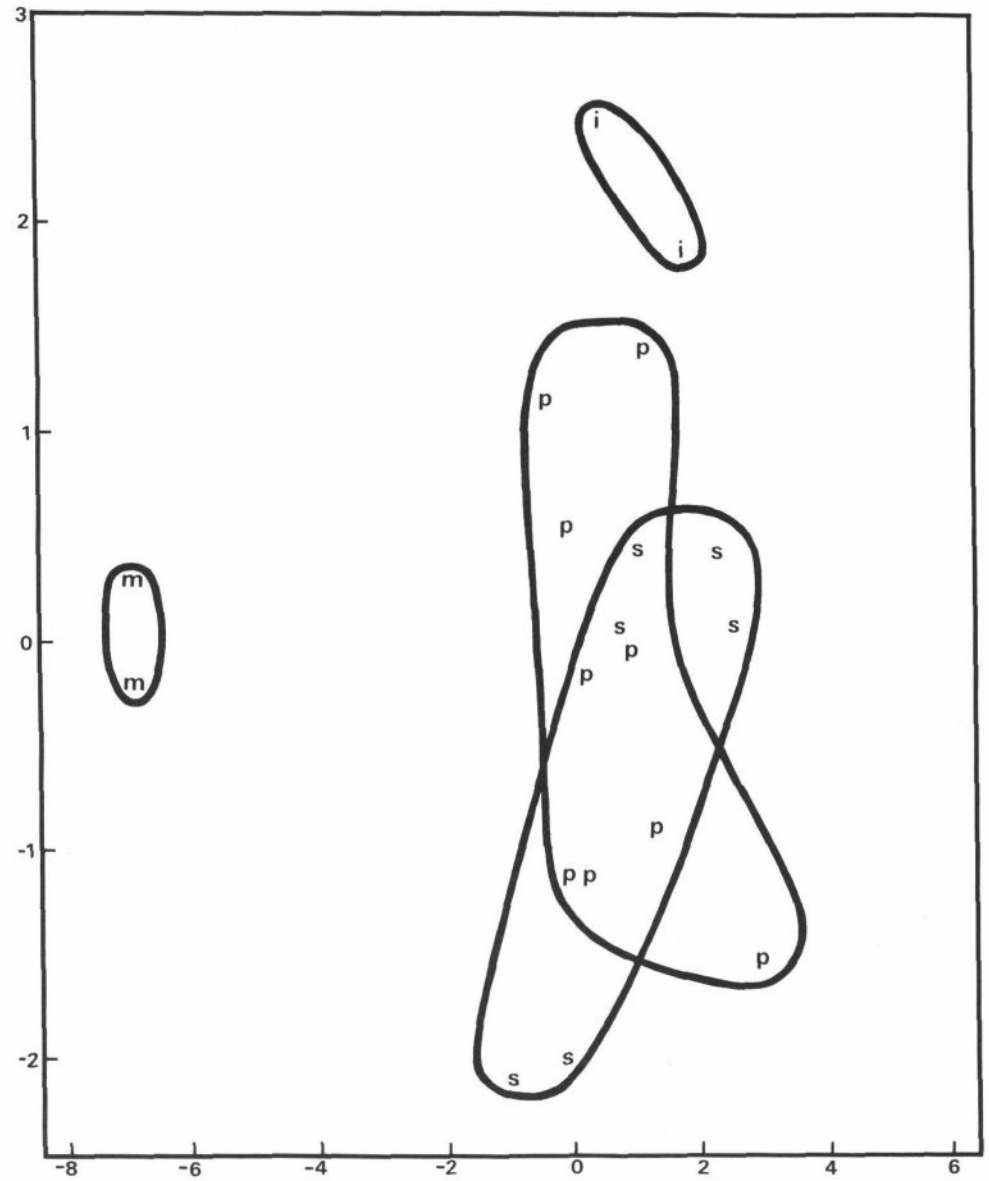


FIG. 40. Plot of group centroids, using first two canonical axes, obtained from discriminate analysis of populations of species of *Trochidrobia* using shell measurements. Males and females of each population are, for the purpose of this analysis, treated as distinct populations. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: SH, 88.75%; SW, 59.20%; AH, 89.98%; AW, 91.18%, BW, 81.96%; TW, 0.56%; PD, 11.13%. Second (vertical) axis: SH, 2.72%; SW, 19.12%; AH, 2.21%; AW, 1.31%; BW, 9.23%; TW, 2.27%; PD, 75.38%.
i, *T. inflata;* m, *T. minuta;* p, *T. punicea;* s, *T. smithi.*

SNK tests (5% level) using pooled data, combined and separate sexes, for each variable used in the discriminate analyses gave the following results:

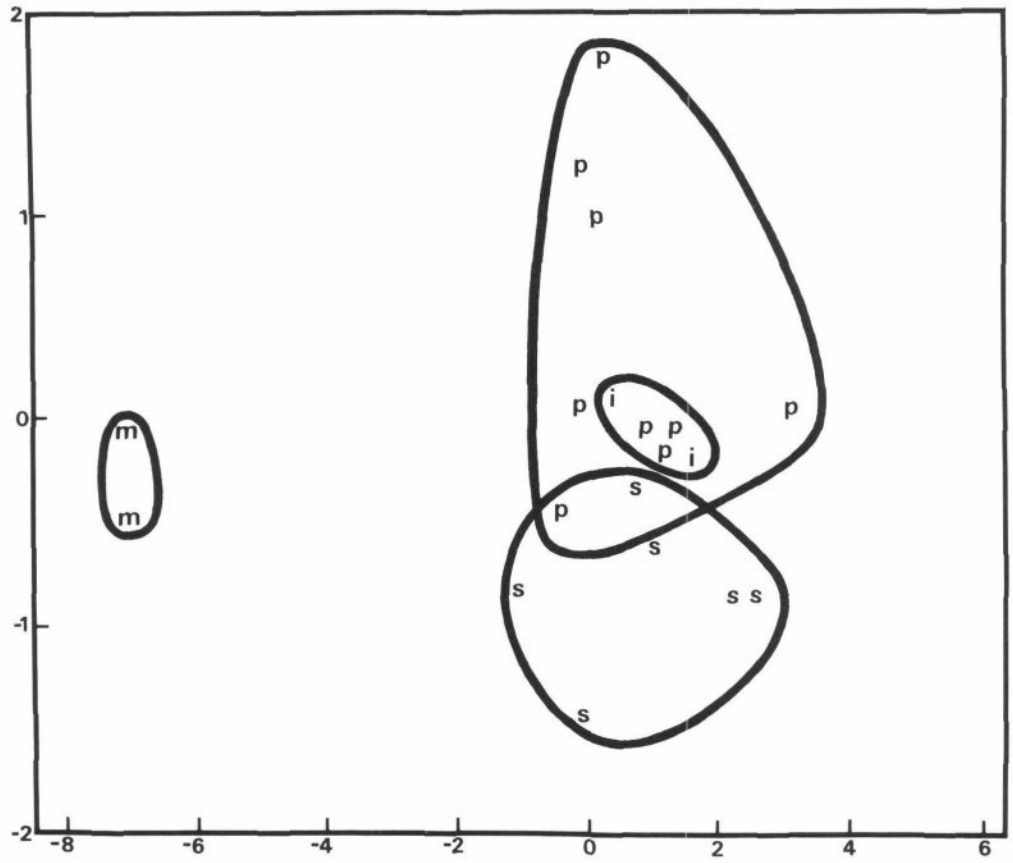


FIG. 41. Plot of group centroids, using first and third canonical axes, obtained from discriminate analysis of populations of species of *Trochidrobia* using shell measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct populations. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: SH, 88.75%; SW, 59.20%; AH, 89.98%; AW, 91.18%, BW, 81.96%; TW, 0.56%; PD, 11.13%. Third (vertical) axis: SH, 0.11%; SW, 0.34%; AH, 5.02%; AW, 5.01%; BW, 0.88%; TW, 93.46%; PD 0.02%.
i, *T. inflata;* m, *T. minuta;* p, *T. punicea;* s, *T. smithi.*

Shell characters:

SH—Combined and separate sexes: *T. minuta* significantly different from all other taxa, which form a single subgroup. There is no sexual dimorphism in this character.

SW—Combined sexes: all means are significantly different. Separate sexes: three discrete subgroups are formed, *T. minuta, T. inflata* + *T. punicea* male, and *T. punicea* female + *T. smithi. T. punicea* is the only species sexually dimorphic (females larger) in this character.

AH—Combined and separated sexes: the only taxon significantly different from the others is *T. minuta.* There is no sexual dimorphism in this character.

AW—Combined sexes: *T. minuta* and *T. smithi* form two separate subgroups with an intermediate, separate group formed by the other two taxa. Separated sexes: discrete subsets are formed by *T. minuta, T. punicea* (male) + *T. inflata* (male), and *T. punicea* female + *T. inflata* female + *T. smithi.* Thus significant sexual dimorphism is apparent in *T. punicea* and *T. inflata* in this character.

BW, TW—Combined and separate sexes: only *T. minuta* is separated as a distinct subgroup. There is no sexual dimorphism apparent in these characters.

PD—Combined sexes: two separate subgroups, *T. minuta* + *T. punicea,* and *T. smithi*

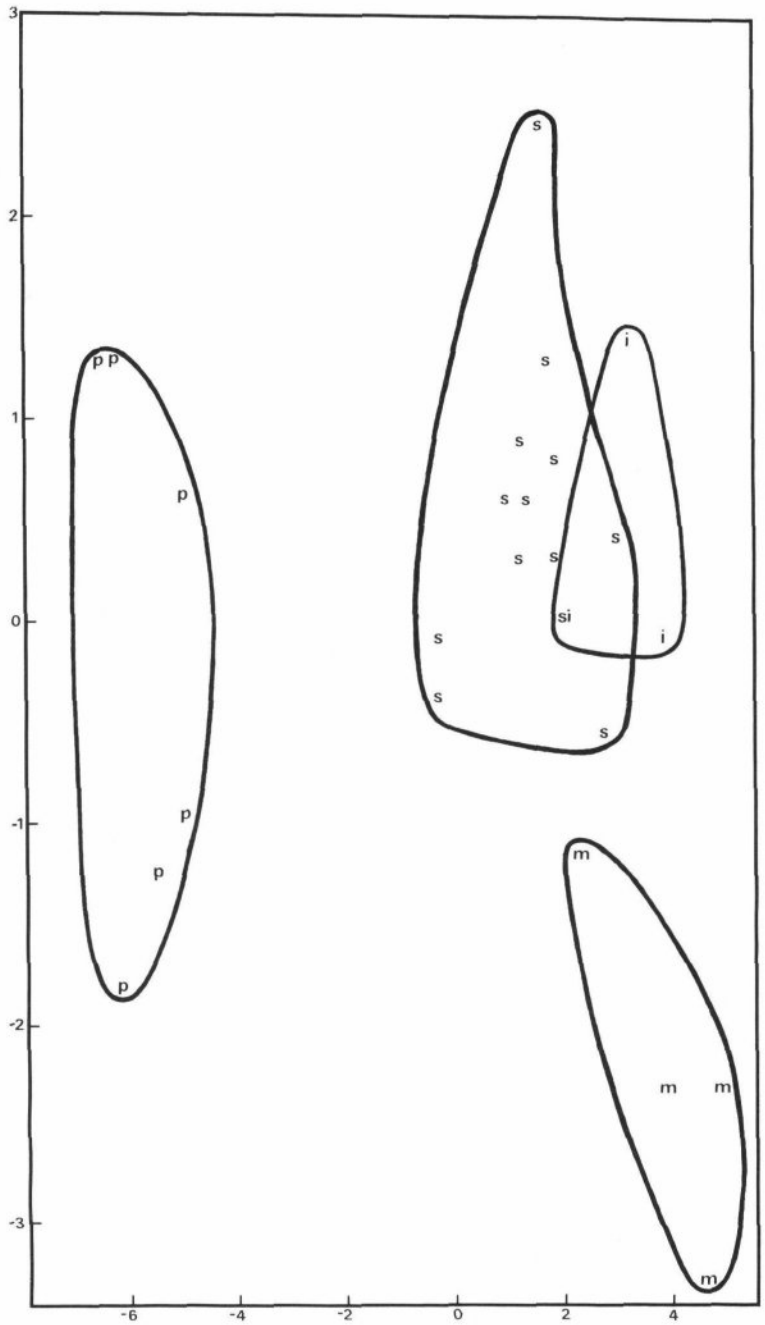


FIG. 42. Plot of discriminate scores for individuals, using first two canonical axes, obtained from discriminate analysis of specimens of *Trochidrobia* using female genital measurements. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: GO, 51.32%; CG, 61.65%; AG, 93.08%; BC, 52.76%; WB, 98.57%; DB, 90.61%; CV, 98.19%; DV, 95.13%. Second (vertical) axis: GO, 39.60%; CG, 37.93%; AG, 3.61%; BC, 43.64%; WB, 0.15%; DB,3.02%; CV, 1.25%; DV, 3.71%.
i, *T. inflata;* m, *T. minuta;* p, *T. punicea;* s, *T. smithi.*

TABLE 9. Summary of results of discriminate analysis of species of *Trochidrobia*. The numbers are the Euclidean (taxonomic) distances between the groups.

	T. punicea	*T. smithi*	*T. minuta*	*T. inflata*
T. punicea	X	0.128 0.271	1.383 1.149	0.239 0.219
T. smithi	0.155 2.646	X	1.462 1.414	0.274 0.385
T. minuta	1.306 4.301	1.437 1.675	X	1.356 1.142
T. inflata	0.243 3.377	0.324 0.744	1.248 0.999	X

Right side:
Female, shell
Male, shell

Left side: Combined sexes, shell
Female, genital

and *T. inflata*. Separate sexes: these two groups are not discriminated, all means falling into overlapping subsets.

Female genital characters:

GO—T. minuta separated from the rest of the species.

CG, AG—no distinct subgroups.

BC, WB, DB, DV—*T. punicea* separated from the other species.

CV—*T. minuta* and *T. inflata* form a subgroup and *T. smithi* and *T. punicea* both significantly different.

Anatomy

Anatomical description of Fonscochlea accepta: Head foot (Fig. 11d). The distally bilobed snout is slightly shorter than the narrow, parallel-sided tentacles. These tentacles move slowly up and down and are held at about 45° to the longitudinal axis of the snout. They are not ciliated dorsally and weakly ciliated ventrally, the cilia beating backwards at right angles to the longitudinal axis of the tentacle. The tentacles have blunt, rounded ends and the conspicuous, black eyes are in bulges at their outer bases. The entire dorsal side of the snout and most of the head are black or grey, and the tentacles are usually grey with a narrow, pale, longitudinal mid-dorsal stripe. The eyes are surrounded by a rim of unpigmented epithelium and immediately behind them is a triangular zone of black pigment. The inner sides of the proximal ends of the tentacles have scattered, minute, opaque white spots, and poorly developed subepithelial pigment gives this area a slight reddish-brown tinge. There is an unpigmented or weakly pigmented, ciliated, narrow rejection tract running down each side of the head-foot, at the junction of the foot and the "neck", to the sides of the foot. The tract on the right is more strongly developed in females than in males. Metapodial and pallial tentacles are absent. The mantle collar has numerous black and a few white subepithelial pigment cells giving it a greyish appearance. The head-foot, by way of contrast, is pigmented by epithelial cells.

The foot is slightly expanded anteriorly, rather short (about two-thirds the shell length), about two and one-fourth times as long as it is wide, and has a prominent slit along the anterior edge. The anterior mucous gland opens by way of this slit and can be seen dorsally through the unpigmented propodium. It is roughly triangular and composed of about 18 simple tubules that lie along the longitudinal axis of the foot. There is a slight lateral constriction in the anterior third of the foot and it is rounded behind. The foot is pale grey to dark grey along the sides and posteriorly but the anterior end is unpigmented mid-dorsally. The sole is pale grey, this colour being imparted by scattered black pigment cells in the connective tissue in the pedal haemocoel. Subepithelial gland cells make up the sole gland. The sole is ciliated, the cilia beating in a posterior direction. Cilial currents around the edges of the foot pass particles posteriorly.

Mantle cavity (Fig. 4F). The mantle cavity is longer than broad and contains a well-developed ctenidium (CT) with triangular filaments (see Table 18B) for statistical details), which extends through almost the entire length of the mantle cavity and occupies about half of the

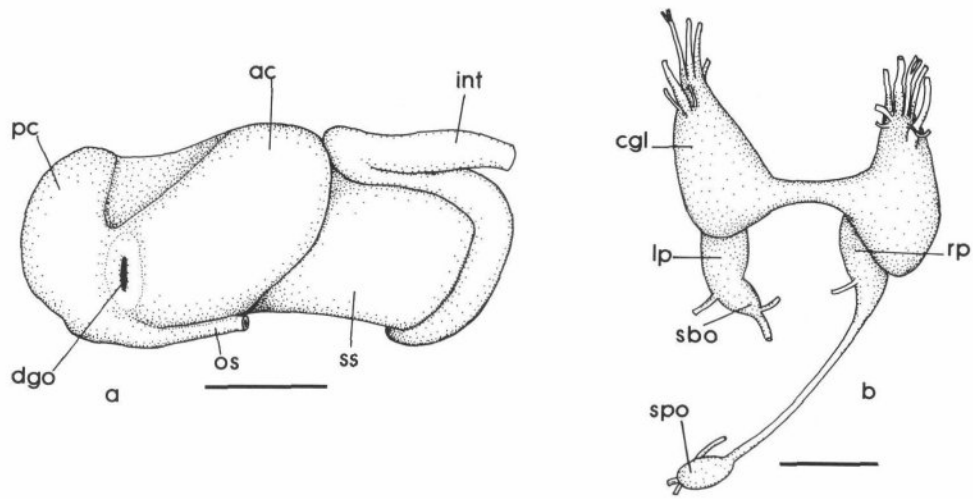


FIG. 43. a. Stomach of *Fonscochlea accepta* form A, Welcome Springs, viewed from its inner (left) side. b. Circum-oesophageal ganglia of *F. accepta* form A, Welcome Springs viewed dorsally (pedal ganglia omitted). ac, anterior chamber of stomach; cgl, left cerebral ganglion; dgo, digestive gland opening; int, intestine; lp, left pleural ganglion; os, oesophagus; pc, posterior chamber of stomach; ss, style sac; rp, right pleural ganglion; sbo, suboesophageal ganglion; spo, supra-oesophageal ganglion. Scale: 0.25mm.

pallial roof in the posterior section, but narrows considerably anteriorly. An oval, unpigmented osphradium (OS) lies to the left of the posterior end of the ctenidium. It is about one-third the length of the ctenidium and consists of a raised, unciliated central portion containing the osphradial ganglion bordered by a slightly lower, weakly ciliated region with longer epithelial cells. Part of this border is separated from the central area by a narrow groove, forming a weak encircling ridge. A very poorly developed hypobranchial gland lies over the posterior end of the rectum. The mantle collar is ciliated, the cilia driving particles outwards.

Alimentary system. A small pair of jaws composed of chitinous rodlets lies in the anterior end of the buccal tube. The buccal mass occupies the length of the snout and the radular sac protrudes behind it. The free portion of this sac is about twice as long as the buccal mass. Two simple, tubular salivary glands open to the buccal cavity and lie dorsal to the nerve ring. The oesophagus is simple, narrow and the anterior part (mid-oesophagus) contains long dorsal folds that coil in a dorsal direction. The dorsal folds are lined with low ciliated cells but the lateral walls are predominantly lined with dark-blue-staining short cells which appear to be glandular.

The stomach (Figs. 43a, 44b; see also Fig. 45, stomach of *F. zeidleri*) is typical of the family in having a style sac (ss), an anterior (ac) and a posterior chamber (pc), and a single, posterior, slit-like digestive gland opening (dgo). There is no caecal appendage. The style sac occupies about 0.6 of the stomach length and contains a crystalline style; the intestine (int) opens to it along about two-thirds of its length. Externally the anterior and posterior chambers are distinguishable only on the inner (ventral) side and the oesophagus (os) and digestive gland open on this side. Internally the major typhlosole (t1) runs to the posterior end of the stomach and is subdivided into two low, strongly ciliated ridges (t1a,t1b). The minor typhlosole (t2) is also subdivided by a deep groove and terminates immediately in front of the gastric shield (gs). Posterior to the gastric shield the posterior chamber is finely transversely ridged on both floor and roof and functions as a sorting area (sa). These narrow, ciliated ridges are in marked contrast to the broad, low ridges (cr), separated by narrow grooves, that cross the roof of the anterior two-thirds of the stomach. These ridges are cuticularized, presumably to protect the epithelium from the rotation of the crystalline style. This ridged area is incorrectly referred to as the sorting area by Davis *et. al* (1982). Fig. 44b illustrates the major fea-

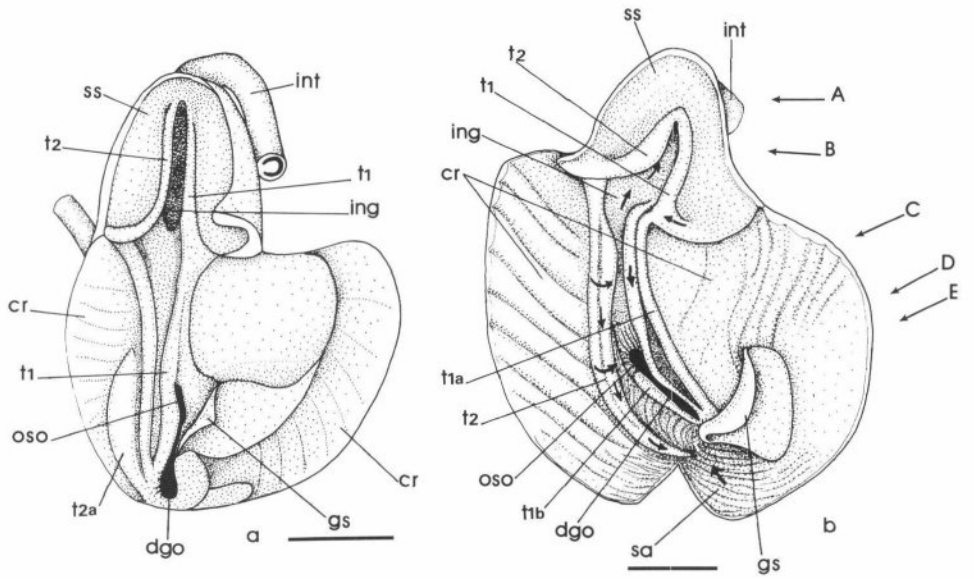


FIG. 44. Stomachs of *Trochidrobia punicea* (a) and *F. accepta* form A (b) opened from outer (right) sides. Arrows in b indicate directions of main ciliary currents; letters A–E correspond approximately to sections with same letters in Fig. 45. cr, chitin-lined ridges; dgo, digestive gland opening; gs, gastric shield; ing, intestinal groove; int, intestine; oso, oesophageal opening; sa, sorting area; ss, style sac; t1, major typhlosole; t1a, t1b, folds developed from major typhlosole; t2, minor typhlosole; t2a, fold developed from minor typhlosole. Scale: 0.25mm.

tures of the stomach with the dorsal (outer) wall opened. The transverse sections of the stomach of *F. zeidleri* (Fig. 45) show the relationships of the typhlosoles to the rest of the stomach and the extent of the ciliated epithelium.

The digestive gland opening (dgo) lies posterior to the oesophageal opening. The digestive gland overlies the posterior end of the inner wall of the stomach and occupies the remainder of the visceral coil. It is composed predominantly of digestive cells with smaller excretory cells, which contain occasional excretory granules, in the creases of the tubules.

The intestine passes around the style sac, loops towards the anterior chamber of the stomach alongside the style sac, and then runs more or less straight to the right side of the mantle cavity. The rectum (Fig. 4F,R) passes along the right side of the mantle cavity and opens a little behind the mantle edge. The proximal part of the intestine contains a large typhlosole but the remainder is simple.

Renal organ and pericardium. The renal organ lies behind the posterior wall of the mantle cavity on the right side and opens to it by way of a short, dorsoventrally orientated slit (Fig. 4F,RO). This slit is located in the middle of the posterior pallial wall and is rendered conspicuous by white lips that surround it. The opening is lined with a ciliated, columnar epithelium and is surrounded by muscle fibres that presumably act as a sphincter. The renal epithelium is thin and simple, composed for the most part of a single layer of irregular cells. A nephridial gland occupies most of the outer wall.

The pericardium also lies immediately behind the posterior pallial wall, but on the left side. It contains the heart, which consists of a well-developed ventrical and auricle. No reno-pericardial opening was observed.

Nervous system (Fig. 43b). The nerve ring is embedded in a mass of spongy connective tissue composed partly of cells containing black pigment granules. The arrangement of the ganglia is essentially similar to that described for *Hydrobia truncata* (Vanatta) by Hershler and Davis (1980). The cerebral ganglia (cgl) are joined by a commissure about as long as the width of a single cerebral ganglion. Each cerebral ganglion gives off seven nerves anteriorly, the base of one of them, the tentacular nerve, being swollen. There is a long right pleuro-supra-oesophageal connec-

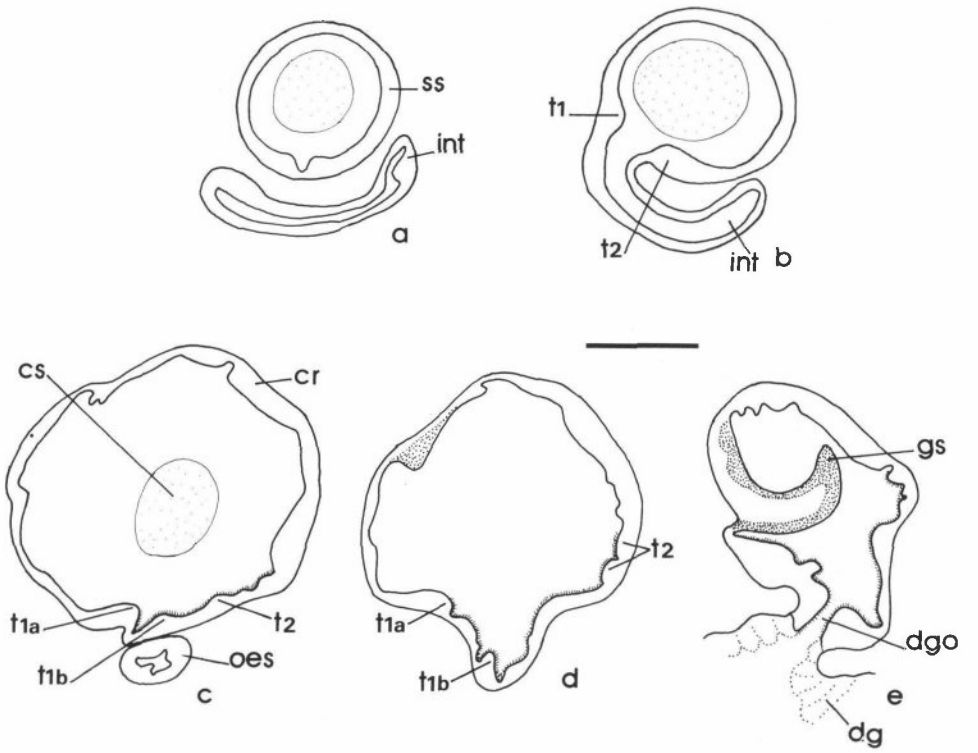


FIG. 45. Sections through stomach of *Fonscochlea zeidleri* form A. Approximate positions indicated in Fig. 44b. cr, chitin-lined ridges; cs, crystalline style; dg, digestive gland; dgo, digestive gland opening; gs, gastric shield; int, intestine; oes, oesophagus; ss, style sac; t1, major typhlosole; t1a, t1b, folds developed from major typhlosole; t2, minor typhlosole.
Scale: 0.25mm.

tive (rp-spo) and the left pleural (lp) and suboesophageal ganglia (sbo) are fused.

The cerebro-pedal complex is also very similar to that described for *H. truncata* except that the cerebropedal connectives are relatively shorter than the pleuropedal connectives. Only the cerebral, pedal and buccal ganglia are pigmented.

Male genital system (Fig. 46a). The testis occupies the upper surface of most of the visceral coil behind the stomach. It is complexly lobed, with five lobes each containing approximately 15 to 20 lobules. The visceral section of the vas deferens forms a seminal vesicle that lies coiled beneath the anterior half to two-thirds of the testis. When straightened the seminal vesicle is about one and two-thirds times longer than the shell. A more or less straight part of the seminal vesicle emerges from beneath the testis and runs across the ventral side of the stomach. This duct narrows before entering the prostate gland immediately behind the posterior pallial wall. This large gland extends partly (0.1 to 0.45 of its total length) into the right side of the mantle cavity. The prostate has thickly glandular walls except in its mid-ventral portion where the vas deferens opens and leaves. The pallial portion of the vas deferens opens immediately in front of the posterior pallial wall and runs as a straight tube along the right side of the mantle cavity until it is close to the base of the penis. Here it undulates for a short distance before entering the penis. The pallial vas deferens lies just beneath the surface of the epithelium, has a simple, ciliated epithelium and is not surrounded by muscle fibers.

The penis (Fig. 46a), coiled twice anticlockwise as seen from above, is attached to the midline behind the head. The distance of the anterior edge of the penial attachment behind the eyes is only slightly less than the distance between the tentacle bases and about two-thirds the length of the snout. The penial duct

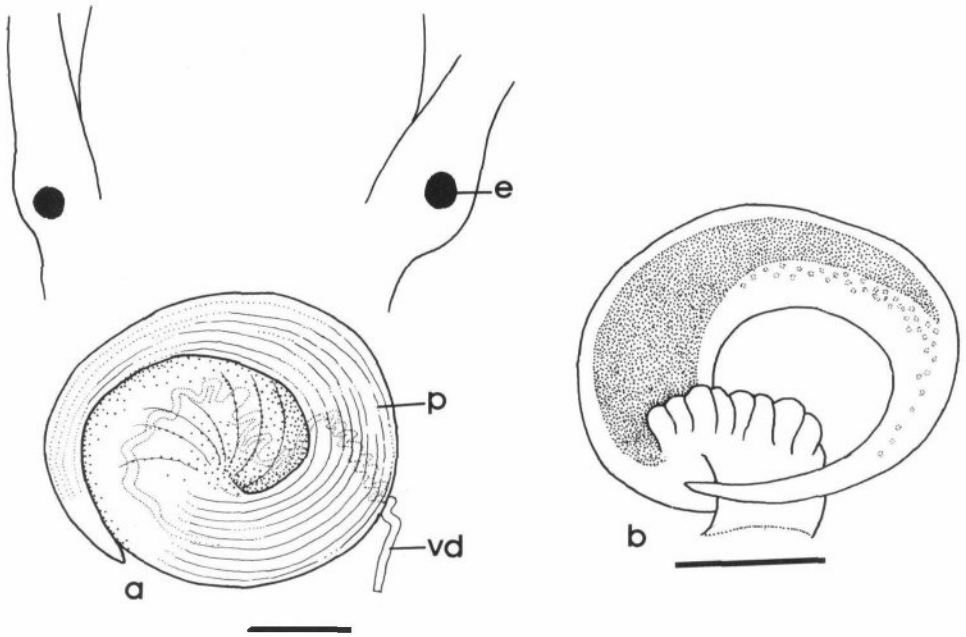


FIG. 46. a. Dorsal view of penis of *Fonscochlea accepta* form A, Welcome Springs, preserved material.
b. Ventral view of living penis of *Fonscochlea zeidleri* form A, Blanche Cup.
e, eye; p, penis; vd, pallial vas deferens.
Scale: 0.25mm.

lies close to the outer edge of the penis and is similar to the pallial vas deferens in structure. It coils in the broad, proximal quarter of the penis and is straight in the remainder. The distal part of the penis is long and tapers to a point. Unlike the basal part it is not transversely ridged and has longitudinal stripes that correspond to strands of longitudinal muscle lying beneath the epithelium. There are no penial glands or cilia; the epithelium is covered with cuticle.

Female genital system (Figs. 12d,g,h, *F. accepta* form A; 47, F. zeidleri). The ovary is a simple sac filled with about 17 eggs in a mature individual. It is about one-half the length of the digestive gland and lies behind the posterior end of the stomach. The thin-walled oviduct is lined with pale-staining, unciliated cells and passes straight across the ventral wall of the stomach to a position just behind the posterior pallial wall. At this point there is a sudden change to a ciliated cuboidal epithelium that is thrown into longitudinal folds marking the commencement of the coiled section of the oviduct.

The longitudinal folds in the first part of the coiled oviduct persist for only a short distance, the lumen becoming oval. The initial section of the coiled oviduct probably represents the renal section of the oviduct. It passes very close to the renal organ but no open reno-gonadial duct was observed in sections or in dissection. There are, however, strands of tissue connecting the most proximal portion of the duct to the kidney wall and some modification of the kidney tissue was apparent in this region. The cells increase in size in the section following the renal part and they are more or less cuboidal with a few blue-staining (in Mallory's Triple Stain) gland cells apparent. The coiled part of the oviduct (co), at this point, is surrounded by a few muscle fibres. It bends sharply upwards and then loops down to run forward along the albumen gland (ag). Near the posterior end of the albumen gland it loops upwards and two spherical sperm pouches open to it. In this region the coiled oviduct is surrounded by an outer coat of circular muscle. The epithelium is thrown into a few low, longitudinal folds and sperm are attached to the ciliated epithelial cells. The oviduct increases in diameter and

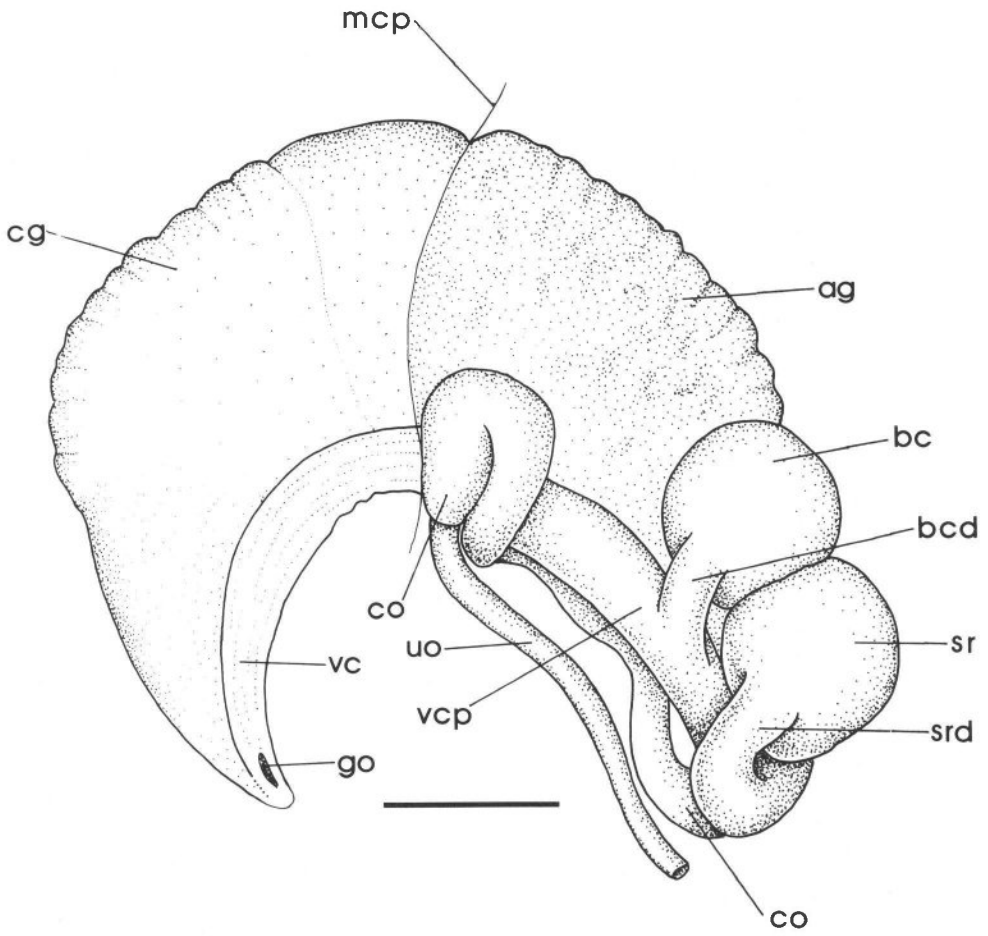


FIG. 47. Female genitalia of *Fonscochlea zeidleri* form A, from the left side.
ag, albumen gland; bc, bursa copulatrix; bcd, duct of bursa copulatrix; cg, capsule gland; co, coiled part of oviduct; go, female genital opening; mcp, posterior limit of mantle cavity; sr, seminal receptacle; srd, duct of seminal receptacle; uo, upper oviduct; vc, ventral channel; vcp, posterior extension of ventral channel. Scale: 0.2mm.

loops upwards to lie behind, and sometimes above, the proximal loop. It then opens ventrally into the posterior end of the capsule gland (cg). This tubular extension (vpc) of the sperm groove in the ventral channel is lined with an epithelium similar to that of the sperm groove, the cuboidal cells bearing conspicuous cilia and occasional blue-staining gland cells.

The two sperm pouches (bc, sr) lie near the posterior end of the albumen gland on the inner (left) side of the gland and their short ducts extend from their ventral walls to open separately into the oviduct. They are identical in histology and appearance and might both be homologous with the bursa copulatrix of other hydrobiids. They are lined with long, purple-staining cells with dense, finely-staining contents and basal nuclei. Unoriented sperm fill the lumen in most specimens and additional sperm have their heads attached to the outer surface of the epithelial cells. Each sperm sac is surrounded by a coat of muscle and their ducts, which also contain sperm with their heads attached to the epithelial cells, are similar in structure to the oviduct in this region.

The oviduct gland of *F. zeidleri* (Fig. 47) is typical of those in all the species of *Fonscochlea*. It consists of a blue-staining albumen

gland (ag), which lies behind the posterior pallial wall, and a red-purple staining capsule gland (cg), which lies in front of this wall. The two glands are, however, externally continuous. The lumen of the albumen gland is continuous with that of the capsule gland and ciliated cells line the lumina of both. The tubular oviduct opens to the thin-walled ventral channel (vc) of the capsule gland, part of which, on the left, is separated from the main channel by a ciliated, nonglandular fold. This fold continues throughout the ventral channel to the small, subterminal, ventral opening and separates the sperm-conducting channel, on the left, from the egg-conducting channel. The very thin ventral wall of the egg-conducting channel is lined with small, cuboidal, unciliated cells. In the vicinity of the oviduct opening the gland cells in the ventral part of the capsule gland change from red- to pale-blue-staining.

The anatomy of *Fonscochlea accepta* is typical of all the species of *Fonscochlea*. The most important character that separates this genus from all other genera in the family is the equal-sized sperm sacs that seem to have been developed from a subdivided bursa copulatrix. Their arrangement differs in detail in the two subgenera of *Fonscochlea*, as described in the taxonomic section (compare Figs. 12c–h and 27a–d with Figs. 12a,b and 47). In most other respects the anatomy of species of *Fonscochlea* is similar to that of other species of the family Hydrobiidae.

Anatomical description of Trochidrobia punicea: Head-foot (Fig. 24h). The snout is about two-thirds the length of the tentacles when at rest but when extended is about the same length. It has a bilobed tip that is slightly narrower than the rest of the snout, and is pigmented dark grey to black, the tip being unpigmented in many specimens. The cephalic tentacles are parallel-sided, held at about 45°, sway slowly up and down through a small arc (species of *Fonscochlea* move their tentacles through a greater arc and more rapidly) and are pigmented light to dark grey, often with a narrow, white median line. A few scattered, dense-white spots lie on the inside proximal end of the tentacles anterior to the eyes and a conspicuous group of these spots lies on the inner side of the eyes and, sometimes, behind them. The large, black eyes are in bulges at the outer bases of the tentacles and are, in some specimens, surrounded by black pigment, but in others the black pigment lies mainly behind the eyes. The dorsal head and 'neck' are grey to black and a ciliated rejection tract runs down both the sides of the head onto the foot.

The foot is almost as long as the shell is wide and is about one-third as wide as long. Only a very short portion extends beyond the operculum and, normally, the foot is invisible when the crawling animal is viewed from above. There are lateral constrictions behind the anterior edge, and the posterior end is evenly rounded. A well-developed pedal gland opens to the anterior edge of the foot and the sole is supplied with subepithelial glands. The entire sole and the lateral edges of the foot are covered with posteriorly beating cilia. The anterior edge has cilia beating towards the outer corners. The foot is pigmented grey to black on the anterior and posterior dorsal surfaces and is paler to unpigmented dorsolaterally. The sole is dark grey to whitish, the colour being imparted by pigment-bearing cells in the connective tissue in the cephalic haemocoel.

The mantle collar is richly supplied with dense-white cells across the outer lip but these are fewer across the inner lip where there is more black pigment. This black pigment is predominantly in subepithelial cells, but, with the exception of the sole, the remainder of the pigment on the head-foot is contained in epithelial cells.

Mantle cavity (Fig. 48). The mantle cavity is short and broad, being slightly wider than it is long. The well-developed ctenidium (ct) is placed diagonally across the cavity and the apices of the filaments lie at their right edge. A short, oval osphradium (os) lies alongside the posterior end of the ctenidium. It is similar in structure to that of species of *Fonscochlea*. There is no hypobranchial gland. The rectum (r) and genital duct (cg) run down the right side of the cavity and the anus (a) lies close to the mantle edge. The ctenidium lies closer to the mantle edge, ending just inside the mantle skirt (me).

Alimentary system. The mouth opens to a short, cuticle-lined oral tube with a pair of small jaws laterodorsally. The well-developed buccal mass occupies most of the snout and a coiled radular sac emerges posteriorly from it.

The anterior part of the oesophagus (mid-oesophagus) has long dorsal folds, which are curved dorsally, occupying most of the lumen. The lateral and ventral walls are lined with a ciliated, cuboidal epithelium with purple-

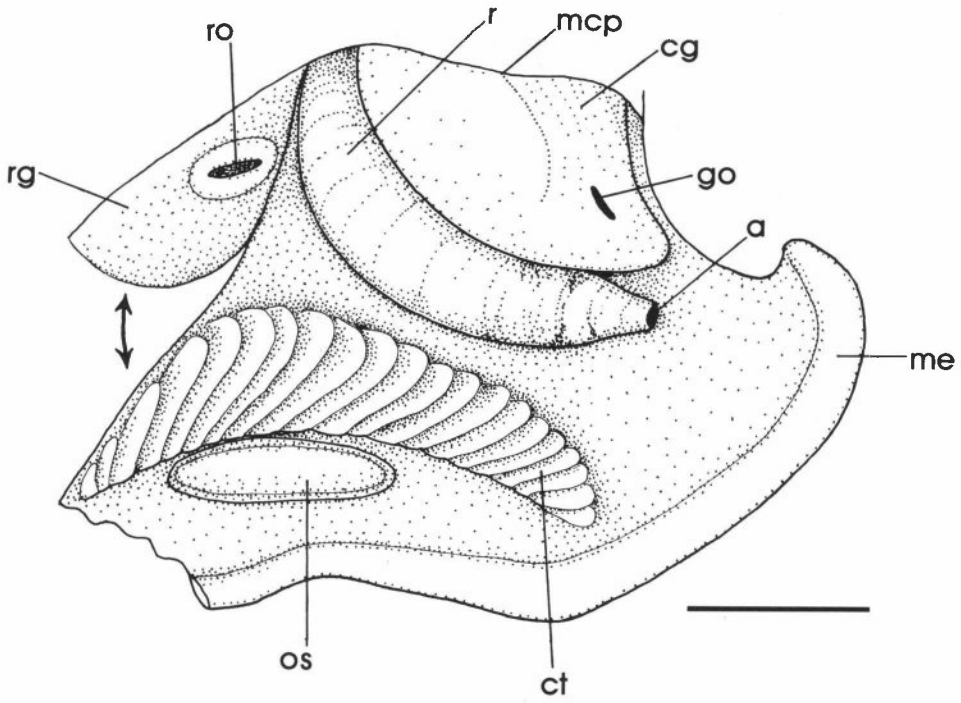


FIG. 48. Dissection of pallial cavity of *Trochidrobia punicea*. Double-headed arrow indicates separation of kidney from dorsal pallial wall. a, anus; cg, capsule gland; ct, ctenidium; go, female genital opening; mcp, posterior limit of mantle cavity; me, mantle edge; os, osphradium; r, rectum; rg, renal organ; ro, renal opening.
Scale: 0.2mm.

staining, granular contents. This section of the oesophagus terminates at the end of the cephalic cavity, the posterior oesophagus being narrower and without the dorsal folds. The simple, tubular salivary glands lie dorsal to the nerve ring.

The stomach (Fig. 44a) is similar in general appearance externally to that of species of *Fonscochlea*. The style sac communicates with the intestine along all of its length. The well-developed typhlosoles (t1, t2) within the stomach are unpigmented and readily discernible against the stomach wall. The major typhlosole (t1) extends to the posterior end of the stomach where it swings around the digestive gland opening after fusing with the minor typhlosole (t2). Short left (t2a) and right branches of the fused minor + major typhlosole are given off that extend onto the roof of the posterior end of the stomach. The gastric shield lies close to the oesophageal (oso) and digestive gland (dgo) openings. These openings lie at either end of a groove that divides the major typhlosole (t1) into two arms. This typhlosole splits into two folds at the anterior end of the oesophageal opening, the right fold running to the anterior edge of the gastric shield and the left fusing with the minor typhlosole near the digestive gland opening at the posterior end of the stomach.

The typhlosoles, style sac, and the posterior end of the stomach are ciliated, the remainder of the gastric epithelium being cuticularized. The pigmented roof of the anterior chamber is very indistinctly marked with widely separated narrow grooves (cr).

The digestive gland and intestine are very similar to those of *Fonscochlea*. The digestive gland covers the inner, ventral, side of the stomach to half-way across the anterior chamber.

Renal organ and pericardium. The renal organ (kidney) lies behind the posterior wall of the pallial cavity. The lumen is severely reduced, particularly in females, by the invagination of the genitalia. The renal opening (Fig.

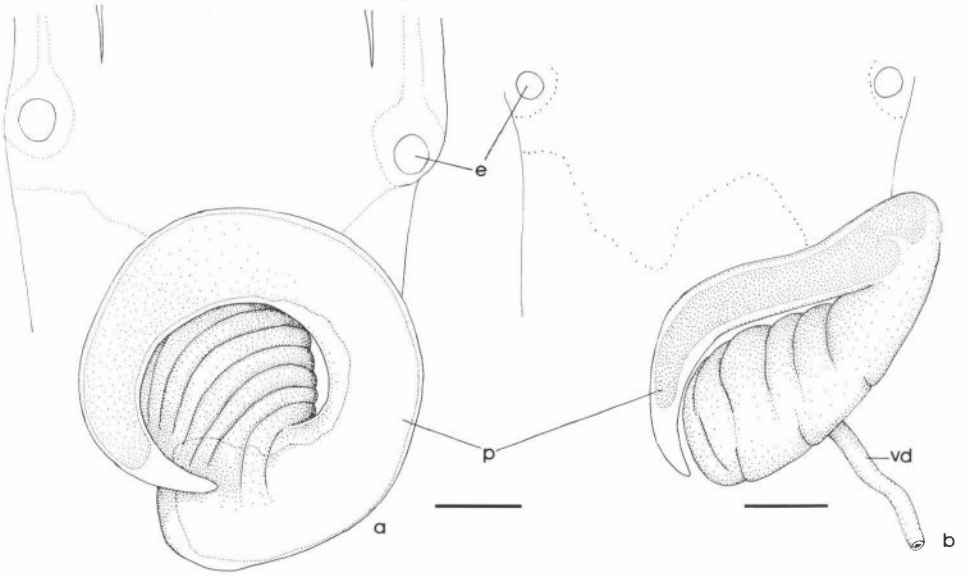


FIG. 49. Penes of *Trochidrobia punicea,* Blanche Cup (a.) and *Trochidrobia smithi,* Outside Springs (b.). a, eye; p, penis; vd, pallial vas deferens.
Scale: 0.1mm

48, ro) lies in the middle of the posterior wall of the pallial cavity. It is a short, vertical slit surrounded by thickened, ciliated, white lips (sphincter muscle). The renal epithelium is simple and very thin except on the outer wall where it forms a thick nephridial gland.

The pericardium lies behind the left side of the posterior pallial wall and the base of the ctenidium. Its posterior face abuts against the anterior end of the style sac. The ventricle and auricle are both well developed.

Nervous system. The cerebral ganglia are joined by a commissure that is slightly shorter than the width of the cerebral ganglia. The pleural ganglia are fused to the cerebral ganglia but a waist-like constriction separates them. The supra-oesophageal ganglion is a little longer than the width of the cerebral ganglia, and the right pleuro-oesophageal connective is about the same length as the cerebral ganglia. The suboesophageal ganglion abuts the left pleural ganglion. All of these ganglia, and the buccal and pedal ganglia, are pigmented except for the supra-oesophageal ganglion.

Male genital system. The testis consists of several lobes, each consisting of numerous lobules, about 45 in the anterior lobe. The vas deferens lies coiled beneath the anterior two lobes of the testis. It runs forward as an almost straight tube, narrows across the inner (ventral) side of the stomach and terminates just behind the posterior pallial wall where it opens to the middle part of the prostate gland. The pallial section of the vas deferens leaves the prostate gland immediately in front of the posterior pallial wall and runs along the groove at the junction of the mantle cavity floor and the mantle roof. It is straight until it nears the base of the penis where it undulates across the right side of the "neck" before entering the penis.

The large prostate gland is reniform, narrowly oval in section, thickly glandular, with a thin ventral wall only in the vicinity of the point of entry and departure of the vas deferens. It lies partly in the pallial roof and partly behind the posterior pallial wall. Its extent of penetration of the pallial roof varies from one-third to one-half of its total length. The penis (Fig. 49a) lies just to the right side of the midline of the head at a distance behind the eyes about equal to the length of the snout. It is coiled twice anticlockwise in preserved material. The base of the penis is swollen and unpigmented, at least in the proximal part, and has clearly defined creases running across its surface. The remainder of the organ is pale to dark grey along much of its length, the proximal part

often being unpigmented. It is smooth and tapers to a point. The inner side of the penis, i.e. the edge on the inner side of the coil, is flattened to almost channelled in some individuals and rounded in others. The penial duct is, like the pallial vas deferens, ciliated, thin-walled and very narrow. The penis is surrounded by an unciliated, non-cuticularized cuboidal epithelium. It contains some pale-blue staining subepithelial gland cells amongst the muscle and connective tissue. Distinct penial glands are absent.

Female genital system (Fig. 36b). The ovary is short relative to the digestive gland. The upper oviduct (uo) is a straight, thin-walled tube that passes across the ventral surface of the stomach before reaching a point close to the pericardium and the renal organ. Here its walls thicken and the ciliated epithelium is raised into longitudinal ridges. There is no gonopericardial or renogonadial duct although a tissue connection (st) with the pericardium can be seen in dissection. The renal section of the oviduct is extremely short and is invaginated within the renal wall.

The coiled oviduct (co), the first, very short part of which is the renal oviduct, is coiled behind the posterior pallial wall (mcp) on the left side of the albumen gland. It is considerably swollen in this species, a character not seen in other species of the genus. It invaginates into the renal organ, considerably reducing the volume of the renal lumen. The outer wall of the coiled oviduct is surrounded by an outer layer of circular muscle fibres and a thicker inner layer of longitudinal fibres and is lined with a ciliated cuboidal epithelium. Spermatozoa are stored in the lumen of the coiled oviduct, and are aligned more or less longitudinally, apparently by ciliary action. The large bursa copulatrix lies behind the coiled oviduct and its right (outer) wall is embedded in the albumen gland. There is a short, free bursal duct (about one-fifth the length of the bursa), the remainder of the duct merging with the coiled oviduct and running back along it. The bursal duct eventually opens to the coiled oviduct but the exact point of opening was not established because the two tubes are enveloped in a common sheath of connective tissue. The bursa copulatrix (bc) is lined with an unciliated, purple-staining columnar epithelium with granular cytoplasm and basal nuclei. In all specimens sectioned, the bursa did not contain sperm.

The oviduct anterior to the bursal duct continues as a short, broad tube, for a distance approximately equal to the length of the bursa, to the posterior wall of the pallial cavity where it opens to the capsule gland (cg) as the ventral channel. This oviducal tube is lined with ciliated cells, amongst which are scattered larger, blue-staining gland cells.

The oviduct gland is clearly divided into a blue-staining albumen gland (ag) lying behind the pallial cavity and, continuous with it, a red-staining capsule gland (cg) in front of the posterior pallial wall. The albumen gland opens to the capsule gland which, immediately in front of the junction of the two glands, receives the oviduct. This tube opens to the ventral channel (vc) of the capsule gland into a ciliated gutter, similar to that in species of *Fonscochlea,* which runs to a slit-like opening (go) situated about one-third of the length of the capsule gland from its anterior end. The capsule gland is, however, relatively shorter and broader than that of species of *Fonscochlea.* In the vicinity of the genital opening the glandular epithelium in the ventral part of the capsule gland forms a pale-blue zone.

The main feature of interest in the anatomy of this genus is the lack of a seminal receptacle and the development of accessory sperm storage in the coiled oviduct. In *Trochidrobia smithi* sperm storage takes place in the ventral channel. In other respects the anatomy is typical of the family Hydrobiidae.

TABLE 10. Shell heights for the snail taxa used in the physiology experiments.

Species	Range of shell heights (means, sexes pooled) among populations (mm)
F. accepta form A	3.16–3.57
F. accepta form B	2.83–3.41
F. aquatica	3.93–4.50
F. variabilis	1.41–2.52
F. conica	1.70–2.18
F. zeidleri	2.97–4.37
T. punicea	1.60–1.91 (shell width)

Physiology

The taxa examined fall into four main groups, distinguished by differences in shell size (Table 10) and habits: 1) *F. zeidleri* form A, the amphibious species; 2) large aquatic species (*F. aquatica* form A and cf. form A, and *F. accepta*); 3) small, aquatic *Fonscoch-*

TABLE 11. Survivorship of snails in dry dishes. Ten snails were used in each experiment. T1 = *Trochidrobia punicea*, F1 = *Fonscochlea accepta*, F2 = *Fonscochlea aquatica*, F3 = *Fonscochlea variabilis*, F4 = *Fonscochlea conica*, F5 = *Fonscochlea zeidleri*. BC = Blanche Cup, CS = Coward Springs Railway Bore, FS = Finniss Springs.

	Species (population)										
Number of hours	T1 (run 1)	T1 (run 2)	F4	F3 (BC)	F3 (CS)	F1	F1b	F2	F5 (FS)	F5 (BC)	F5 (CS)
1	8	5	2	7	8	10	10	9	10	10	10
2	5	2	0	4	5	7	10	9	10	8	10
4	2	0	0	1	4	6	10	9	9	9	10
6	0	0	0	0	3	1	8	6	10	9	10
12	0[1]	0	0	0	0	0	5	5	9	10	7[4]
24	0[1]	0	0	0	0	2	4	3	9[3]	9	9
48	0[2]	0	0	0	0	0	0	0	8[3]	9	6
Date & time commenced	27–8 11:30AM	2–9 8:15AM	3–9 10:15AM	21–8 9:00AM	1–9 8:00AM	3–9 9:25AM	29–8 8:00AM	31–8 9:30AM	28–8 8:00AM	30–8 8:40AM	1–9 7:45AM

[1]commenced at 6:30PM [2]commenced at 3:34PM [3]commenced at 8:40AM [4]dish checked after 10 minutes, but not after one hour.

lea species (*F. conica, F. variabilis* form A); and 4) *Trochidrobia punicea*, small and aquatic.

Desiccation. During the 48 hours that these experiments were run, there was no mortality in any of the wet, control dishes of any of the species. The results for the moist dishes were the same, except that at 48 hours the two populations of *F. variabilis* tested had 90% (Coward Springs Railway Bore) and 100% (Blanche Cup) mortality (results significantly different from those for the other species, Fisher's Exact Test, $P < 0.005$). The results are summarized in Table 11.

Only *F. zeidleri* survived well (60–90% in the three populations tested) after 48 hours in the dry dishes (Figs. 50–52). *Fonscochlea aquatica* cf. form A (Kewson Hill) had 10% survival after 48 hours (significantly less than that of any *F. zeidleri* population, $P < 0.05$) and 50% mortality after only one hour. The other species had higher mortalities. *F. conica* had 80% mortality after one hour and 100% mortality after two hours, *T. punicea* 50–80% mortality after two hours and 100% mortality after 6 hours, *F. variabilis* 50% mortality after two hours and 100% mortality after 12 hours and *F. aquatica* and *F. accepta* 100% mortality after 48 hours (see below for details). After 24 and 48 hours, all three *F. zeidleri* populations had significantly higher survival than that of the next best "survivor", *F. accepta* form B (for all pairwise comparisons, $P < 0.05$). At 12 hours, only the Blanche Cup *F. zeidleri* population had a significantly higher survival than that of *F. accepta* form B ($P = 0.025$). There was no significant difference in survival amongst the three *F. zeidleri* populations at any time.

Survival of two of the three large aquatic *Fonscochlea* taxa, *F. accepta* form A, *F. accepta* form B and *F. aquatica,* was good through 12 hours (50%) and higher than that of the small aquatic *Fonscochlea* species (*F. conica* and *F. variabilis*): for *F. accepta* form B, this difference was significant at two, four, six, 12, and 24 hours (for all pairwise comparisons, $P < 0.05$), for *F. aquatica,* the difference was significant at four and 12 hours ($P < 0.05$). Both *F. accepta* form B and *F. aquatica* had higher survival than the other large aquatic species, *F. accepta* form A, after six and 12 hours (all pairwise comparisons, $P < 0.05$), but not at 24 hours. At no point during the experiments did the former two taxa differ significantly from each other in survival.

There were no significant differences in survival seen in any of the pairwise comparisons for any time between the two populations of *F. variabilis* and the two runs of *T. punicea* (Finniss Springs), except for that between *T. punicea* and *F. variabilis* from Coward Springs Railway Bore after four hours ($P = 0.05$). Both of these species showed a fairly rapid onset of mortality. Yet after two hours both of the above species had a signif-

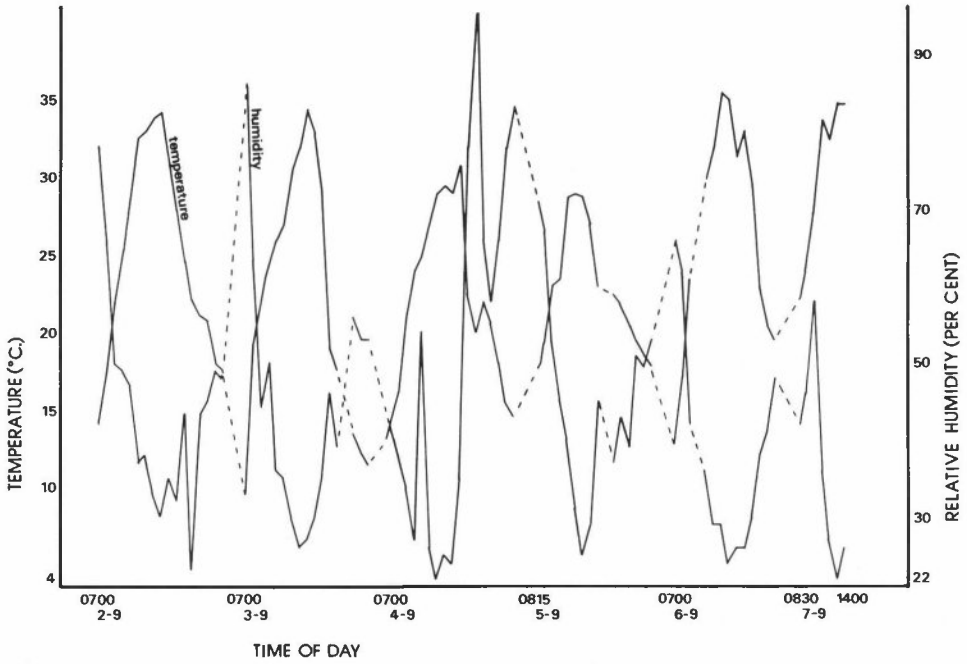


FIG. 50. Running record of air temperature and humidity in tent for duration of experiments. Readings taken hourly, generally from 0600 to 2200; dashed lines indicate intervals at night during which readings were not taken.

icantly higher survival than *F. conica* (all comparisons, $P < 0.05$), which already had 100% mortality at that time.

Fonscochlea aquatica from Kewson Hill showed the peculiar pattern of fairly rapid onset of mortality (50% after one and two hours), followed by survival of 10% of the snails after 12, 24, and 48 hours.

Salinity: Nearly 100% of the snails, for all species, remained active in the control jars for the duration of the experiment. At 24 hours, 98% of the snails (for all species pooled) were active. The results for salinities of 6, 9, and 12‰ are given in Table 12.

In 6‰ salt water, nearly 100% of the specimens of *F. zeidleri, F. aquatica,* and *F. accepta* form B remained active throughout the experiment: after 24 hours, for these species pooled, 91% of the snails were active and there were no significant differences in activity among these species. However, activity did decline markedly in *F. variabilis* after two hours and in *T. punicea* after 24 hours. At 12 and 24 hours, the number of active snails of *F. variabilis* (either population) was significantly less (Fisher's Exact Test, $P < 0.05$) than that of the species listed above for all pairwise comparisons but one (*F. accepta* form B–*F. variabilis,* Coward Springs Railway Bore). For *T. punicea,* at 12 hours, the number of active snails was significantly less than that of only *F. aquatica* from Kewson Hill and *F. zeidleri* and Coward Springs Railway Bore ($P < 0.005$). At 24 hours, the number was significantly lower than that seen in any of the above group of species ($P < 0.005$). A significantly larger number of *T. punicea* were active than *F. variabilis* (both populations) at two, three, six, and 12 hours (for all comparisons, $P < 0.025$).

In 12‰ salt water, activity of *F. zeidleri* and the large aquatic species remained high. After 24 hours, for all species pooled, 80% of the snails were active and there were no significant differences among species. There were, however, several significant differences seen in the early hours of the experiment when acclimitization was apparently occurring. There was no activity for both *F. variabilis* and *T. punicea* for the duration of this experiment. At six, 12, and 24 hours, the number of active snails for these species (0) was significantly lower than that of the above group of species (for all comparisons, $P < 0.025$).

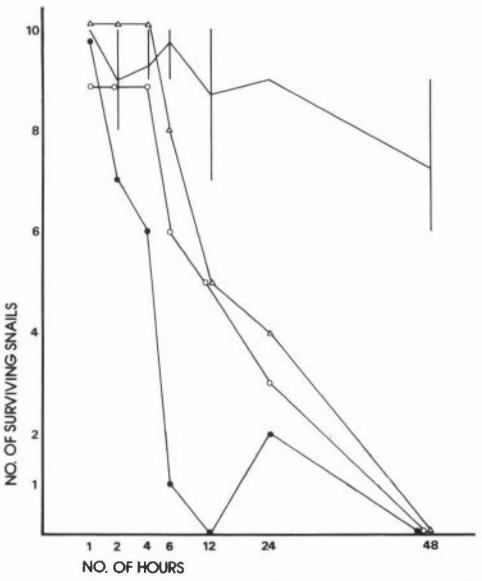


FIG. 51. Survivorship of large-sized species of *Fonscochlea* in dry dishes. *Fonscochlea accepta* form A, solid circles; *F. accepta* form B, open triangles; *Fonscochlea aquatica* form A, open circles; *F. zeidleri* form A represented by line with error bars, representing range of results among populations of that species.

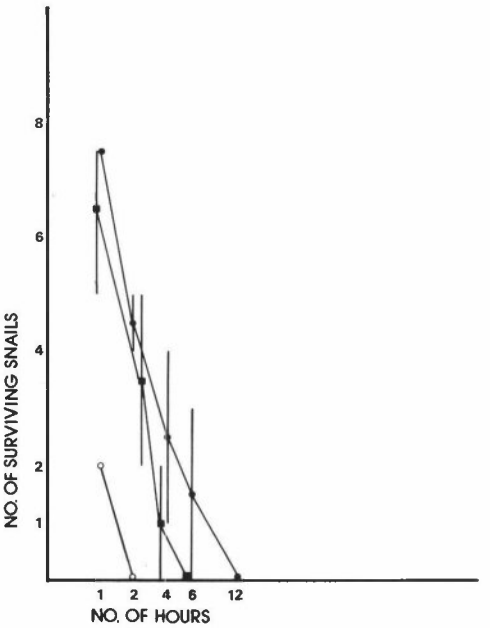


FIG. 52. Survivorship of small-sized species of *Fonscochlea* and *Trochidrobia punicea* in dry dishes. *Trochidrobia punicea,* solid squares (two runs pooled); *Fonscochlea conica,* open circles; *Fonscochlea variabilis* form A, solid circles (runs for different populations of this species pooled). Error bars represent ranges of results.

At 24‰ salt water, with two exceptions (in which case a few snails were active at only one point in the experiment), activity was nil for all species throughout the experiment.

Deoxygenated water. The results are given in Table 13. In the control tubes, initially supplied with oxygenated water, activity generally decreased markedly by six hours, and only 26% of the snails (for all species pooled) were active by 20 hours. In four experiments, the snails in the control tubes were tested for survival, in the same manner as were those snails in the tubes with deoxygenated water, after 20 hours; 90% of these snails (all species pooled, N = 80) were alive, although some were sluggish. The decrease in activity and occasional mortality could have been due to deoxygenation of the water in the small 15 cc test tubes during the course of the experiment.

In the test tubes initially supplied with deoxygenated water, again activity decreased markedly during the course of the experiments, with only 26% of the snails (all species pooled) active at six hours, and 13% at 20 hours. Despite this decrease in activity, survival for all species, except *T. punicea,* was near 100% at all times. In general, the snails became active during the first ten minutes after being placed in oxygenated water. Survival of *T. punicea* was significantly less than that of all other species tested at four hours (all pairwise comparisons, Chi-Square Test of Independence, one-tailed, $P < 0.005$), six hours ($P < 0.05$) and 20 hours ($P < 0.005$). There were no significant differences in survival between any two of the other species.

Temperature. The results (Table 14) indicate that, in general, almost all individuals of all species tested remained active at 10–32°C., and a large percentage of individuals were active at 5° (76% for all species pooled), 35° (77%) and 37° (41%). At the lower end of the temperature range, the snails generally became more and more sluggish, whereas at the upper range of the temperature range, activity greatly increased and, at a slightly higher temperature, was followed by sluggishness and cessation of activity.

Considerable variation was seen in the instances in which several populations of a spe-

TABLE 12. Activity of snails over time in water of salinities of 6‰, 9‰, and 12‰. Ten snails were used in each experiment unless otherwise indicated. The approximate natural salinity of the water used in the experiments is given for each sample (calculated from the conductivity).
FS = Finniss Springs, CSRB = Coward Springs Railway Bore, BC = Blanche Cup.

Species (population)	Salinity	6‰ Number of hours						9‰ Number of hours						12‰ Number of hours						Date, time commenced
		1	2	3	6	12	24	1	2	3	6	12	24	1	2	3	6	12	24	
F. zeidleri (FS)	1.8	9	6	10	9	6	10	4	5	8	5	9	9	2	4	9	6	9	9	29.8 10:55AM
F. zeidleri (CSRB)	2	10	10	10	10	10	9	10	10	10	10	10	10	2	3	7	8	9	8	1.9 9:30AM
F. zeidleri (BC)	3.6	10	10	10	10	9	10	10	10	10	7	8	9	10	9	8	7	6	9	30.8 10:20AM
F. aquatica	3.6	10	10	8	10	9	10	8	8	7	7	8	9	9	6	6	5	3	7	30.8 12:52PM
F. accepta form B	1.8	10	10	9	7	7	9	9	9	9	7	4	10	8	2	5	5	5	9	29.8 9:10AM
F. variabilis (BC)[1]	3.6	6	9	9	9	6[1]	9	0	4	1	2	0[1]	0	0	0	0	0	0	0	31.8 10:50AM
F. variabilis (CRSB)	2	10	9	9	7	10	7	10	2	0	0	1	2	0	0	0	0	0	0	2.9 9:30AM
T. punicea	1.8	10	10	9	9	10	10	8	10	8	9	6	2	0	0	0	0	0	0	28.8 8:20AM

[1]11 specimens used

TABLE 13. Survivorship and activity of snails in deoxygenated water. Activity of snails in control tubes (initially supplied with oxygenated water) also shown. Twenty snails were used in each experiment unless otherwise indicated.
FS = Finniss Springs, BC = Blanche Cup, and CS = Coward Springs Railway Bore.

Species (population)	% of snails surviving Number of hours					% of snails active in tube Number of hours					% of snails active in control tube Number of hours					Date, Time Comm.
	1	2	4	6	20	1	2	4	6	20	1	2	4	6	20	
F. zeidleri (CS)	100	100	100	100	100	45	40	45	75	0	100	100	80	95	5	1.9. 11:05AM
F. zeidleri (BC)	100	100	100[18]	100[16]	100	87	15	30	0	0	100	90	90	85	80	30.8. 12:00PM
F. zeidleri (FS)	100	100	100	90	100	15	10	5	0	0	100	100	80	25	10	28.8. 10:30AM
F. accepta form B (FS)	100	100	100[19]	100	100	95	95	30	60	10	100	100	80	75	20	29.8. 10:55AM
F. variabilis (10 snails/tube)	90	100	100	100	100	30	30	40	10	0	100	100	100	45	0	31.8. 11:25AM
F. conica	100	100	100	90	100	60	90	90	30	0	100	100	100	90	50	3.9. 12:30PM
T. punicea	95	100	50	60	35	65	60	10	10	0	90	60	30	25	5	2.9. 3:00PM

[16]16 specimens used [18]18 specimens used [19]19 specimens used

cies were tested. For *F. zeidleri,* at 2° the Blanche Cup population had a significantly larger number of individuals active than did the other two populations ($P < 0.0005$ Chi-Square); at 35° the Coward Springs Railway Bore population had significantly larger number of active snails than did the other two ($P < 0.01$, Chi-Square); at 37°, the Coward Springs Railway Bore population had significantly higher activity than did the Blanche Cup population ($P = 0.025$, Fisher's Exact Test), which in turn had higher activity than did that of Finniss Springs ($P < 0.01$, Chi-Square); at 40 and 42° the Coward Springs Railway Bore population had a significantly higher activity than had the other two populations ($P < 0.0005$, Chi-Square). While *F. accepta* form B had significantly higher activity than did *F. ac-*

TABLE 14. Numbers of snails active at various water temperatures. Twenty snails were used for each experiment unless otherwise indicated.
FS = Finniss Springs, BC = Blanche Cup, CS = Coward Springs Railway Bore.

Species (population)	Temperature (°C)																				Date Comm.
	0	.12	.25	.50	1	2	5	10	15	20	25	30	32	35	37	40	42	45	47	50	
F. zeidleri (FS)	—	0	2	3	5	7	20	20	20	20	20	20	20	7	6	0	—	—	—	—	2.9
F. zeidleri (BC)	0	—	3	2	3	20	20	20	20	20	20	20	18	11	15	8	0	—	—	—	30.8
F. zeidleri (CS)	—	—	—	—	0	9	15	20	20[1]	20	20	20	20	19	20	20	1	0	—	—	1.9
F. aquatica	0	—	—	2	4	4	17	19	20	20	20	20	18	16	18	0	—	—	—	—	30.8
F. accepta form B	—	—	—	0	9	16	20	20	20	20	20	20	20	15	11	2	4	0[2]	—	—	1.9
F. accepta form A	—	—	0	2	3	5	19	20	20	20	20	20	20	20	20	10	4	0	—	—	3.9
F. variabilis (BC)	—	—	—	—	0[3]	1	4	20	20	20	20	19	20	20	19	3	0	—	—	—	30.8
F. variabilis (CS)	—	—	—	—	—	0	2	19	19[1]	20	20	20	20	20	20	16	5	0	—	—	1.9
F. conica	—	—	—	—	—	0	10	19	29	29	29	29	29	19	19	19	18	0	—	—	3.9
T. punicea	—	—	—	0	1	8	20	20	20	20	20	20	20	18	5	0	—	—	—	—	1.9

[1]14.5° [2].44° [3]1.5°

cepta form A (and *F. aquatica*) at 2° ($P < 0.005$), *F. accepta* form A had significantly higher activity at 37° ($P = 0.006$, Fisher's Exact Test) and 40° ($P < 0.01$, Chi-Square Test).

The *F. variabilis* population from Coward Springs Railway Bore had a significantly higher activity than did that from Blanche Cup at 40° ($P < 0.0005$, Chi-Square) and 42° ($P = 0.025$, Fisher's Exact Test), probably reflecting the higher water temperature at the bore.

There were no consistent significant differences in activity between *F. zeidleri* and the large aquatic *Fonscochlea* species at any temperature. *Fonscochlea aquatica* from Kewson Hill, though, did show a reduced level of activity in high temperatures relative to the other species: at 37° its activity was significantly less than that of all these other species (plus the small *Fonscochlea* species, $P < 0.01$, Fisher's Exact Test). *Fonscochlea conica* had a significantly higher activity than did *F. variabilis* at 42° ($P < 0.0005$, Chi-Square). *Trochidrobia purnicea* had significantly less activity at 37° than had all other taxa except *F. zeidleri* from Finniss Springs, *F. aquatica* from Kewson Hill, and *F. accepta* form B ($P < 0.005$, Chi-Square).

Submergence tolerance. All populations were tested for submergence tolerance except those from Coward Springs Railway Bore and Welcome Springs. For all of these populations, except *F. zeidleri* from Finniss Springs, nearly all of the snails were active throughout the experiment (at 72 hours, for all species pooled, 95% of the snails were active). *Fonscochlea zeidleri* from Finniss Springs showed reduced activity at 24 hours (40% of snails active), 48 hours (50%), and 72 hours (30%). The number of active snails for this population was significantly less than that of all other populations at all three of these time periods (for all pairwise comparisons, $P < 0.005$, $P < 0.05$, $P < 0.005$, respectively, Chi-Square).

Submergence preference. The results are given in Table 15. For two of the three *F. zeidleri* populations tested, those from Finniss Springs and Blanche Cup, over 50% of the individuals moved to the top of the plate; many moved far beyond the water meniscus and became dry. Although these two populations did not differ significantly in proportion of individuals on the top of the dish, the Blanche Cup population did have a significantly larger proportion of individuals on the bottom of the plate (32% v 8%, $P < 0.005$, Chi-Square). Both of these populations had a significantly larger number of individuals on the rim of the dish than did the aquatic population of *F. zeidleri* from Coward Springs Railway Bore, which had only 16% ($P < 0.025$, Chi-Square).

For *F. aquatica* from Kewson Hill and *F. accepta* form A, again more than half of the individuals migrated to the top (52% and 76%,

TABLE 15. Results of the submergence preference experiments for snails. "Bottom", "sides" and "top" refer to positions in the plate. Fifty snails were used in each experiment unless otherwise indicated. FS = Finniss Springs, BC = Blanche Cup, and CS = Coward Springs Railway Bore.

Species (population)	NUMBER OF SNAILS		
	Bottom	Sides	Top
F. aquatica	2	19	9
F. accepta form B (N = 103)	9	51	43
F. accepta form A	3	9	38
F. variabilis (BC)	27	17	6
F. variabilis (CS)	41	9	0
F. zeidleri (FS)	4	19	29
F. zeidleri (BC)	16	9	25
F. zeidleri (CS)	25	17	8
F. conica	18	32	0
T. punicea (N=52)	30	22	0

respectively), but it was noted that for these species, and for those discussed below, the individuals on the top of the dish tended to cluster at or just above the water level, in some cases actually dragging the meniscus upward, and did not dry out. The three large *Fonscochlea* aquatic taxa tested differed significantly from one another in proportion of individuals on the top of the dish. *Fonscochlea accepta* form A had a higher proportion (76%) than did *F. accepta* form B (42%, $P < 0.005$, Chi-Square), which in turn had a higher proportion than did *F. aquatica* (18%, $P < 0.05$, Chi-Square). For *F. aquatica,* a significantly larger proportion of the individuals stayed at the bottom of the dish (44%) than for both of the forms of *F. accepta* (6–9%, $P < 0.05$, Chi-Square).

Apart from 12% of the *F. variabilis* from Blanche Cup, none of the individuals of the small aquatic *Fonscochlea* species and *T. punicea* migrated to the top of the dishes. For all pairwise comparisons, except *F. variabilis* (Blanche Cup)–*F. aquatica* and *F. variabilis* (Blanche Cup)–*F. zeidleri* (Coward Springs Railway Bore), the proportion of individuals of these species on the top of the dish was significantly less than that of all other taxa tested ($P < 0.005$, Chi-Square). *Fonscochlea variabilis* from Coward Springs Railway Bore, in particular, tended to stay on the bottom of the dish, rather than the sides or top (82%, significantly higher proportion than that of all other species and populations tested, $P < 0.05$, Chi-Square).

Response to light. The results of these experiments are given in Table 16. Significant differences between runs, in the nine cases in which the experiments were repeated, were seen only for *F. zeidleri* (Finniss Springs and Coward Springs Railway Bore populations) and *F. accepta* (both forms).

Of the other species tested, *F. aquatica, F. variabilis,* and *F. conica* all tended to cluster in the dark zones (at least 78% of the individuals). *Fonscochlea aquatica,* in particular, showed this tendency, with an average, for the two runs, of 93% of the individuals clustered in the extreme dark zone. *Fonscochlea accepta* tended to be distributed more evenly between the light and dark zones and had a significantly lower proportion of individuals in the dark zones than did all of the above group of species (all pairwise comparisons, $P < 0.01$, Chi-Square). *Trochidrobia punicea* was the only species that showed a strong attraction to light, with an average of 85% (two runs) of the individuals in the light zones, and had a significantly larger proportion of individuals in the light zones than did all other populations and species tested (all pairwise comparisons, $P < 0.05$, Chi-Square).

DISCUSSION

Evolution and relationships of fauna

The attempt to explain the origin and distribution of the hydrobiid species in the mound springs raises three questions: that of the origin of the fauna, that of the mechanisms available for that fauna to achieve its present distribution, and that of the factors maintaining the present patterns. These questions are all discussed below in some detail.

Geological history: The geological history of the mound springs is poorly understood.

TABLE 16. Results of the light response experiments for snails. The significance level for difference in results between runs (when two runs were done for a taxon) is given (Chi-Square Test, unless otherwise indicated). One hundred snails were used in each experiment.
FS = Finniss Springs, CS = Coward Springs Railway Bore, BC = Blanche Cup.

Species (population)	NUMBER OF SNAILS IN GIVEN ZONES								
	Light	Light-Middle	Dark-Middle	Dark	Light & Light-Middle	Dark & Dark-Middle	S.L.	Date, Time Commenced	
F. accepta form A	41	6	11	42	47	53		28.8	
	50	14	17	18	64	35	P <0.02	28.8	6:20PM
F. accepta form B	23	16	14	47	39	61		3.9	8:45AM
	42	11	8	35	53	43	P <0.05	3.9	5:35PM
F. aquatica	1	0	0	99	1	99		30.8	
	2	4	6	88	6	94	NS (Fisher's Exact Test)	28.8	4:15PM
F. variabilis (BC)	11	0	3	86	11	89	—	31.8	
F. variabilis (CS)	2	2	2	94	4	96		2.9	2:50PM
	1	6	26	67	7	93	NS	1.9	
F. conica	14	7	24	55	21	79		3.9	2:50PM
	10	9	17	64	19	81	NS	3.9	
F. zeidleri (FS)	58	12	8	22	70	30		2.9	10:25AM
	7	3	15	75	10	90	P <0.001	28.8	10:55AM
F. zeidleri (CS)	4	27	28	41	31	69		1.9	8:45AM
	27	30	30	13	57	43	P <0.001	2.9	1:00PM
F. zeidleri (BC)	16	25	32	27	41	59	—	30.8	
T. punicea	67	14	9	10	81	19	NS	2.9	11.25AM
	74	15	6	5	89	11		28.8	12.30PM

Three large hills in the middle of the Lake Eyre group, Hamilton Hill and North and South Beresford Hills, are extinct mound springs. They were formed on a weathered Pleistocene land surface which lay 10–50 m above the present land surface (Wopfner & Twidale, 1967). Jessup and Norris (1971) have suggested that these fossil mounds are approximately equivalent in age to the Etadunna Formation (Miocene) but Wopfner and Twidale (1967) suggest that they commenced activity when gypsite sediments were being deposited over much of the Lake Eyre Basin between 80,000 and 40,000 years ago. Wopfner and Twidale postulate that spring activity began after uplift of the eastern rim of the Great Artesian Basin, when the wetter Pleistocene increased the amount of water held in the aquifers. They suggest that the (Pleistocene) freshwater limestones and travertines were formed in "shallow pools surrounding these springs." They also record reed casts and *"Coxiella"* from the limestones. It is likely that at least North Beresford Hill was raised at least several metres above the land surface that existed at that time. The fossil snails found in the limestones are closely similar to those living in the mound springs nearby, both *Fonscochlea* and *Trochidrobia* being present (i.e. apart from one very small site on North Beresford Hill, they are not the salt lake-inhabiting *Coxiella*). Many Recent springs have similar snail and plant "fossils" in the limestones composing their mounds. We favour a Pleistocene age for these springs because of the lack of erosion on them.

Habermehl (1982) has briefly discussed the theories that might account for the greater height and considerable size of the extinct mounds represented by Hamilton and Beresford Hills. He argues that the "great and ancient" mounds are related not to a much more abundant water discharge but to prolonged, stable hydraulic conditions and that later unstable conditions led to lower, relatively small mounds.

A drier, windier period in the Quaternary followed and the land surface was lowered partly by deflation and partly by erosion fol-

lowing tectonic movements (Wopfner & Twidale, 1967). The formation of new springs at lower levels ensued in a stepwise manner (Habermehl, 1980, 1982) following the progressive lowering of the pressure heads in the spring areas. Springs will tend to form at lower levels further reducing the pressure head in higher springs. Reduced flow will cause the outlets to clog and hasten the extinction of the spring and clogging is accelerated by vegetation trapping windblown sediments (Habermehl, 1980, 1982).

As erosion lowers the ground surface the north-dipping aquifer is moved, relative to the ground surface, farther north. Thus if any Tertiary springs existed they might have been located to the south of the present springs. To date no evidence of such springs exists, with the possible exception of some fossil hydrobiid snails (Ludbrook, 1980) found in limestones, of presumed Miocene age, that cap plateaus near the Billa Kalina homestead approximately 50 kilometres south of the nearest active mound springs. Ambrose and Flint (1981) have interpreted these limestones as part of a Miocene lake more than 100km wide. It is possible, however, that artesian springs could have been associated with this lake just as they are today in several dry salt lakes in the Lake Eyre basin. Some evidence for this view is the general similarity of the Billa Kalina snails to the large species of *Fonscochlea* and their apparent concentration in large numbers only in a small area, a few tens of metres in extent, about 4km north of the Billa Kalina homestead, and their rarity or absence elsewhere in the outcrop (our observations). Casts and moulds of snails similar to those found at Billa Kalina are also known from Malbooma to the southwest of Billa Kalina (Ludbrook, 1980; verified by W.F.P.).

At least two other species of presumed Miocene hydrobiids are known from nonmarine limestones in the Northern Territory and western Queensland (one recorded by McMichael, 1968, the other an unpublished observation by W.F.P.) but these do not appear to have any similarity to the mound spring species.

There is, as far as we can ascertain, no direct evidence for mound spring activity in the Paleogene, although this is hardly surprising given the climatic, erosional and tectonic changes that have occurred. The unusual fauna that the springs contain does suggest, however, that artesian springs or some equivalent habitat, might have been in existence for much of the Tertiary. Early to Middle Tertiary uplift in the Great Divide (Ollier, 1982) on the eastern side of the Great Artesian Basin could have provided the water head necessary for spring activity.

During the Early and Middle Miocene the vegetation of much of the interior of Australia was dominated by temperate rainforest (Kemp, 1978; Martin, 1978) and the climate was warm and humid (McGowran, 1979). By the Late Miocene to Early Pliocene marked aridity generally correlated to the marine transgression (Bowler, 1976, 1982) but it was not until about one million years ago that southern Australia became arid. Periods of wet and dry climates followed four or five times during the last 500,000 years. The climate over the last 400,000 years underwent very large and, perhaps, rapid hydrologic oscillations affecting large areas of the continent (Bowler, 1982). The considerable variation between wet and dry imposed a set of new stresses on habitats and the animals and plants living in them.

The main "imprint of aridity on the landscape" of Australia is of Quaternary age with a peak period about 18–16,000 B.P. (Bowler, 1967, 1982). Nevertheless Bowler (1967, 1982) points out that the trend towards aridity began as early as the Middle Miocene. Kemp (1978) proposed that the climate during the Miocene became increasingly arid in the north and northwest of Australia. The Miocene xerophytic fossil flora from near Billa Kalina supports this hypothesis (Ambrose & Flint, 1981). Thus, although it is possible that adequate freshwater habitats existed in central Australia up until the formation of the first known mound springs, these habitats would have, presumably, tended to become increasingly scarce and reduced in size. If the mound springs were in existence throughout this period of change they would have provided an aquatic refuge for animals that would otherwise have perished at the first onset of aridity (Ponder, 1986; DeDeckker, 1986).

Relationships of mound-spring invertebrates: The two genera of the Hydrobiidae found in the springs between Marree and Oodnadatta are endemic to these springs. *Trochidrobia* is not closely related to any known genus and its general relationships are unclear. The other genus, *Fonscochlea*, is closely related to an undescribed genus in Dalhousie Springs to the north of Oodnadatta, and is a member of the Australasian *Hemistomia* group of genera (Climo, 1974; Ponder,

1982). The female reproductive system and the radular characters of species of *Fonscochlea* set it apart from any others in the group with the exception of the undescribed genus from Dalhousie Springs.

The crustacean fauna also contains some endemics of considerable interest. The phreatoicid isopod *Phreatomerus latipes* (Chilton, 1922) and the ostracode *Nagarawa dirga* DeDeckker, 1979 (family Cyprididae) both belong in endemic subfamilies. Two additional endemic ostracodes have been found amongst the material collected on this survey (DeDeckker, pers. comm.).

The Phreatoicoidea occur throughout Australia and are best represented in Tasmania (Williams, 1981). *Phreatomerus* is probably the least specialized and least typical of the surface-living phreatoicids (Nicholls, 1943) and is the only member of this group known to live in a desert environment. The Cyprididae contain the majority of the nonmarine ostracodes and have a worldwide distribution.

An endemic amphipod is an undescribed species of *Austrochiltonia* and is morphologically very similar to congeners living in other habitats in South Australia, including hypersaline environments (W. Zeidler, pers. comm.).

A small macrostomid flatworm was discovered during the latter part of our study at Elizabeth Springs and Old Finniss Springs and is now described (Sluys, 1986). It is one of only two records of this order from Australia.

A substantial microfauna and microflora exists, at least in some spring groups, and is largely unstudied (Mitchell, 1985; Ponder, 1986).

Evolution of species within mound springs: The mound-springs fauna probably became adapted to living in artesian springs early in its history, given the lack of similar faunas in freshwater ecosystems, including non-artesian springs, in central Australia (personal observation, W.F.P.). In addition, the fauna of mound springs does not live in naturally occuring water holes, dams or bore drains, with the exception of the old, large artesian bore at Coward Springs railway siding. Springs in the Flinders Ranges have been extensively sampled by one of us (W.F.P.) and W. Zeidler, as have the artesian springs to the east of these ranges. No closely related invertebrates have been found in these springs. One of us (W.F.P.) examined the artesian springs in the Queensland part of the Great Artesian Basin and, although some hydrobiids were discovered, they are not congeneric with the South Australian species.

Their present distribution, which generally coincides with the distribution of the major spring groups (Table 1), suggests that the species had their origin in springs with a similar grouping to those existing at present. The location of the faults responsible for the creation of many of the springs might have resulted in a relatively stable pattern of spring development. There is certainly little evidence to suggest that the groups and complexes of mound springs existing today extended much beyond their present distributions in the recent past. Extinct mounds are found in every group but, as far as we know, very few or none are found between them.

Small, isolated springs should be ideal habitats for speciation, as in the case of the fish fauna of the springs of western North America (Miller, 1950; Turner, 1974; Soltz & Naiman, 1978; Naiman & Soltz, 1981). Migration of small numbers of individuals to such a habitat could, in theory, result in rapid genetic change (Mayr, 1942, 1954; Templeton, 1980). According to some workers (e.g., Wright, 1931, 1978; Crow & Kimura, 1970; Cohan, 1984), the subdivision of a population into isolated units will result in genetic differentiation, even in the absence of different selection pressures, owing to random genetic drift. Others (e.g., Cain, 1977) have argued strongly against using drift as an explanation as it cannot be proved.

Apart from the endemic forms at the well-isolated Emerald and Big Cadnaowie Springs (*F. accepta* form C and *F. zeidleri* form B) there is, surprisingly, no observable local endemism among minor spring groups or isolated springs. There is, however, minor differentiation between populations, not all of which might have a genetic basis, but this differentiation is subtle and difficult to measure. Why have these local forms not progressed to the point at which distinct morphological taxa can be recognised and why do other populations not appear to have markedly differentiated? Five scenarios are briefly considered below that may account for these observations.

First, the mound springs only recently became subdivided into groups. Whereas some extinct mounds can be recognised between existing groups of springs, there is little evidence to suggest that there was much greater continuity of springs in the recent past (see

above). Spring formation requires suitable geological conditions, faulting of confining beds or outcropping of aquifer that do not appear to be met in areas outside the present spring groups.

Second, there is a high level of gene flow (see Slatkin, 1985, for a recent review) between populations. This might be occurring between populations inhabiting adjacent springs, or even springs in the same group, in a variety of ways. Crossing of outflows during flooding or the accidental transportation on large mammals (including man) and birds as they move from one spring to another are obvious ways for snails to be dispersed. Such dispersal, resulting in gene flow, is unlikely, however, between groups separated by more than a few kilometres (e.g., between Welcome and Davenport Springs, Appendix 1, Figs. 62, 63B) because of the probability of dehydration during transport, as indicated by the desiccation experiments. In addition there are two important steps after the transportation of an individual to a new location: the successful establishment of this individual and then its interbreeding with an individual in that population.

While we have no information on migration rates between any springs or spring groups, it seems likely, considering the available dispersal agents and mechanisms, that there would be a low level of interchange between all but adjacent springs in the same group, but virtually none between groups. A higher level of interchange might be expected to result in the mixing of species between the spring complexes but there is no evidence that this occurs. There might be, however, other reasons that such immigration, if it did occur, might fail (see discussion below on community structure). Dispersal agents are discussed below. Slatkin (1985) points out that differences in levels of gene flow cannot account for morphological stasis and that very low levels of gene flow do not allow the spread of new combinations of genes to other populations (see also the fourth scenario).

Another consideration is that the "superpopulation" represented by the spring group, composed of discrete populations in each spring, is probably the level at which evolution is occurring. If the population of a single spring differentiated, the chances of this genome's being successfully transferred to other populations within the life of the population might be small, particularly in the case of the relatively unstable sand mound springs and those periodically devastated by floods. Slatkin (1985) points out that the extinction and recolonization of local populations is a form of gene flow and might be more effective than dispersal between established populations in preventing local differentiation.

In the third scenario the fauna only recently invaded the springs and is still differentiating. The complexity of the communities, the unique fauna and the existence of probable Pleistocene fossils at Hamilton Hill and the two Beresford Hills are but some of the lines of evidence suggesting that the fauna has some antiquity. It is, however, possible that some of the spring groups might have acquired their fauna recently from other, older spring groups.

Fourth, genetic variability exists but is not readily observed in the phenotype. Hydrobiid snails are not richly endowed with the kinds of morphological characters that provide clues to minor differentiation. Our measurement data shows that some populations differ significantly from the rest of the species in one or more characters. Electrophoretic studies might provide useful information about interpopulation differentiation but have not been attempted in this study. Phenotypic variation in some populations might possibly have a genetic basis and probable genetic differences occur. For example, a number of albinos were observed in a sample from one of the springs in the Elizabeth Springs group but were very rare in other populations. In another population from Elizabeth Springs the right tentacle in both sexes was much longer than the left in a high proportion of the sample. These observations suggest that some degree of genetic differentiation exists between populations.

Fifth, there is very low genetic variability, i.e. a very stable genotype. Speciation accompanied by very low levels of genetic divergence, as determined by electrophoresis, together with marked phenotypic differences, is known to occur in some desert fishes (Turner, 1974). Turner (1974) suggested that this stability was due to the fact that electrophoresis samples a portion of the genome coding for a coadapted "core" of enzymes that have not been affected by selective pressures in the evolution of allopatric species. There is a large body of data suggesting that the structural genes sampled by electrophoresis are not the genes involved in the speciation process. In the case of the moundspring snails, there might be genetic and phe-

notypic stability coupled with low level intra- and interpopulation genetic variability.

Ehrlich and Raven (1969) suggest that failure to speciate is not caused by excessive gene flow but by uniform selection regimes over the entire range of the species. The diversity of spring types and of habitats within the springs, appears, however, to have resulted in little ecophenotypic variation (with a few exceptions, see below). Perhaps the habitat variation encountered by the snails in any one spring is sufficiently broad and variable to counter the selective pressures associated with local habitat and microclimate differences in different springs. A generalist genotype might well have considerable selective advantages in such a system.

The densities of the snails and other invertebrates in many springs can be very high (> 1 million per sq.m. in Blanche Cup Spring) and the total number of snails in any spring of reasonable size could therefore be considerable. Thus, given these circumstances, the snails inhabiting the average spring cannot be equated with the classic, small population favoured by some geneticists as the focal point of evolutionary change. However, when the springs were first colonised, or following an event causing destruction of the majority of the population, the population sizes would have been small and the founder effect (Mayr, 1954) might affect genetic change then (although see Barton & Charlesworth, 1984, who have questioned the evolutionary importance of this effect). A rapid increase in numbers, a stable, generalist genome and no deviation from the supposedly normal range of environmental parameters would presumably largely negate the potential for a founder effect to operate.

In order that some of the above ideas can be tested we put forth two hypotheses.

The first of these is that the generally observed phenotypic uniformity of the mound-spring snails throughout their ranges is due to a low level of genotypic variability, with environmental conditions generally having little effect on the genome. This idea can be readily tested by comparing electrophoretically several populations within the range of the species and from different spring types.

The second hypothesis is that differentiation between populations is reduced because most populations are large and each is relatively short lived. This can be tested by, first, comparing the level of genetic difference within a spring group between large populations (in large springs) and small populations (in small springs), second, comparing genetic differences between relatively long-lived springs on hard mounds and short-lived springs on sand mounds and third, comparing genetic differences in populations in old mound springs with those in young springs in the same group.

Dispersal: The dispersal mechanisms available to the mound spring aquatic fauna can be divided into three main categories: flood dispersal, transportation by other animals and wind dispersal.

Flooding is a periodic occurrence in the study area (Kotwichi, 1986), with, perhaps, a major flood every ten to 25 years and significant local flooding every eight to ten years. Local storms produce local flooding on a smaller scale. There are few data, apart from the rainfall information from Marree and Oodnadatta, on the detailed rainfall in the area.

On a broad scale the direction of flow of the flood channels indicates that flood transportation alone would not account for the present distribution of the hydrobiids. The drainage system cuts across most of the groups of mound springs such that flooding, apart from local transportation within a spring group, would tend to carry organisms away from suitable habitats rather than to them. Glover and Sim (1978b) believe that fish are primarily distributed by flooding. This might be true for the fish, which are much more mobile than the endemic invertebrates. The fish could presumably survive in Lake Eyre South, when flooded, and reach adjacent drainage channels. The fish are also able to survive in creek-bed pools and bore drains but none of the mound-spring endemic invertebrates appears to be able to do this, with the notable exception of those in the Coward Springs Railway Bore. W. Zeidler (pers. comm.) has found a single specimen of what appears to be the mound-springs *Austrochiltonia* in Charles Angus Bore near Hermit Hill and another solitary individual in Finniss Creek following the 1974 floods. These observations might give extra weight to the flood-dispersal hypothesis but do not represent exceptions to the rule that the invertebrate fauna is restricted to natural springs.

In our view the most important type of dispersal is accidental transportation by other animals. This type of dispersal has long been known to be important in small, flightless, aquatic animals (see review by Rees, 1965, for examples involving molluscs). Birds are

the obvious choice for long-distance dispersal, invertebrates being attached to their feet, legs and feathers as they feed in the springs. Their relatively rapid movement would enable them to transport individuals successfully between springs at least occasionally. Ponder (1982) has argued that this method of transportation was the most likely in the establishment of the Lord Howe Island hydrobiid fauna and involved transportation over at least 500 km of ocean. Mammals, such as kangaroos, might also carry invertebrates from one spring to the other within the same complex. Since the advent of European man, cattle, camels and horses are certainly important in this regard. Man himself would carry living snails in mud attached to his feet; certainly biologists' boots would be excellent dispersal agents. There are instances in which large aquatic insects, particularly water beetles, have been known to transport molluscs but the aquatic insects in the springs in the study area are small.

Wind dispersal might be important, although we have no data to support this contention. Strong winds are common in the area and could disperse animals such as the ostracodes and snails. It is unlikely that the larger crustaceans and snails would survive such dispersal except over short distances (see results of desiccation experiments for data on snails).

The hypothesis that species diversity is stabilized as the result of balanced rates of species immigrations and extinctions (Preston, 1962; MacArthur & Wilson, 1967) has received strong support. The number of species remains constant but because of extinctions and immigrations the species composition constantly changes. Faeth and Connor (1979) point out that the existence of immigration and extinctions resulting in "turnover," i.e. changes in species composition, while the species number remains constant, is crucial to this theory of "dynamic equilibrium." It is of interest in this regard to note that the springs within each spring complex have essentially a uniform fauna, the total number of species and the species composition being the same for most springs. If the "dynamic equilibrium" model be accepted for the springs, this uniformity appears to be in contrast to the observation that there is a low level of interchange between springs. There are, however, different distributions between spring complexes, suggesting that these major groups of springs can be regarded as archipelagos with very low rates of interchange, whereas spring groups can be regarded as "super islands" on which interchange might be sufficient to maintain the constant species composition observed.

Migration into very isolated springs from other springs appears to have occurred in only two cases. Emerald and Big Cadnaowie Springs have, in both cases, only a single snail species (Big Cadnaowie Spring does not have isopods or amphipods) and in both cases the hydrobiids there are clearly derived from species found in other spring groups. This situation appears to meet the predictions of the theory of island biogeography (MacArthur & Wilson, 1967) which state that the effect of area (in this case, size of spring) decreases as distance from the source areas increases and that islands (i.e. springs) at great distances from species sources will have few species, if any.

Environmentally-induced variation: The most obvious variation encountered in the mound-spring snails is the reduction of body size in some populations or parts of populations. Examples are the small form of *F. variabilis* (see discussion under *F. variabilis* form A) and the stunted forms of *F. aquatica, F. conica* and *F. zeidleri* occurring at Kewson Hill (Fig. 53).

Fryer *et al.* (1983) suggest that simultaneous change in several taxa would be a likely phenotypic response to environmental stress. It is thus likely that attainment of similar shell forms by the three species of *Fonscochlea* in the springs on Kewson Hill are similar ecophenotypic responses to the same environmental stress, presumably, in this case some factor related to the small, shallow, steep springs and the lack of shade. It is, however, noteworthy that apparently major differences between the springs (e.g., size of spring, amount of vegetation, substrate type, conductivity; total dissolved solids, pH, slope of outflow, etc.) do not appear to induce marked differences in the phenotype in most instances. An exception to this would be the stunting of some specimens of *F. zeidleri* in the outflows of several of the taller mounds in the middle group of springs (e.g., Blanche Cup, Horse Springs East).

Ecology and behaviour

There is evidence, in most springs, of a difference in the relative abundance of the species found in different zones in the spring. The

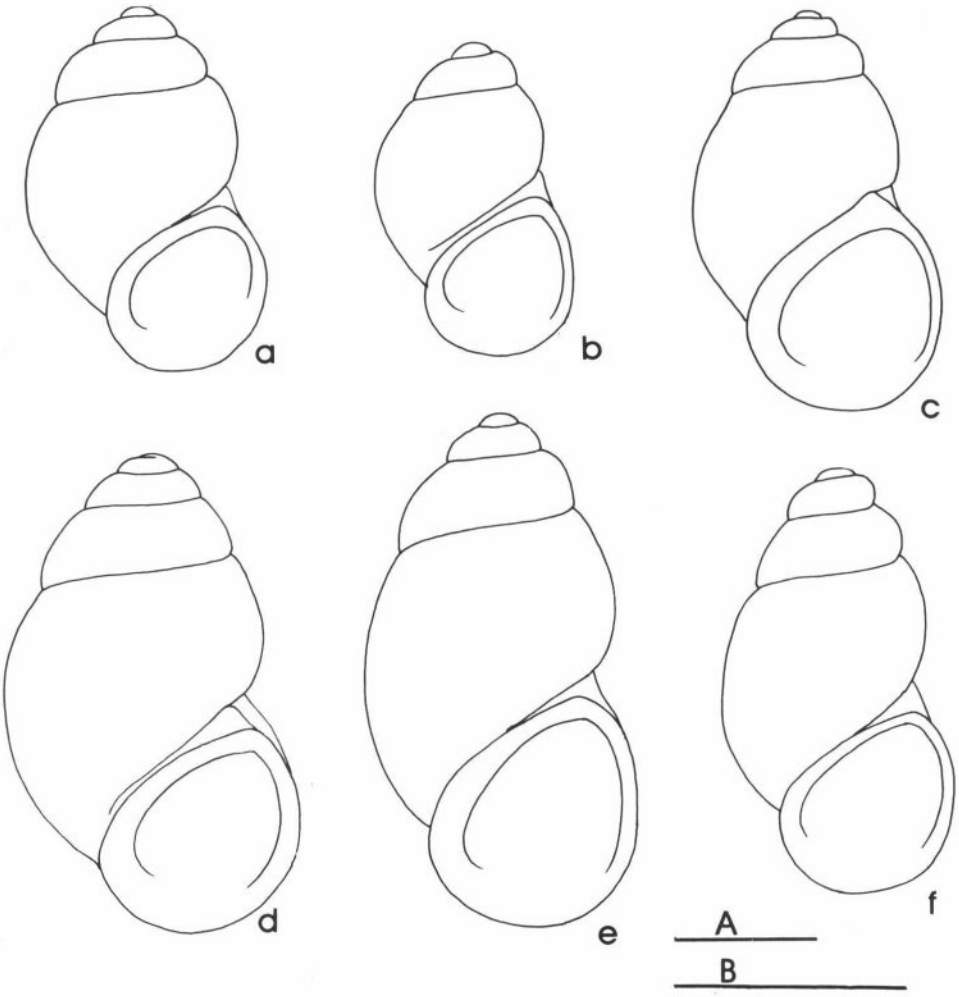


FIG. 53. Comparison of shell shape between specimens from Kewson Hill Springs (Stn 742, a–c) and Elizabeth Springs (Stn 024, d–f; 767, e).
a,d. *Fonscochlea zeidleri* form A (a, AMS, C.152976; d, AMS, C.152975).
b,f. *Fonscochlea conica* (b, AMS, C.152971; f, AMS, C.152972).
c,e. *Fonscochlea aquatica* cf. form A (c, AMS, C.152973; e, AMS, C.152974).
Scale: 1mm; a,c–e Scale A; b,f Scale B.

percentage frequency data obtained for a number of springs representing most of the spring complexes is plotted in Fig. 54. This shows that there is a considerable amount of variation between springs, and that in all of the examples and in virtually all of the springs sampled there were substantial differences between the zones sampled, i.e. the head of the spring, the upper outflow and the outflow proper.

The difference in habitat preference between *F.zeidleri* and the large aquatic species of *Fonscochlea* is illustrated in Fig. 55. These data clearly illustrate that *F.zeidleri* prefers exposure on the edges of the springs and the large aquatic species prefer submergence.

One of the most noticeable aspects of the mound-spring fauna is that it is generally restricted to the outflows and spring head; pools and swamps at the base usually contain very low numbers of the spring endemics, with the possible exception of isopods. These lower parts undoubtedly experience the greatest environmental stresses, salinity and temper-

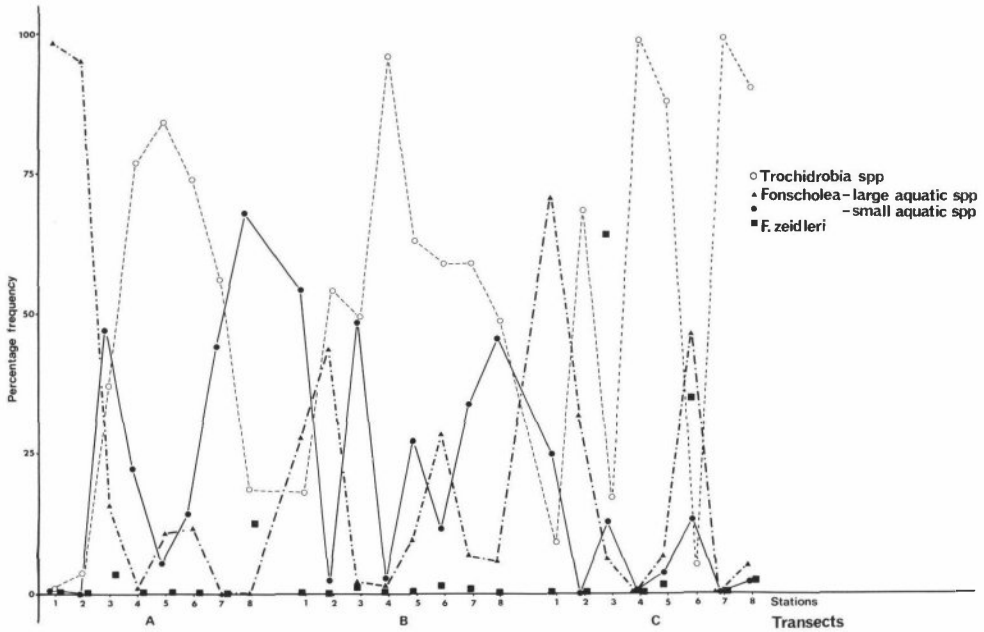


FIG. 54. Percentage frequencies of hydrobiids in three zones, demonstrating lack of any preference for a particular zone by any of the main aquatic groups, large aquatic *Fonscochlea*, small aquatic *Fonscochlea* and *Trochidrobia*. Data summarized from eight springs. Zone A, head of spring; Zone B, upper part of outflow; Zone C, middle to lower part of outflow. These qualitative samples were taken mainly in the water, hence the low numbers of *F. zeidleri* in most of the counts.
1, Welcome Springs (756); 2, Old Woman Spring, Hermit Hill (733); 3, Horse Springs East (748); 4, Little Bubbler Spring (744); 5, Julie Springs (772); 6, Strangways Springs (679); 7, Francis Swamp (717); 8, Hawker Springs (670).

ature fluctuations, and would be more ephemeral. Behavioural adaptations and/or physiological responses are probably responsible for ensuring that the animals remain in the most favourable parts of the spring but we have little information on the nature of these responses. The information we do have was obtained from the simple physiological experiments that were carried out in the field and described above (see physiology section of methods and results).

Hydrobiids generally feed by removing from sediment particles bacteria and diatoms that they ingest. The size of the particles has been shown to be correlated with the size of the snail in species of *Hydrobia* (Fenchel & Kofoed, 1976). It is possible that a similar relationship will be found in the mound-spring hydrobiids.

We have, at this point, no information on growth rates, fecundity or mortality. Egg capsules containing a single egg are laid singly and attached to the substrate or to vegetation. One species of *Trochidrobia (T.punicea),* places egg capsules in the umbilicus of its shell or (possibly) in that of other individuals of the same species. Mature gonads and the presence of juveniles in samples collected in different seasons suggest that the snails might be reproductively mature all year round. Egg capsule production appears to be low as these are uncommon in samples. Certainly the number of capsules produced in the laboratory is very small.

Community structure: The general pattern involving the presence of one large aquatic species, the lone amphibious species and one small aquatic species of *Fonscochlea,* as well as one or sometimes two species of *Trochidrobia* in each spring (Table 1) is so well established that it could be argued that the niche potential of the springs, as far as the hydrobiid snails are concerned, is fully exploited. Further species packing would presumably involve either dietary or microhabitat shifts or

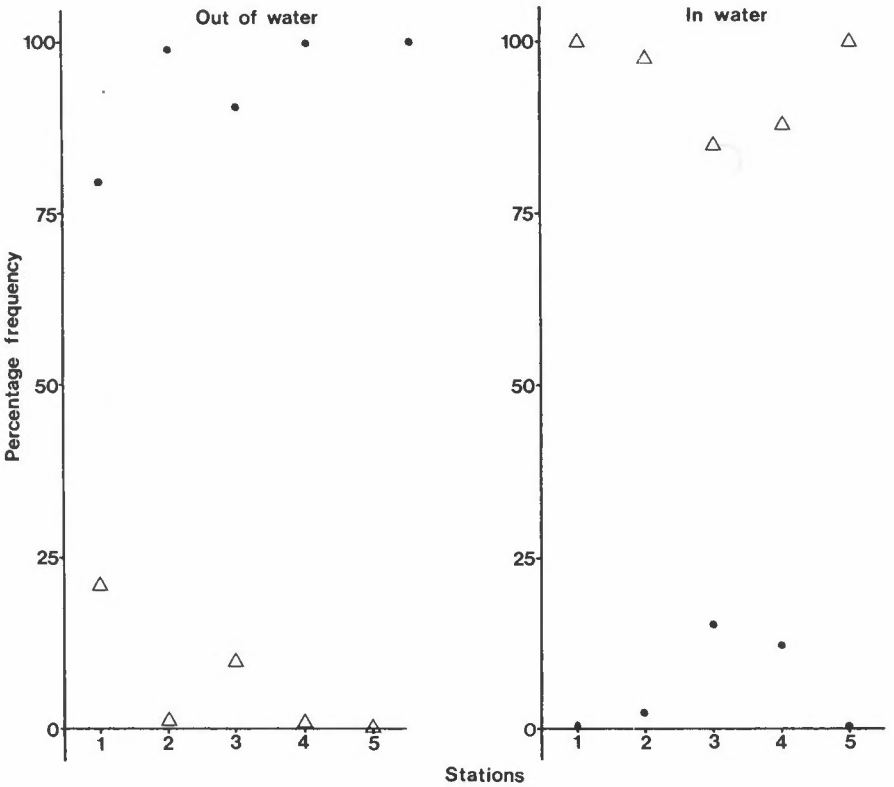


FIG. 55. Percentage frequencies of *Fonscochlea zeidleri* form A, closed circles; large aquatic species *Fonscochlea accepta* and *F. aquatica,* open triangles, out of, and in, water in five springs. Data from quantitative samples. 1, Welcome Springs (755); 2, Julie Springs (772); 3, Elizabeth Springs (771); 4, Jersey Springs (770); 5, Hawker Springs (670).

further reduction or increase in body size. In order that a sufficient size separation be achieved to allow more species to "fit" into the community, the snails would have to reach sizes close to the limits observed in hydrobiids. With such a tight-knit community structure, the successful introduction of species from other springs into springs with an established fauna would seem to be unlikely.

There are several views on the maintenance of species diversity in communities. One school argues that resources are limiting and therefore coexisting species must differ in the utilization of these resources to avoid competitive exclusion (e.g., Roughgarden, 1983). Another school argues that competitive exclusion does not occur because densities of dominant potential competitors are kept low by predation or some other form of cropping (Paine, 1966; Connell, 1970), or by environmental disturbance (Connell, 1972; Dayton, 1975).

The mound-spring hydrobiids appear to conform, in the main, to the limited resources-species packing model. According to the limited resources school several competing species can more easily outcompete and eliminate a species than can a single competitor (MacArthur, 1972). Thus, with increasing numbers of neighbouring species sharing the same niche space the observed overlap would be expected to decrease (Lande, 1980).

Firstly, the snails and other invertebrates often achieve very high densities (> million per sq m in their most favoured areas). Densities can be even higher in summer because of increased evaporation causing habitat shrinkage. These high densities suggest to us that competition could be an important factor in this ecosystem. The maximal number of species in any one spring is five, as in Freeling Springs and some of the northern group of springs, with four being the usual number.

Generally there are three species of *Fonscochlea* and one of *Trochidrobia,* but Freeling Springs, and some northern springs, have two species of *Trochidrobia* (Table 1).

Because five species can coexist in a few springs, there would appear to be possibilities for further addition of species, at least in *Trochidrobia,* in other springs south of Freeling Springs, which have only one species of this genus. This addition has indeed occurred, one of the Freeling Spring species *(T.minuta)* being found in the closest springs. The reason that *T. minuta* is absent from the other springs is not clear, but a recent dispersal event is, in our opinion, the most likely hypothesis. If this be the case, detailed studies on the interactions between the two *Trochidrobia* species in these springs would be of considerable interest.

Presumably the Freeling fauna evolved in greater isolation than prevails today, allowing the evolution of the endemics that this group of springs contains. The two species of *Trochidrobia* were presumably allopatric and, when included together in the same system, previous divergence in size or in behaviour might have been accentuated, allowing the coexistence of these species. *Trochidrobia punicea* and *T.smithi* are similar in size to each other and there do not appear to be any noticeable differences in habitat preference between them. These factors suggest that the long-term coexistence of *T.punicea* and *T.smithi* following an introduction would be unlikely, following the competitive exclusion principle (Gauss, 1934; Lack, 1947). This principle has, however, been questioned by some workers (e.g., Ayala, 1970) who argue that competing species can coexist even with limited resources. The widely divergent reproductive anatomy in these two otherwise almost indistinguishable species is difficult to explain without invoking a past sympatry. Perhaps they were sympatric in an environment in which resources were not limited or in which they were separated ecologically. It is possible that such coexistence is indeed occurring now, as species determinations have been made by dissecting only a small number of specimens from each locality.

Interaction between the small species of *Fonscochlea* and species of *Trochidrobia* might be avoided by subtly different choices of habitat. Preliminary analysis of the distribution of the snails in the springs shows that they are distributed differently, although with some overlap. Percentage frequency data of snails in various zones within the springs suggest that springs that have fewer species show less zonation in the fauna, thus favouring the idea that the observed distributions are the result of interaction between species. A third possibility, differential mortality, seems unlikely.

Differences in body size allowing differing use of limiting resources, such as food and shelter, are one way in which competition between sympatric species might be reduced (Hutchinson, 1959; Fenchel, 1975; Roth, 1981; Williams, 1972). Whenever size differences do not occur the species must differ in other ecological dimensions. The species of *Fonscochlea* are separated into two size groups, one consisting of *F.accepta, F.aquatica* and *F.zeidleri,* the other, smaller in size, consisting of *F.variabilis, F.billakalina* and *F.conica* (Table 17). Likewise, the two sympatric species of *Trochidrobia* at Freeling Springs show a marked difference in size (Table 17), although the size difference is not so large as in the species of *Fonscochlea.* This difference is even less between the sympatric species of *Trochidrobia* in the northern springs. These species seem to predominate in different parts of the outflow, thereby probably reducing the level of interspecific interaction. One weakness in this model is that juveniles of the larger species would obviously overlap with the small species, although this would not be significant if the juveniles reached maturity quickly and the adults were long-lived. Unfortunately we lack growth rate and lifespan data. Fenchel's (1975) demonstration of displacement in size in two sympatric species of *Hydrobia* has been contested by more recent work (Roth, 1981; Simberloff & Boecklen, 1981; Levinton, 1982; Cherrill & James, 1987). Some indirect evidence indicating size displacement was obtained in a study of the hydrobiids of Lord Howe Island (Ponder, 1982).

Variation in environmental factors might allow a greater species diversity than would a system that is stable and shows little or no variation (Levins, 1979). The large species of *Fonscochlea* are separated ecologically whenever they occur together, as *F. zeidleri* is amphibious and lives in the same spring with only one of the other large species that is aquatic. As noted above, the habitat separation of these two species was very noticeable in all of the springs examined (Fig. 55). At the Coward Springs Railway Bore, in which *F.aquatica* is not found, the normally amphib-

TABLE 17. Comparison of shell heights and ratios of shell heights for pairs of sympatric congeners.

Species	Station	Shell Height (mm) $\bar{x}$	s	$\bar{x}$(large)/$\bar{x}$(smaller)
F. accepta form A	755	3.43	0.17	1.92
F. conica		1.79	0.16	
	003	3.16	0.15	1.48
		2.14	0.13	
F. aquatica form A	739	4.31	0.17	1.92
F. variabilis form A		2.25	0.21	
F. aquatica form A	032–033	4.24	0.18	1.47
F. variabilis form B		2.88	0.28	
F. aquatica form A	679	3.96	0.27	1.45
F. billakalina		2.73	0.15	
F. aquatica form A	764,020	3.93	0.18	1.80
F. conica		2.18	0.24	
F. aquatica form B	045,046	3.88	0.15	1.41
F. variabilis form C		2.75	0.34	
	665	4.23	0.22	1.57
		2.69	0.21	
T. inflata	043	1.49	0.16	1.35
T. minuta	045	1.10	0.06	

ious *F. zeidleri* lives both on the edges and in the water to a depth of several centimeters.

Species in the second group, the small species, have never been found in the same spring, although they do live in closely adjacent springs in the Blanche Cup complex, and are markedly different in size from the larger aquatic species sharing the spring.

Predation does not appear to be significant in determining the densities of the aquatic invertebrates in the springs. Predation by birds might occur, but we know of no other potential predators apart from small mammals and reptiles. Predation from all of these sources would, however, be at a low level, given the small numbers of these animals in the vicinity of the springs. Birds have regularly been observed feeding on the springtails where the endemic invertebrates are normally rare or absent but aquatic insects are common. They are rarely seen feeding in the outflows in which the endemic invertebrates are abundant. The fishes in the springs do not appear normally to eat the snails, their gut contents being mostly vegetable matter, snails only rarely being found (J. Glover, pers. comm.).

There is, in the mound springs, marked diurnal and seasonal variation in temperature (Ponder, 1986; Figs. 3, 50), some variation in rates of flow (from observation), evaporation (and hence salinity) and, presumably, algal cover etc., as well as spatial variation in substrate, slope, vegetation, water flow and depth within and between springs. Although this heterogeneity is a characteristic feature of the springs, this ecosystem, compared with many other aquatic ecosystems, particularly in arid environments, is probably a relatively uniform one (Naiman, 1981). Any analysis of the niche limitations of individual species would have to take account of these temporal oscillations and the spatial complexity. In addition, destruction of part of the population can occur from sudden changes in flow rate and/or unusually high evaporation, leaving all or part of the outflow dry. Trampling by animals not only reduces numbers indiscriminately (although, perhaps, favouring species living beneath rock), but also results in temporary habitat destruction. Floods also have a devastating effect on springs in water courses, as observed at the Hermit Hill complex following the January, 1984, floods. An analysis involving all of these variables is well beyond the scope of this paper. It could be inferred, however, that this ecological variability might be a contributing factor in allowing a rather high number of closely similar species to coexist. Indeed it is very unusual to have three sympatric congeners of hydrobiids. It might also be suggested that, if instability were shown to be a major feature of the

mound spring ecosystem, niche separation might be important only in times of overcrowding or of critically limited resources. We favour this marriage of the two views on the maintenance of species diversity.

Physiology

The mound-spring habitats are generally small and subject to harsh and highly variable climate: temperatures in the area frequently fall below 0° C in winter and surpass 40° C in summer, and rainfall is scant and variable. The springs contain hard water that is slightly saline (2–8‰) but with the high evaporation encountered, locally salinities probably exceed this range. Given these conditions, one would predict that mound-spring snails would be fairly tolerant to a range of temperatures and salinities, as well as to desiccation and, possibly, to deoxygenated water. Species should vary in their tolerances to these variables, as well as in their responses to light and submergence in water, according to their microhabitat and, possibly, body size. In particular, the amphibious snail species should be more tolerant than the aquatic species to desiccation. The ability to withstand desiccation has important implications for their potential to survive dispersal and temporary cessation of water flow.

The experiments described above were carried out in an attempt to gain an understanding of the responses of hydrobiids to some of the important environmental parameters encountered in the mound springs. The purposes of these experiments were first, to provide data on the tolerance of the mound spring hydrobiids to desiccation, salinity, deoxygenated water, temperature, and submergence in water; and the response of the snails to light and submergence in water; second, to discuss these data as they relate to the ecology of the snails; and third, to compare the results of these experiments with similar studies of other hydrobiids. Similar experiments were also carried out on the endemic isopod and amphipod; a summary of the results is given in Kinhill-Stearns (1984).

The results of the physiological experiments indicate that there are significant differences among species, and among some populations, in tolerance and response to the environmental parameters studied. Many of these differences appear to be related to the ecology and/or the body size of the snails. The primary ecological division of the mound spring snails is into amphibious *(F. zeidleri)* and aquatic species (all others) (Fig. 56). *Fonscochlea zeidleri* typically inhabits the narrow band of moist habitat on the sides of an outflow or surrounding a spring pool. At most localities, more than 80% of living *F. zeidleri* are found out of the water and the reverse is true of the aquatic species (Fig. 55). The exception is at Coward Springs Railway Bore in which a substantial part of the population of *F. zeidleri* is fully aquatic.

We have noted three possible morphological adaptations of *F. zeidleri* to the amphibious habit. The cephalic tentacles, typically elongate in the aquatic species, and in most hydrobiids, are short relative to those of the other species. Observations of *F. zeidleri* crawling in a film of water indicated that their short tentacles were maintained in approximately their normal position, oriented about 45° to the longitudinal axis of the snout, whereas under similar conditions the tentacles of *F. aquatica* were bent backwards by the surface tension. Thus the shortened tentacles of *F. zeidleri* might have adaptive value whenever the snail is crawling about in a thin film of water, the forward-pointing tentacles being able to maintain their sensory function in the region lateral to the anterior end of the snout. The calcareous opercular pegs, which are small to almost absent in the aquatic species, are massive in *F. zeidleri,* providing a relatively large muscle attachment area that presumably enables the operculum to be held tightly against the aperture whenever the snail is retracted into the shell, and thus help resist desiccation. The gill filaments are fewer, shorter, and thicker relative to body size than those of the aquatic species. Whenever a snail is out of the water it is likely that the pallial cavity will contain air bubbles as well as water. Such air bubbles could abut against long gill filaments, and cause them to fold over, which folding would inhibit the lateral ciliary activity and hence the flow of water through the mantle cavity, and, consequently, interfere with respiratory activity. It is less likely that the air bubbles would so affect the shortened, stubby filaments of *F. zeidleri.* Also note that an air bubble held in a damp mantle cavity could also assist in maintaining a lower body temperature compared to snails with a water-filled cavity. This has been found to be the case in experiments with land snails (Schmidt-Nielsen *et al.,* 1972). As predicted, *F. zeidleri* in all three populations tested had a significantly higher tolerance to desiccation

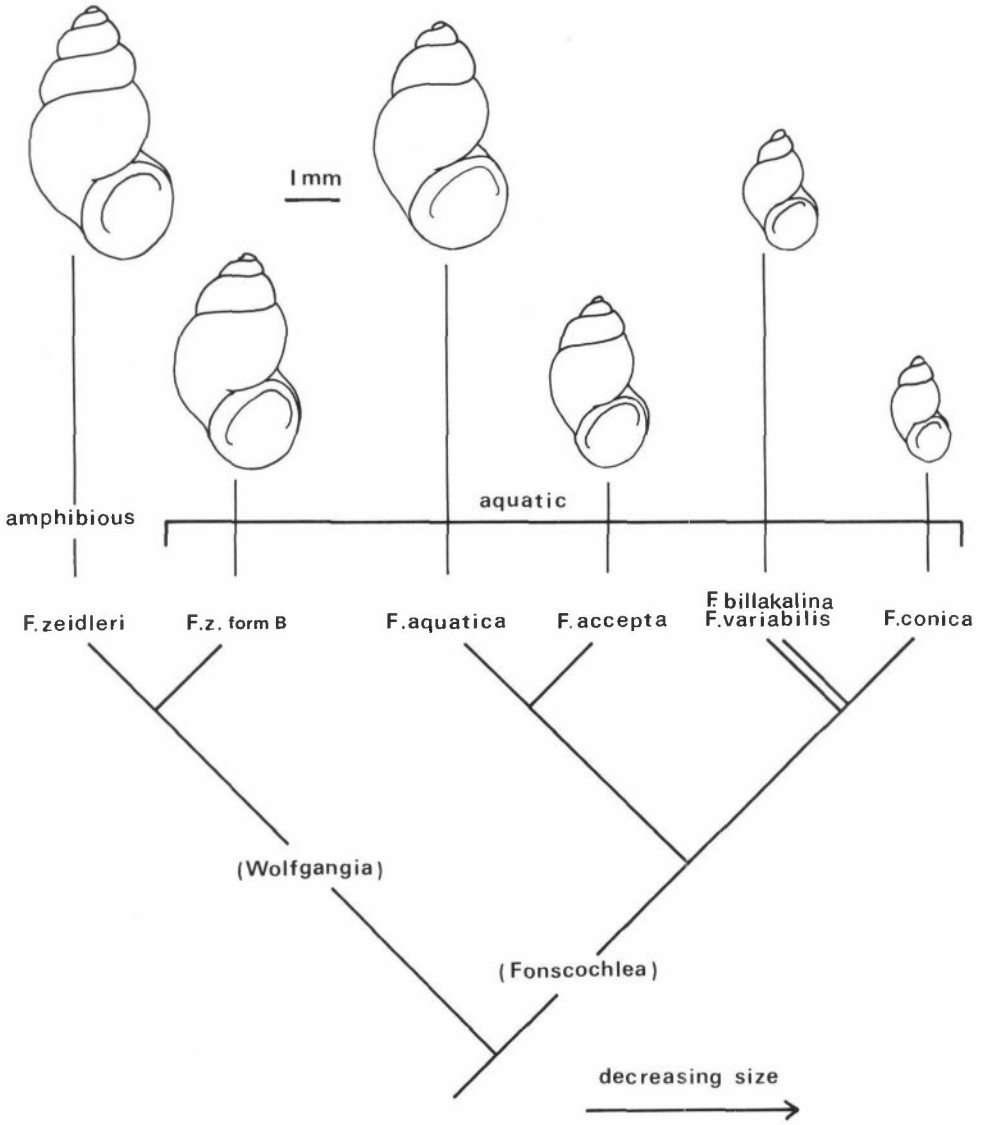


FIG. 56. Diagrammatic representation of probable relationships of species of *Fonscochlea*, as well as sizes and habitats. This figure is not a cladogram and the distances between branches are not intended to indicate degree of taxonomic separation.

than had the aquatic species tested. Apart from *F. zeidleri,* only *F. aquatica* from the small, harsh Kewson Hill springs survived for 48 hours in the dry dishes.

Considering their amphibious habit, it was not surprising that, for two of three populations, large percentages of *F. zeidleri* crawled out of the water in the submergence preference experiments. While large numbers of snails of some of the aquatic species also crawled to the tops of the dishes, they did not venture beyond the meniscus and remained at least partly submerged.

The differences in results between populations of *F. zeidleri* in the submergence preference and light response experiments can be explained partly by differences in microhabitat of these populations. Blanche Cup is a

large calcrete mound, with a spring pool on top and outflow to one side. *Fonscochlea zeidleri* lives there on moistened rock, and most of the individuals are fully exposed to the sun. At Finniss Springs, the mound is soft, being composed of a sandy substrate, allowing the snails to burrow to shallow depths. The population of *F. zeidleri* at the Coward Springs Railway Bore has been introduced, presumably recently, from a nearby spring, but *F. aquatica* has not been introduced in the 80–90 years that the bore has been flowing. *Fonscochlea zeidleri* occupies both the amphibious and aquatic microhabitats at this locality, possibly because *F. aquatica,* which is similar in size to *F. zeidleri,* is absent. The specimens on which the experiments were conducted were all submerged when collected. These microhabitat differences correlated well with the results of the submergence preference experiments. Over 50% of *F. zeidleri* from Blanche Cup and Finniss Springs crawled out of the water in these experiments, but only 16% of the snails from Coward Springs Railway Bore did so.

Despite its reduced ctenidium, *F. zeidleri* did not show significantly higher mortality or reduction in activity than did the aquatic species during the experiments on tolerance to deoxygenated water and submergence. In the controls of the deoxygenation experiment, too, the activity of *F. zeidleri* did not decrease faster than that of the aquatic species. This fact might suggest that the differences observed in the ecology of these snails might not be due soley to simple physiological limitations, at least in the ability of *F. zeidleri* to tolerate a submerged existence. Certainly the existence of an aquatic population at Coward Springs Railway Bore would support this observation.

Given the variation seen amongst runs of *F. zeidleri* from Coward Springs Railway Bore and Finniss Springs, it is difficult to generalize as to the response of these snails to light. One possible explanation for the variable results is that the snails from these populations are adapted to avoid light in their natural habitats, as their microhabitat distribution would suggest, but while held in sunlight-exposed containers, the snails used in one of the runs might have become light adapted and hence did not avoid light during the experiment. It is also possible that the snails used for the separate runs were collected from slightly different habitat types. The Blanche Cup population of *F. zeidleri* lives exposed to the sunlight, but only 41% of the snails tested for this population were in the light zones.

The two similar-sized forms of *F. accepta* differ in the height of the gill filaments; *F. accepta* form B has shortened gill filaments, similar to those of *F. zeidleri,* whereas *F. accepta* form A has tall filaments like those of *F. aquatica.* Their habitats are generally similar as both species are abundant in shallow waters in outflows, but *F. accepta* form A is commonly found in deeper pools as well, whereas *F. accepta* form B does not seem to prefer this habitat. As might be predicted from their morphology, *F. accepta* form B survived better than did *F. accepta* form A during the desiccation experiments.

Trochidrobia punicea is often found on exposed surfaces in the water whereas most of the other aquatic species seem to prefer shaded microhabitats. This difference corresponds well with the fact that *T. punicea* was the only species tested that had a strongly positive response to light. The aquatic *Fonscochlea* species, however, are also frequently encountered in the open, often in large numbers, but were negatively phototropic in the experiments. Their natural occurence might be due, in part, to the lack of suitable shelter.

The tolerances of the various species to desiccation and salinity might be determined, in part, by body size. Desiccation rate is partly a function of exposed surface area of tissue. When retracted in the shell, a snail can lose water either through the shell or through, or around the edges of, the operculum. A small snail has larger ratios of shell surface area to shell volume and shell apertural area to shell volume than has a large snail of similar shell geometry. Small snails therefore should desiccate more rapidly than large snails. This would be accentuated by the fact that, for the mound-spring snails, small snails have thinner shells than do large snails. The desiccation experiments clearly showed that the large-sized species, apart from *F. accepta* form A (see above), had higher survival in the dry dishes than did the small-sized species *(T. punicea, F. variabilis, F. conica).* As noted above, these differences obviously are at least partly due to divergent adaptation as well.

Salinity tolerance was also correlated with body size among the species tested. The large species were fully active in 12‰ salt water whereas the small species had reduced activity in 9‰ and no activity in 12‰. It is not clear the extent to which body size itself is

responsible for these differences. Although osmotic problems of water loss and salt uptake encountered in high-salinity water are again dependent on surface area, and hence related to body size, physiological adaptations might be more important. The maximal salinity known for the spring groups from which the snails were collected for these experiments is about 4.5‰ and about 5.2‰ for springs known to contain hydrobiids (Kinhill-Stearns, 1984). It is noteworthy that the snails can tolerate salinities that are twice this value. The mound-spring snails are members of a large group of freshwater animals that can tolerate salinities of approximately 3–10‰ (Bayly, 1972). As discussed below, their salinity tolerances do not approach those of the inhabitants of athalassic nonmarine waters (salinity of 10–300‰, *sensu* Bayly, 1972).

It would be of great interest to compare the tolerances of mound-spring snails to temperature, salinity, and water oxygenation with fluctuations of these parameters within the springs from which the snails came. Unfortunately such habitat data are not generally available, although we do have some data concerning temperature. For an 11-day period during winter, beginning 26/8/83, the temperature in one of the largest of the Finniss Springs varied from 11.0–27.8° C. just below the springhead, and from 13.0–31.0° C. in a downstream pool. The air temperature varied from 3.0–36.0° C. during the same period. Maximal diurnal fluctuations were 16.1° near the springhead and 15° in the downstream pool, values approaching the maximal such fluctuations recorded in desert aquatic habitats (Deacon & Minckley, 1974; Hershler, 1984).

An aspect of snail morphology that might bear on thermal tolerance is body pigmentation. In most of the populations of mound-spring snails the degree of pigmentation of the head/foot is highly variable but some conspicuous trends have been observed. In general, there is an increase in black pigment (melanin?) in populations inhabiting the most exposed habitats (e.g., Kewson Hill) where shelter (e.g., vegetation) is virtually absent. Individuals exposed on hard rock outflows tend to be darker than those that can gain shelter by burrowing in the sand. This coloration does not appear to be in any way cryptic because in many outflows the dark snails are very conspicuous against the pale sediment or rock.

Hydrobiids living in caves and other phreatic habitats are always unpigmented (Vandel, 1965), whereas species living in surficial waters are often pigmented, usually black. This pattern, together with our observations on the pigmentation of mound-spring snails, suggests that the degree of pigmentation is correlated with exposure to sunlight. As the pigment in the mound spring snails is largely restricted to the upper visceral mass (including the gonad), head/foot and snout, areas that are exposed to the sunlight, and hence ultraviolet rays, it is likely that such pigment has a screening function in this group.

While there are no data available on tolerance to environmental parameters in other spring-dwelling hydrobiids, some data are available for species in the related family Pomatiopsidae, which inhabit ephemeral water bodies in arid lands (*Coxiella* in Australia, *Tomichia* in Africa) (Bayly & Williams, 1966; DeDeckker & Geddes, 1980; Davis, 1981), and moist amphibious habitats in non-arid regions (*Oncomelania* in Asia, *Pomatiopsis* in North America) (van der Schalie & Getz, 1963). Some information is also available for hydrobiids of brackish waters *(Hydrobia, Potamopyrgus)* (Newell, 1964; Avens, 1965; Winterbourn, 1970; Bayly, 1972; Fenchel, 1975; Wells, 1978). These various data sets can be compared only in a general fashion because of differences in experimental design and methods.

Tomichia and *Coxiella* typically tolerate at least several months of desiccation, and a 10 to 20-fold change in water salinity. These tolerances are considerably broader than those of the mound-spring hydrobiids, although the desiccation tolerance of *Fonscochlea zeidleri* can approach that of the permanent stream-dwelling *Tomichia differens* (Davis, 1981). Such broad tolerances are expected, considering the typical habitats of *Tomichia* and *Coxiella,* ephemeral water bodies subject to extreme salinity fluctuations. The mound-spring habitat, while often quite shallow, is permanent and not subject to great salinity fluctuations. *Fonscochlea zeidleri* does not occupy dry habitats, nor do any of the mound-spring snails inhabit downstream pools, possibly because they might be subject to high temperature and salinity fluctuations and might even dry up in summer. *Pomatiopsis* and *Oncomelania* appear to have temperature tolerances slightly broader than those of the mound spring snails. While *Fonscochlea zeidleri* had no mortality after submersion for 72 hours, there was significant mortality after

this lapse of time in some of the species of *Oncomelania* and *Pomatiopsis,* perhaps reflecting more specialization for a terrestrial existence in the latter group. Most of the species of *Oncomelania* and *Pomatiopsis* tested appear to survive desiccation better than do *F. zeidleri,* again implying more specialization for near-terrestrial life. After 48 hours in dry dishes, there was mortality in *F. zeidleri* whereas there was 100% survival in all species of *Pomatiopsis* and *Oncomelania*. While it is unlikely that *F. zeidleri* would survive 30 or 42 days in dry dishes, it might well survive a week and therefore be as tolerant to desiccation as *Pomatiopsis cincinnatiensis*.

Hydrobia totteni and the mound-spring hydrobiids were active throughout a similar range of temperatures. The *Hydrobia* and *Potamopyrgus* species tested had high percentages of snails active in a range of salinities exceeding 17‰ and as much as 33‰ (Winterbourn, 1970), whereas the mound spring snails were active throughout a salinity range of only 12 o/oo. This difference is probably a reflection of the estuarine habitat of *Hydrobia* and *Potamopyrgus*. *Fonscochlea zeidleri,* but not the other mound-spring species, appears to have a higher tolerance to desiccation than has *Potamopyrgus* (an average of 73% survival versus 0% survival in dry dishes after 48 hours) and possibly *Hydrobia totteni*, but probably not *H. ulvae*. Obviously the estuarine *Hydrobia* would not be exposed to the semi-dry conditions that *F. zeidleri* experiences for more than the length of a tidal cycle. Fish and Fish (1977) have shown that the embryonic development of *Hydrobia ulvae* has an optimal temperature/salinity combination. At temperature/salinity combinations differing from the optimum, hatching was prolonged and mortality increased. It is probable that temperature and salinity changes in the mound springs have similar effects on the development of the hydrobiid eggs.

Hydrobiid fauna

The discussion thus far has concentrated on the general problems and theoretical considerations concerning the fauna as a whole. A scenario is suggested within the framework proposed above to provide an explanation for the differentiation of the taxa.

The mound springs provide a gradation of degrees of isolation from completely isolated, through single springs, to local spring groups with scattered to interconnected springs. Any hypothesis that attempts to explain the evolution of a taxon only in terms of the details of present-day spring distribution would be inadequate but, as suggested above, the general pattern of spring distribution is likely to be fairly stable. Obviously any links between, or greater isolation of, present groups would have been of significance. Other past events that might have been important in the development of the present-day taxa are changes in climate, drainage patterns and, possibly, different ecological and physiological requirements of the hydrobiid fauna, perhaps enabling some of the species to live in other water bodies. This last possibility we consider unlikely and, consequently, do not develop it further. A possible exception is the amphipod, *Austrochiltonia*, which might have invaded the springs recently from other water bodies, closely similar species being found farther south.

The sympatric species of snails occurring in the majority of the springs represent four radiations. One radiation is that of *Trochidrobia* with two very distinct sympatric species at Freeling Springs, one of which is endemic and the other, as noted above, also found in some of the northern springs to the south of Freeling Springs, and two morphologically similar, allopatric species in the other springs. *Fonscochlea* (Fig. 56) has radiated in two main directions, one toward an amphibious species, *F. zeidleri* from which the aquatic form, *F. zeidleri* form B, is secondarily derived, and the other, probably less derived, including all the other taxa. These groupings are reflected in the subgeneric classification. The larger, aquatic group split into two groups that radiated in parallel with each other but differ markedly in size. The species in these two "aquatic" radiations are very similar morphologically and differ from *F. zeidleri* in a number of important characters. It is thus likely that the two subgenera in *Fonscochlea* represent an ancient speciation. The species distributions within the radiations follow the existing pattern of springs closely enough to indicate that the speciation events are similar in antiquity to the present major spring groups.

There are several patterns of distribution demonstrated by the mound-spring hydrobiids (Figs. 13, 26, 31, 39; Appendix 1, Figs. 57–63; Table 1). These fall into three main groups. The first pattern is restriction to a single spring. This applies to only two infraspecific forms (*F. zeidleri* form B not included in

distribution maps but occurring at Big Cadnaowie Spring, Fig. 63A; and *F.accepta* form C, Fig. 13). The evolution of both of these forms is presumably quite recent as they are not greatly differentiated from related taxa. They presumably differentiated in isolation after dispersal, or might be relictual populations.

The second pattern is restriction to a single spring group or complex. Three of the taxa occurring at Freeling Springs (Fig. 58), *T. inflata*, *F. aquatica* form B and *F. variabilis* form C fall into this category, as do *F.accepta* form B (Fig. 13) and *F.variabilis* form A (Fig. 26). The "taxa" of *Fonscochlea* in this category are considered to be of infraspecific status only, i.e. "forms" that might be subspecies, and their relatively recent divergence is probable. Whether these forms represent differentiation following dispersal or the partial fragmentation of a wider-ranging taxon following greater isolation of spring groups, is unclear. The two species of *Trochidrobia* found at Freeling Springs are, on the other hand, very different from their congeners and no close relatives occur elsewhere, facts suggesting a considerable period of isolation and continuity with the ancient spring habitat of a group different from the rest of the mound springs. If this were indeed the case, the endemic forms of *Fonscochlea* found at Freeling Springs would probably be of relatively recent origin and derived from the springs to the south. The occurrence of *T.minuta* in some of the northern springs might be due to recent dispersal events.

The third pattern is occurrence in several spring complexes. The majority of taxa, including geographic forms, fall into this category. *Fonscochlea accepta* form A (Fig. 13) is found in Welcome and Davenport Springs (Figs. 62, 63B), whereas the species *(F. accepta)* ranges from Welcome to Emerald Springs, a range of about 82 km (Figs. 13, 61, 63B). *Fonscochlea aquatica* form A ranges through the Blanche Cup group to the northern springs south of Freeling Springs (165 km range) (Figs. 13, 61, 63B), with a closely related form (subspecies?) in Freeling Springs (Figs. 13, 58). The amphibious *F.zeidleri* form A has the largest range of any species (270 km) and is found from Freeling Springs to Welcome Springs (Figs. 31, 58, 63B). One of the smaller species of *Fonscochlea*, *F. variabilis*, has differentiated into what we are regarding as forms but which might well be equivalent to subspecific taxa. One form is found in the scattered northern springs, another even farther north in Freeling Springs (Fig. 58), and another in the Blanche Cup spring group (Figs. 26, 61). *Fonscochlea conica,* on the other hand, while showing some morphological variation, ranges from Beresford Spring to Welcome Springs (124 km) (Figs. 26, 61, 63B). *Fonscochlea billakalina* ranges through the Billa Kalina-Francis Swamp-Strangways spring complexes (Figs. 26, 60, 61). The two species of *Trochidrobia* that occur in the springs south of Freeling Springs are distributed differently from the *Fonscochlea* species (Table 1; Fig. 39). *Trochidrobia smithi* extends from the northern springs to the Billa Kalina complex and the Beresford group (Figs. 60, 61). *Trochidrobia punicea*, like *F.conica*, is found in the middle springs and extends to Welcome Springs (Fig. 63B) but, unlike that species, is found in most of the springs in the area.

The different distributions of the larger aquatic species of *Fonscochlea, F. accepta* and *F. aquatica*, compared with *T. punicea* and *F.conica* suggest that there might have been an extinction of the fauna in the middle springs followed by the differential invasion of *F.aquatica* form A and *F. variabilis* from the northern springs and *T.punicea* and *F.conica* from the south. It is possible that the original population of *F. aquatica* in the area is still represented by at least some of the populations in the Jersey-Elizabeth-Kewson Hill Springs area (Fig. 61), as these appear to have differentiated (see discussion in taxonomic section under *F. aquatica* form A). *Fonscochlea variabilis* has been successful in establishing itself only in the larger springs in the Blanche Cup spring group (Fig. 61) whereas the very similar *F.conica* occurs throughout the rest of the middle group. This hypothesis would also help to explain the lack of noticeable differentiation in the species found in the middle spring group, with the exception of *F.variabilis* form A. Fossil specimens from the middle of the area (from the top of Hamilton Hill, Fig. 61) include only *F.zeidleri* and a species of *Trochidrobia* that could be either *T.smithi* or *T.punicea*, whereas small-sized *Fonscochlea* are abundant on North Beresford Hill (Fig. 60), a similar fossil mound on the northwest edge of the middle springs.

Absence of fauna

Several springs and groups of springs in the study area did not contain hydrobiids (Appendix 1) and many of these same springs

also lacked the endemic crustaceans. Individual springs in some spring groups also lacked the snails and crustaceans whereas neighbouring springs did not. Water chemistry does not appear to explain the absence of fauna in many cases (see Kinhill-Stearns, 1984, for details of water chemistry of most of the relevant springs), although poor water quality and the lack of running, oxygenated water is certainly relevant in some cases. At least two springs, Pigeon Hill Spring and Dead Boy Spring in the Hermit Hill Spring Complex (Fig. 62), are closely associated with fauna-bearing springs but have sulphate-rich water that renders them unsuitable for the mound-spring invertebrates.

Several springs along the southern edge of Lake Eyre South (Jacobs, Fred, Smiths, Gosse and McLachlan, Fig. 62) are similar in water chemistry to the Hermit Hill springs and, at least in most cases, have potentially good habitat available. The invertebrates do not appear to have become established in these springs in the recent past as there were no traces of snail shells in the spring sediments. Flooding in this area results in the submergence of many of these springs (our observations and C. Woolard, pers. comm., based on the Jan. 1984, floods) and it seems likely that even if one of the invertebrates were occasionally introduced naturally and if a population were established, it would not be successful in the long term. Some of the smaller, more isolated springs might never have achieved a successful introduction or, perhaps, because of their small size, are much more susceptible to devastating stock damage or occasional natural fluctuations in flow which might obliterate the habitat.

Conservation

The importance of the mound springs as unique natural ecosystems that contain a variety of endemic biota has been addressed elsewhere (Casperton, 1979; Mitchell, 1980, 1985; Harris, 1981; Kinhill-Stearns, 1984; Ferguson, 1985; Ponder, 1985, 1986). The fragility of these ecosystems, their susceptibility to damage by livestock and, particularly, the real probability of their extinction as a result of the extraction of larger amounts of artesian water from the aquifers of the Great Artesian Basin, would suggest that special provisions for their maintenance are required. To date none of the springs of the Lake Eyre Supergroup that contain endemic fauna is offered special protection apart from a few springs that recently have been fenced to prevent stock damage.

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APPENDIX 1

List of stations

The stations are listed in order of our station numbers and are referred to in the text and tables by these numbers. The spring name is followed by the latitude and longitude, the name of the appropriate 1:250 000 map sheet and the grid reference for that sheet. A reference for Cobb (1975) or Williams (1979) is given if appropriate although the citing of these references does not imply that exactly the same spring was sampled. Additional chemical and flow data are given by Kinhill-Stearns (1984) for many of the springs listed. The collectors and the date of collection are given as are brief details about the substations. The numbers in brackets following the substation data for some of the Southern Springs are the numbers allocated to these springs by Roxby Management Services during their survey. Full data about each station are not given. Generally information on the dimensions of the spring, the substrate, habitat, vegetation cover, condition, and details of the substations were noted for each station. In many temperature and, in some, pH, were recorded.

Abbreviations used: BJ—B. Jenkins, CW—C. Woolard, DB—D. Bushell, DW—D. Winn, EH—E. Hershler, helic—helicopter, RH—R. Hershler, WP—W. Ponder, WPj—W. Ponder Jnr, WZ—W. Zeidler.

002 (=41) Welcome Springs-northern one. 29°40.09′S, 137°44′E. Curdimurka 594324 (Cobb, 1975:1). Coll. WZ, 10 Sept.81. General.

003 (=42) Welcome Springs-southwest. 29°40.77′S, 137°49.75′E. Curdimurka 594324. (Cobb, 1975:1). Coll. WZ, 11 Sept.81. General.

004 (=49A) Davenport Springs. 29°40.09′S, 137°35.31′E. Curdimurka 567325. (Cobb, 1975: 11). Coll. WP, WZ and BJ. 13 May 81. General.

005 (49B) Davenport Springs. 29°40.09′S, 137°35.56′E. Curdimurka 567325. (Cobb, 1975: 11). Coll. WP, WZ, WPj and BJ, 13 May 81. General.

006 (=71) Mount Hamilton Homestead ruins. 29°29.71′S, 136°53.95′E. Curdimurka 496346. Coll. WP, WZ, BJ and WPj, 16 May 81. Pool at top.

007 (=69) Strangways Spring, E. of Blanche Cup. 29°29.06′S, 136°53.64′E. Curdimurka 495357. Coll. WP, WZ, BJ and WPj, 16 May 81. Upper part of outflow.

008–012 (=65) Blanche Cup Spring. 29°27.35′S, 136°51.57′E. Curdimurka 491351 (Cobb, 1975:51). Coll. WP, WZ, BJ and WPj, 15 May 81. 008: In pool. 009: Upper outflow. 010: Middle outflow. 011: Outflow at base of mound. 012: Near end of outflow.

013–017 (=66) The Bubbler Spring. 29°26.8′S, 136°51.4′E. Curdimurka 492352 (Cobb, 1975:49). Coll. WP, WZ, BJ and WPj, 15 May 81. 013: Upper outflow, just below pool. 014: Lower outflow. 015: Swampy pool at base. 016: In seep on edge of pool at top. 017: On sedges and algae in pool at top.

018 (=63) Coward Springs Railway Bore. 29°24.21′S, 136°48.89′E. Curdimurka 357486. Coll. WP, WZ, BJ and WPj, 15 May 81. General.

019–022 (=64) Coward Springs. 29°24.78′S, 136°47.28′E. Curdimurka 484357 (Cobb, 1975:56). Coll. WP, WZ, BJ and WPj, 15 May 81. 019: Pool at top. 020: Upper outflow. 021: Outflow near base of mound. 022: Lower outflow.

023 (=64E) Coward Springs. 29°24.78′S, 136°47.28′E. Curdimurka 484357 (Cobb, 1975:56). Coll. WP, WZ, BJ and WPj, 15 May 81. Separate seepage at top of mound.

024 (=52) Elizabeth Springs. 29°21.36′S, 136°46.30′E. Curdimurka 482363. (Cobb, 1975:59). Coll. WP, WZ, BJ and WPj, 14 May 81. General.

025 (=60) Jersey Springs. 29°20.81′S, 136°45.37′E. Curdimurka 481364. Coll. WP, WZ, BJ and WPj, 15 May 81. General.

026–027 (=53) Old Billa Kalina Spring. 29°27.66′S, 136°29.75′E. Billa Kalina 453350. Coll. WP, WZ, BJ and WPj, 14 May 81. 026: Top of outflow. 027: Lower outflow.

028 (=75) Beresford Spring (N. side of Beresford Hill). 29°16.0′S, 136°39.7′E. Curdimurka 471374 (Cobb, 1975:65). Coll. WZ, 10 Sept. 81. Near top of outflow.

029–030 (=76) Strangways Springs (near Irrapatana). 29°09.9′S, 136°33.1′E. Curdimurka 458387 (Cobb, 1975:68, Williams, 1979:64). Coll. WZ, 5 Sept. 81. 029: Near top of outflow. 030: Outflow.

031–033 (=77) The Fountain Spring. 28°21.1′E, 136°17.0′E. Warrina 431485 (Williams, 1979:14). Coll. WZ, 9 Sept. 81. 031: Top of outflow. 032: Near outflow of top pond. 033: Near bottom of outflow.

034 (=78) Big Perry Springs (West). 28°20.4′S, 136°20.6′E. Warrina 438487 (Williams, 1979:16). Coll. WZ, 9 Sept. 81. Top and middle of outflow.

035–037 (=79) Twelve Mile Spring. 28°18.5′S, 136°15.4′E. Warrina 427490 (Williams, 1979:13). Coll. WZ, 6 Sept. 81. 035: Top of spring. 036: Base of mound. 037: Near top of outflow.

038–040 (=80) Outside Springs (middle one). 28°16′S, 136°12.5′E. Warrina 422496 (Williams, 1979:8). Coll. WZ, 6 Sept. 81. 038: Top of outflow. 039: Middle of outflow. 040: Near bottom of outflow.

041 (=81) Outside Springs (southern one). 28°17′S, 136°12.7′E. Warrina 422495 (Williams, 1979:8). Coll. WZ, 6 Sept. 81. Middle of outflow.

042–044 (=82) Freeling Springs (southernmost). 28°4.3'S, 135°54.4'E. Warrina 390518 (Williams, 1979:27). Coll. WZ, 7 Sept. 81. 042: Top of outflow. 043: Middle of outflow. 044: Near bottom of outflow.

045–046 (=83) Freeling Springs (one crossing track). 28°4.3'S, 135°54.4'E. Warrina 390518 (Williams, 1979:27). Coll. WZ, 7 Sept. 81. 045: Near top of outflow. 046: Near bottom of outflow.

047 Lodden (=Louden) Spring. 28°35.2'S, 136°24.0'E. Warrina 443456 (Williams, 1979:48). Coll. WZ, Sept.81. Spring dry.

048 Melon Spring. 28°15.3'S, 136°4.9'E. Warrina 408496. Coll. WZ, Sept. 81. General.

049 Levi Spring. 28°22.9'S, 136°09'E. Warrina 416482. Coll. WZ, Sept. 81. General.

050 Spring in creek bed NE of Nilpinna Springs. 28°14'S, 135°43'E. Warrina 367503. Coll. WZ, Sept. 81. General.

051 The Vaughan Spring. 28°17.4'S, 136°10.1'E. Warrina 426493 (Williams, 1979:12). Coll. WZ, Sept. 81. General.

659 Unnamed spring. 27°47.1'S, 135°39.9'E. Oodnadatta 364553 (Williams, 1979:49). Coll. WP and WZ, 1 June 83. General.

660 Okenden Spring and Bore. 27°50.8'S, 135°44.0'E. Oodnadatta 372547 (Williams, 1979: 54). Coll. WP and WZ. 1 June 83. General.

661 Big Cadnaowie Spring. 27°51.5'S, 135°40.1'E. Oodnadatta 364545 (Williams, 1979:53). Coll. WP and WZ. 1 June 83. Outflow and top pool.

662 Little Cadnaowie Spring. 27°47.4'S, 135°56.5'E. Oodnadatta 367554 (Williams, 1979: 51). Coll. WP and WZ, June 83. General.

663 Freeling Springs, main spring (southernmost). 28°4.3'S, 135°54.4'E. Warrina 390518 (Williams, 1979:27). Coll. WP and WZ, 2 June 83. Quantitative samples taken.

664 Freeling Springs, "Well Spring". 28°4.1'S, 135°54.3'E. Warrina 389518 (Williams, 1979:27). Coll. WP and WZ, 2 June 83. A1: Pool, mud and weed on bottom. A2: Pool on calcrete near water surface. B: Beginning of outflow. C: ca.50m down outflow.

665 Freeling Springs, near "Well Spring". 28°4.2'S, 135°54.5'E. Warrina 390518 (Williams, 1979:27). Coll. WP and WZ, 2 June 83. A:Head of spring. B:21m down outflow. C:50m down outflow.

666 Unnamed spring, ca.2.5km N. of Freeling Springs. 28°2.0'S, 135°44.1'E. Warrina 389521 (Williams, 1979:29). Coll. WP and WZ, 3 June 83. General. In Peake Creek bed.

667 Tidiamurkuna waterhole-spring. 28°2.3'S, 135°48.9'E. Warrina 380523. Coll. WP and WZ, 3 June 83. General.

668 Melon and Milne springs. 28°15.3'S, 136°4.9'E. Warrina 408496 (Williams, 1979:7). Coll. WP and WZ, 4 June 83. General.

670 Hawker Springs, 4.1km from N. turnoff on N. side of track. 28°24.4'S, 136°11.0'E. Warrina 419478 (Williams, 1979:20). Coll. WP and WZ, 4 June 83. A:Head of spring. B: Beginning of outflow. C:Outflow.

671 Hawker Springs, 6.3km from N. turnoff, N.E. of track. 28°25.3'S, 136°11.3'E. Warrina 421484 (Williams, 1979:20). Coll. WP and WZ, 4 June 83. General.

672 Hawker Springs, 7.3km from N. turnoff, W. of track. 28°26.0'S, 136°11.6'E. Warrina 421475 (Williams, 1979:20). Coll. WP and WZ, 4 June 83. A:Head of spring. B:12m down outflow. C:40m down outflow. D:Outflow of subsidiary spring.

673 Hawker Springs. 8.3km S.E. from N. turnoff to springs. 28°26.8'S, 136°11.6'E. Warrina 421474 (Williams, 1979:20). Coll. WP and WZ, 4 June 83. General.

674 Spring Hill Springs, S. side of Spring Hill. 28°25.3'S, 136°9'E. Warrina 416476 (Williams, 1979:23). Coll. WP and WZ, 5 June 83. General.

675 Edith Spring. 28°28.0'S, 136°5.4'E. Warrina 409472 (Williams, 1979:24). Coll. WP and WZ, 5 June 83. General.

676 Talton Springs. 28°31.6'S, 136°5.7'E. Warrina 410463 (Williams, 1979:46). Coll. WP and WZ, 5 June 83, General.

677 Brinkley Springs. 28°30.4'S, 136°16.9'E. Warrina 432466 (Williams, 1979:44). Coll. WP and WZ, 5 June 83. General.

678 Strangways Springs (near Irrapatana), ca.100m S.W. of ruins. 29°9.88'S, 136°33.09'E. Warrina 458386 (Cobb, 1975:68, Williams, 1979: 64). Coll. WP and WZ, 6 June 83. A:Upper outflow. B:Pool on top of mound.

679 Strangways Springs (near Irrapatana), ca.200m S.W. of ruins. 29°9.79'S, 136°33.09'E. Warrina 458386 (Cobb, 1975:68, Williams, 1979: 64). Coll. WP and WZ, 6 June 83. A1:Pool at top of mound on edges out of water. A2:Pool and upper outflow. A3: Lower outflow.

680 Strangways Springs (near Irrapatana), ca.130m N.W. of ruins. 29°9.98'S, 136°32.87'E. Warrina 458386 (Cobb, 1975:68, Williams, 1979: 64). Coll. WP and WZ, 6 June 83. General.

681 Warburton Spring. 29°16.68'S, 136°40.31'E. Curdimurka 471373 (Cobb, 1975:65). Coll. WP and WZ, 7 June 83. A: Pool at top, A1 on edge, A2 in pool. B:Upper outflow, B1 from edges, B2 from water. C: Lower outflow.

682 Unnamed spring near Warburton Spring. 29°16.57'S, 136°40.19'E. Curdimurka 472373. Coll. WP and WZ, 7 June 83. General.

683 Jersey Springs. 29°20.81'S, 136°45.37'E. Curdimurka 481364. Coll. WP and WZ, 7 June 83. A: Beginning of seepage. B:Outflow.

684 Coward Springs Railway Bore. 29°24.21′S, 136°48.89′E. Curdimurka 357486. Coll. WP and WZ, 7 June 83. Exit from pool and upper outflow.

685 Blanche Cup Spring. 29°27.35′S, 136°51.57′S. Curdimurka 491351 (Cobb, 1975:51). Coll. WP and WZ, 7 June 83. Quantitative samples. Also quantitatively sampled 29 Jan. 84.

686 Priscilla Spring. 29°34.30′S, 137°13.52′E. Curdimurka 528336 (Cobb, 1975:41). Coll. WP and WZ, 8 June 83. General.

687 Venable Spring/bore. 29°40.78′S, 137°22.03′E. Curdimurka 544323 (Cobb, 1975:28). Coll. WP and WZ. 9 June 83. General. Low mound with bore.

688 Beatrice Spring/bore. 29°37.46′S, 137°21.95′E. Curdimurka 544330 (Cobb, 1975:25). Coll. WP and WZ, 9 June 83. Bore and large mound with seepages.

689 Dead Boy Spring. 29°36.08′S, 137°24.44′E. Curdimurka 547333. Coll. WP and WZ, 9 June 83. General. Very small spring in large abiotic spring (HDB005).

690A Finniss Swamp West. 29°35.68′S, 137°24.66′E. Curdimurka 549333 (Cobb, 1975:19). Coll. WP and WZ, by helic., 9 June 83. Small spring—general (HWF039).

690B Finniss Swamp West. 29°35.68′S, 137°24.66′E. Curdimurka 549333 (Cobb, 1975:19). Coll. WP and WZ, by helic., 9 June 83. Small spring—general (HWF042).

690C Finniss Swamp West. 29°35.68′S, 137°24.66′E. Curdimurka 549333 (Cobb, 1975:19). Coll. WP and WZ, by helic., 9 June 83. Small spring—general (HWF041).

691A Finniss Swamp West. 29°35.68′S, 137°24.66′E. Curdimurka 549333 (Cobb, 1975:19). Coll. WP and WZ, by helic., 9 June 83. A:Head of spring in swampy, shallow pool. B:Upper outflow. C:Upper part of middle outflow. D:Lower outflow (HWF031).

692A Bopeechee (or Zeke) Springs. 29°36.49′S, 137°23.15′E. Curdimurka 547332 (Cobb, 1975:21). Coll. WP and WZ, 9 June 83. Very small mound and seepage, ca.40m S.S.W. of 692B (HBO003).

692B Bopeechee (or Zeke) Springs. 29°36.49′S, 137°23.15′E. Curdimurka 547332 (Cobb, 1975:21). Coll. WP and WZ, 9 June 83. General (HBO002).

693 Old Finniss Springs. 29°34.97′S, 137°26.79′E. Curdimurka 553336. Coll. WP and WZ, by helic., 12 June 83. Quantitative samples. Also sampled in Aug.1983 (non-quantitative) and Jan.1984 (quantitative) (HHOF092).

694 Old Finniss Springs. 29°34.97′S, 137°26.79′E. Curdimurka 553336. Coll. WP and WZ, by helic., 10 June 83. General. A: Spring 13×24m (HOF089). B:Spring 15×37m (HOF088). C:Spring 8×17m (HOF087). Three small springs grouped together.

695 Smith Springs. 29°30.37′S, 137°21.42′E. Curdimurka 544344 (Cobb, 1975:31). Coll. WP and WZ, by helic., 11 June 83. General examination of all springs.

696 Gosse Springs. 29°28.0′S, 137°20.6′E. Curdimurka 542349 (Cobb, 1975:34). Coll. WP and WZ, by helic., 11 June 83. General (3 separate springs examined). Main spring also examined 29 Jan. 84.

697 McLachlan Springs. 29°27.8′S, 137°19.0′E. Curdimurka 539349 (Cobb, 1975:37). Coll. WP and WZ, by helic., 11 June 83. General (a large sand mound).

698–9 Unnamed springs near McLachlan Springs. 29°28′S, 137°19.1′E. Curdimurka 540348. Coll. WP and WZ, by helic., 11 June 83. General.

700 Unnamed spring 1.5km S.E. of McLachlan Springs. 29°28′S, 137°19.1′E. Curdimurka 540348. Coll. WP and WZ, by helic., 11 June 83. General—several small seeps.

701 Unnamed spring in W. Lake Eyre South. 29°19.9′S, 137°10.9′E. Curdimurka 526366. Coll. WP and WZ, by helic., 11 June 83. General.

702 Unnamed spring in S. end of Lake Eyre South. 29°21.60′S, 137°16.54′E. Curdimurka 535363. Coll. WP and WZ., by helic., 11 June 83. General.

703 Emerald Spring. 29°23.14′S, 137°3.70′E. Curdimurka 513359 (Cobb, 1975:45, Williams, 1979: 61). Coll. WP and WZ, by helic., 11 June 83. A: Upper outflow. B:Middle outflow.

704 Fred Springs West. 29°31.08′S, 137°16.85′E. Curdimurka 536344 (Cobb, 1975:38). Coll. WP and WZ, by helic., 11 June 83. General. Very little surface water. Fred Springs East was also visited but no station number was allocated.

710 Old Finniss Springs (nearest ruin). 29°35.08′S, 137°27.0′E. Curdimurka 553336. Coll. WP and WZ, by helic., 12 June 83. General (one of several similar mounds examined) (HOF081).

711A Hermit Hill Springs. 29°34.32′S, 137°25.56′E. Curdimurka 551336 (Cobb, 1975:16). Coll. WP and WZ, by helic., 12 June 83. General (HHS172). Several similar mounds examined (B–V).

711W Hermit Hill Springs. 29°34.24′S, 137°25.86′E. Curdimurka 552336 (Cobb, 1975:16). Coll. WP and WZ, by helic., 12 June 83. General (HHS149). Firmer sediment in outflow than 711A.

712 Hermit Hill Springs (E.group). 29°34.24′S, 137°25.86′E. Curdimurka 552336 (Cobb, 1975:16). Coll. WP and WZ, by helic., 12 June 83. General (HHS064–077). Group of 3 small springs with common outflow.

714 Cardajalburrana Spring. 28°11.1′S, 135°33.1′E. Warrina 352505 (Williams, 1979:31). Coll. WP and WZ, by helic., 13 June 83. General.

715 Weedina Springs. 28°23.6′S, 135°38.6′E. Warrina 362480 (Williams, 1979:37). Coll. WP and WZ, 13 June, 83. General.

716 Eurilyana Spring, on S. side of Lake Cadibarrawirra. 28°55.5'S, 135°26.9'E. Warrina 341416 (Williams, 1979:43). Coll. WP and WZ, 13 June, 83. General.

717 Loyd Bore, Francis Swamp. 29°7.3'S, 136°17.7'E. Warrina 432393 (Cobb, 1975:1, Williams, 1979:58). Coll. WP and WZ, 13 June, 83. A:At point of outlet. B:General swamp around main outlet. C:In outflow draining out of main part of spring.

718 Anna Springs East (?bore). 29°31.90'S, 136°59.32'E. Curdimurka 506345. Coll. WP and WZ, by helic., 13 June 83. General.

719 North West Springs. 29°33.51'S, 137°24.11'E. Curdimurka 548337. Coll. WP and WZ, by helic., 13 June 83. General. A-C:3 small springs in S.E. of group (HNW005,007,010).

719D North West Springs. 29°33.51'S, 137°24.11'E. Curdimurka 548337. Coll. WP and WZ, by helic., 13 June 83. General. Small spring in N. of group (HNW003).

720 Francis Swamp, one of springs in middle part of swamp. 29°8.6'S, 136°17.3'E. Billa Kalina 433 388 (Cobb, 1975:1). Coll. WP and WZ, by helic., 14 June 83. A:In middle of spring outlet area. B:In swamp surrounding outlet. C:In outflow.

721 Francis Swamp, springs near south end. 29°10'S, 136°19.2'E. Billa Kalina 434386 (Cobb, 1975:1). Coll. WP and WZ, by helic., 14 June 83. Three springs samples (A-C).

722 Margaret Spring. 29°13.2'S, 136°20.8'E. Billa Kalina 436739. Coll. WP and WZ, 14 June 83. General.

723 Fenced Spring (Billa Kalina). 29°29.1'S, 136°26.9'E. Billa Kalina 447347. Coll. WP and WZ, by helic., 14 June 83. A:Pool at top. Mostly open water. B:Upper outflow. C:Middle outflow. D:Edge of outflow.

730 Finniss Swamp West, near main road. 29°35.92'S, 137°24.57'E. Curdimurka 548333. Coll. RH and EH, 27 Aug. 83. General collection (HWF048).

731 Old Woman Springs. 29°35.41'S, 137°27.35'E. Curdimurka 554334. Coll. WP and BJ, 30 Aug. 83. General (HOW024). Small spring reactivated after seismic work in area.

732A Old Woman Springs. 29°35.46'S, 137°27.35'E. Curdimurka 554334. Coll. WP and BJ, 30 Aug. 83. General-small mound near 732B (HOW015).

732B Old Woman Springs. 29°35.46'S, 137°27.35'E. Curdimurka 554334. Coll. WP and BJ, 30 Aug. 83. General (HOW013).

733 Old Woman Springs, main spring. 29°35.57'S, 137°27.28'E. Curdimurka 554334. Coll. WP and BJ, 30 Aug. 83. A:Top pool. B:Beginning of outflow. C:Upper part of outflow. D:Lower outflow. E:Seepage at head of pool (HOW009).

734 Old Finniss Mound Spring. 29°35.00'S, 137°28.18'E. Curdimurka 556335. Coll. WP and BJ, 30 Aug. 83. General (HOF094).

735 Sulphuric Springs. 29°36.51'S, 137°24.20'E. Curdimurka 548333. Coll. WP and BJ, 30 Aug. 83. General (HSS016).

736 Sulphuric Springs. 29°36.68'S, 137°24.20'E. Curdimurka 558332. Coll. WP and BJ, 30 Aug. 83. General (HSS014).

737 Sulphuric Springs. 29°36.61'S, 137°24.01'E. Curdimurka 547332. Coll. WP and BJ, 30 Aug. 83. General (HSS006).

738 Jacobs Spring. 29°29.38'S, 137°8.95'E. Curdimurka 523347 (Cobb, 1975:44). Coll. WP, RH and DB, 31 Aug. 83. General.

739 Blanche Cup Spring. 29°27.35'S, 136°51.57'E. Curdimurka 491351 (Cobb, 1975:51). Coll. WP, RH and DB, 31 Aug. 83. Transect of pool.

740 Kewson Hill Springs. 29°22.31'S, 136°47.13'E. Curdimurka 484362. Coll. WP, RH and DB, 31 Aug. 83. General. On side of very large mound.

741 Kewson Hill Springs. 29°22.28'S, 136°47.16'E. Curdimurka 484362. Coll. WP, RH and DB, 31 Aug. 83. Upper 10m of outflow.

742 Kewson Hill Springs. 29°22.23'S, 136°47.16'E. Curdimurka 484362. Coll. WP, RH and DB, 31 Aug. 83. A:Upper outflow. B:Lower outflow.

742B Kewson Hill Springs. 29°22.23'S, 136°47.16'E. Curdimurka 484362. Coll. WP, RH and DB, 31 Aug. 83. Lower outflow.

743 Coward Springs Railway Bore. 29°24.21'S, 136°48.89'E. Curdimurka 357486. Coll. WP, RH and DB, 31 Aug. 83. Beginning of outflow. A:Pool at bore on edge. B:On surface of damp mud near large clump of bullrushes. C:In water near large clump of bullrushes.

744 Little Bubbler Spring. 29°27.35'S, 136°51.91'E. Curdimurka 492351 (Cobb, 1975:51). Coll. WP, BJ and CW, 1 Sept. 83. A:Beginning of outflow. B:34m down outflow. C:Lower outflow.

745 Strangways Spring E. of Bubbler group. 29°29.06'S, 136°53.64'E. Curdimurka 495357. Coll. WP, BJ and CW, 1 Sept. 83. A:Upper outflow. B:Middle outflow.

746 Horse Springs West. 29°29.50'S, 136°54.80'E. Curdimurka 497347 (Cobb, 1975:48). Coll. WP, BJ and CW, 1 Sept. 83. A:General—mostly upper outflow. B:In solution hole on side of mound.

747 Horse Springs East. 29°29.50'S, 136°55.25'E. Curdimurka 498347 (Cobb, 1975:48). Coll. WP, BJ and CW, 1 Sept. 83. A:Top pool, mostly under stones. B:Outflow.

748 Horse Springs East. 29°29.58'S, 136°55.25'E. Curdimurka 498347 (Cobb, 1975:48). Coll. WP, BJ and CW, 1 Sept. 83. A:Crater-like pool at top. B: Outflow. C:Outflow at base of mound.

749 Spring at Mt. Hamilton ruins. 29°29.71′S, 136°53.95′E. Curdimurka 496346. Coll. WP, BJ and CW, 1 Sept. 83. Pool at top.

750 Anna Springs West. 29°32.04′S, 136°59.26′E. Curdimurka 506345. Coll. WP, BJ and CW, 1 Sept. 83. Pool.

751 Anna Spring/bore East. 29°31.90′S, 136°59.32′E. Curdimurka 506345 (Cobb, 1975:47). Coll. WP, BJ and CW, 1 Sept. 83. General.

752 Main bore/spring, Davenport Springs. 29°40.09′S, 137°35.31′E. Curdimurka 567325 (Cobb, 1975:11–1). Coll. WP, RH and DW, 2 Sept. 83. A:15m down outflow. B:25m down outflow. C: 60m down outflow.

753 Davenport Springs. 29°40.09′S, 137°35.56′E. Curdimurka 567325 (Cobb, 1975:11–1). Coll. WP, RH and DW, 2 Sept. 83. A:Head and uppermost outflow. B:Lower outflow.

754 Welcome Springs. 29°40.09′S, 137°49.44′E. Curdimurka 594324 (Cobb, 1975:1–3). Coll. WP, RH and DW, 2 Sept. 83. A:Uppermost outflow. B: 20m down outflow. C:Pool 25m down outflow. D: 80m down outflow.

755 Welcome Springs. 29°40.42′S, 137°49.75′E. Curdimurka 594323 (Cobb, 1975:1–3). Coll. WP, RH and DW, 2 Sept. 83. A:Head of spring. B:20m down outflow. C:50m down outflow. D:12m down outflow.

756 Welcome Springs. 29°40.77′S, 137°49.75′E. Curdimurka 594323 (Cobb, 1975:1–3). Coll. WP, RH and DW, 2 Sept. 83. A:Pool 4m from beginning. B:Upper outflow. C:Lower outflow.

757 Wangianna Spring/well/bore. 29°40.55′S, 137°42.65′E. Curdimurka 581323 (Cobb, 1975:8). Coll. WP, RH and DW, 2 Sept. 83. General.

758 Welcome Bore/spring. 29°21.02′S, 136°37.38′E. Curdimurka 465364. Coll. WP, RH and DB, 3 Sept. 83. General.

759 Spring at Old Billa Kalina ruin. 29°27.66′S, 136°29.75′E. Billa Kalina 453350. Coll. WP, RH and DB, 3 Sept. 83. A:Pool at top. B:Upper outflow. C:Lower outflow.

760 Spring near Old Billa Kalina ruin. 29°27.66′S, 136°29.75′E. Billa Kalina 453350. Coll. WP, RH and DB, 3 Sept. 83. A:Pool at top. B:Upper outflow.

761 Billa Kalina, 1.8km S. of ruins. 29°27.98′S, 136°28.40′E. Billa Kalina 451349. Coll. WP, RH and DB, 3 Sept. 83. A:Seep at head. B:Pool at top. C:Outflow.

762 Billa Kalina Springs. 29°27.98′S, 136°28.40′E. Billa Kalina 451349. Coll. WP, RH, DB, 3 Sept. 83. A:Pool at top. B:Upper outflow.

763 Billa Kalina Springs. 29°28.53′S, 136°27.22′E. Billa Kalina 848348. Coll. WP, RH and DB, 3 Sept. 83. A:Upper outflow. B:Lower outflow.

764 Coward Springs. 29°24.78′S, 136°47.28′E. Curdimurka 484357 (Cobb, 1975:56). Coll. WP, RH and DW, 5 Sept. 83. A:Small seepage on top of mound. B:Beginning of outflow. C:Outflow at base of mound.

765 Spring near W. side of Kewson Hill. 29°22.17′S, 136°46.79′E. Curdimurka 483362. Coll. WP, RH and DW, 5 Sept. 83. General.

766 E. side of Elizabeth Springs mound. 29°21.36′S, 136°46.30′E. Curdimurka 482363 (Cobb,1975:59).Coll. WP, RH and DW, 5 Sept. 83. A:Head of spring. B:Outflow from top seep. C:Second spring on outflow. D:Outflow, terrace area. E: Outflow, lower end of terraces. F:On steep side of hill in outflow. G:Base of outflow.

767 Elizabeth Spring/bore. 29°21.30′S, 136°47.04′E. Curdimurka 483363 (Cobb, 1975:63). Coll. WP, RH and DW, 5 Sept. 83. A:Upper outflow, under wood. B:Outflow on sedge. C:Outflow under wood.

768 Jersey Springs. 29°20.81′S, 136°45.52′E. Curdimurka 671753. Coll. WP, RH and DW, 5 Sept. 83. A:Beginning of outflow. B:End of outflow.

769 Jersey Springs. 29°20.81′S, 136°45.52′E. Curdimurka 481365. Coll. WP, RH and DW, 5 Sept. 83. A:Head of spring. B:Outflow.

770 Jersey Springs. 29°20.81′S, 136°45.37′E. Curdimurka 481364. Coll. WP, RH and DW, 5 Sept. 83. A:Top of seepage. B:Outflow. C:Small seep.

771 Elizabeth Springs, N.W. side of hill. 29°21.30′S, 136°21.14′E. Curdimurka 483364 (Cobb, 1975:59). Coll. WP, RH and DB, 7 Sept. 83. A:Head of spring. B:Upper outflow. C:Lower outflow.

772 Julie Springs, S.E. side of hill, between Kewson and Elizabeth springs. 29°21.75′S, 136°46.67′E. Curdimurka 483363 (Cobb, 1975:63). Coll. WP, RH and DB, 7 Sept. 83. A:Pool at head. B:Upper outflow. C:On steep fall, upper outflow. D:Bottom of hill, lower outflow.

773 Julie Springs, S.W. side of hill, between Elizabeth and Kewson hills. 29°21.68′S, 136°45.06′W. Curdimurka 483363 (Cobb, 1975:63). Coll. WP, RH and DB, 7 Sept. 83. A:Upper pool. B:Upper outflow. C:Lower outflow.

785 Seepages in mound S.W. of Little Bubbler Spring, Blanche Cup Group. 29°27.36′S, 136°51.91′E. Curdimurka 491351. Coll. WP and WZ, 27 Nov. 83. A and B in two very small seeps on mound.

786 Spring N.W. of Little Bubbler Spring, and N.E. of Blanche Cup. 29°27.34′S, 136°51.56′E. Curdimurka 491351. Coll. WP and WZ, 27 Nov. 83. A:In outlet of spring. B:In upper part of outflow. C:In smaller outflow on same mound.

787 Spring N.N.E. of Blanche Cup. 29°27.35′S, 136°51.57′E. Curdimurka 491351. Coll. WP and WZ, 27 Nov. 83.

1000 Strangways Springs, near Irrapatana, large spring on southern end of hill. 29°10′S, 136°33′E. Curdimurka 458386. Coll. WP and DW, 31 May 85. A:Pool at head. B:Beginning of outflow. C:Lower outflow.

1001 Big Perry Spring. 28°20.45′S, 136°20.7′E. Warrina 438487. Coll. WP and DW, 31 May 85. A:Beginning of outflow. B:Middle part of outflow. C-D:Small seeps on same mound.

1002 The Fountain Spring. 28°21.1S, 136°17′E. Warrina 431485. Coll. WP and DW, 31 May 85. A:Pool at head. B:Beginning of outflow. C:Middle part of outflow. D:Lower outflow.

1003 Twelve Mile Spring. 28°18.5′S, 136°15.4′E. Warrina 427490. Coll. WP and DW, 1 June 85. A, B:Seeps on same mound as main spring. C:Upper outflow, main spring. D:Middle outflow, main spring.

1004 The Vaughan Spring. 28°17.4′S, 136°10.1′E. Warrina 426493. Coll. WP and DW, 1 June 85. General.

1005 Outside Springs (most southern and eastern). 28°17.39′S, 136°12.69′E. Warrina 422495. Coll. WP and DW, 1 June 85. General.

1006 Outside Springs (middle one of group). 28°16′S, 136°12.5′E. Warrina 422496. Coll. WP and DW, 1 June 85. A:Upper outflow. B:Middle outflow.

1007–8 Nilpinna Springs (at homestead). 28°13′S, 135°42′E. Warrina 366502 (Williams, 1979:35). Coll. WP and DW, 16 June 85. General.

Several additional nominal springs were visited which proved to be dry and no station numbers were allocated. These included:

Oodnadatta Sheet:
Unnamed. 365552 (Williams, 1979:50).

Peake and Denison Geological Map 1:150,000.
Oodloodlana and Oortooklana Springs. To the West of Mt. Denison. Sand Creek, Blind, Coppertop and Mud Springs. To the East of Mt. Denison.

Warrina Sheet
Kerlatroaboorntallina Springs (Mt. Kingston Bore). 388527 (Williams, 1979:26).

List of springs not sampled

There are several springs that, for various reasons, have not been sampled. They are grouped in the list below according to the 250,000 map sheet on which they are found. Springs that are found in spring groups that have been subsampled are not included in this list. Some of these have been recently visited by consultants from Social and Environmental Assessment (SEA) while preparing a report for the South Australian Govt. on the mound springs.

Oodnadatta:
Unnamed spring near Big Cadnaowie Spring (=Cadna-owie Springs or MacEllister Springs). 365546. Williams (1979:52) lists this spring but did not visit it. Visited by SEA, no snails reported. Mt. Toondina Spring. 330534. Listed by Williams (1979: 56) but not visited by him.

Warrina:
Primrose Spring. 441509. Small spring and seeps; described by Williams (1979:5).

Fanny Springs. 425488. Small seeps and ponds; described by Williams (1979:10).

Little Perry Spring. 440494. Bore on spring, flow very small (Williams, 1979:15).

Several springs West of Lat.135.40′S. on the Warrina Sheet have not been visited. The few springs sampled in this area did not contain any invertebrates and were mostly just saline pools. Some examined only from the air appeared to be very similar to those sampled. Oolgelima Spring was visited by SEA, no snails were reported.

Billa Kalina:
William spring. 442405. Listed by Williams (1979: 58), but was not visited by him. Visited by SEA, no snails reported.

Emily Spring. 443401. Listed by Cobb (1975:3) but not visited by him.

Curdimurka:
Walcarina Spring. 508346. Cobb (1975:46) lists this "spring" and states that it is a small seepage. Attempts to locate this spring from the air have failed.

Stations at which no hydrobiids were collected

During the course of the survey of mound springs a large number of springs within spring groups were examined that, mainly because of time constraints, were not allocated station numbers. Some of these springs were rejected because they lacked invertebrates. Thus, with the exception of a few stations in the Hermit Hill area, the following list of springs that were found not to contain hydrobiids applies only to isolated springs or whole spring groups.

Oodnadatta Springs:
Okenden (660), Little Cadnaowie (662), unnamed (659).

Northern Springs:
Melon and Milne (048, 668), Levi (049), The Vaughan (051), Edith (675), Talton (676), Brinkley (677).

North Western Springs:
Tidiamurkuna (667), Nilpinna (050, 1007-8), Cardajalburrana (714), Weedina (715), Eurilyana (716).

Middle Springs:
Anna (718, 750, 751).

Southern Springs:
Jacobs (738), unnamed in Lake Eyre South (701), McLachlans (697, 698–700), Gosses (696), Fred (704), Smith (695), Beatrice (688), North West (719), Wangianna (757), Hermit Hill area: Old Woman Group (731, 732), Old Finniss Group (734).

Springs to the East of Marree:
(Numbers refer to grid references on the 1:250,000 sheets)

Marree Sheet: Hergott Spring (now a bore) (620328), Wirringina Springs (650314), Rocky (233343) and Reedy Springs (233341).

Note: Most of the extant springs to the East of Marree have been sampled. W. Zeidler has visited Lignum Dam and Spring and Four Mile Spring and Bore and in both no evidence of the original spring

remains. In our experience, and from the information provided by Cobb (1975) regarding these springs they are all either heavily degraded by bores being placed on the springs or they are reduced to very small seeps. The one exception is Reedy Springs.

Callabonna Sheet: Public House Spring (not named on map) (241314) and Petermorra Springs (246313).

Note: Springs in the Northern Flinders Ranges and east and northeast of the Northern Flinders Ranges are not listed here, although many have been sampled. None contain the invertebrate fauna seen in the Lake Eyre Subgroup.

Locality maps

The locations of the informal spring systems are given in Fig. 2, the more detailed locality maps in Figs. 58–63 and the key to the locations of the locality maps in Fig. 57. The distributions of the taxa are shown in Figs. 13, 26, 31 and 39 in the taxonomic section. In each map the main drainage channels and the main points of reference are shown. Lake Eyre is a salt lake that contains water only after flooding, filling only once in several years (Kotwicki, 1986). The general topography is flat.

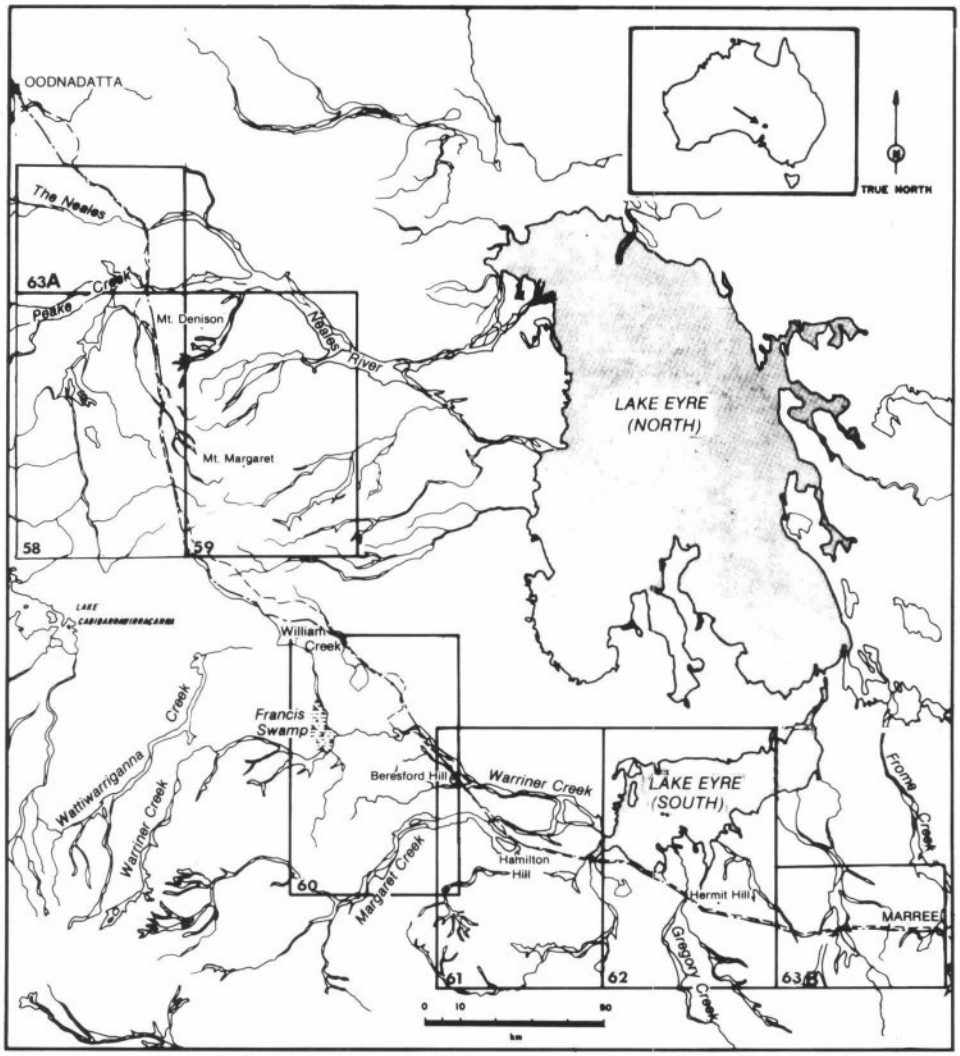

FIG. 57. General location map. Numbered rectangles refer to Figs. 58–63. On each of the following maps only sampled springs are indicated.

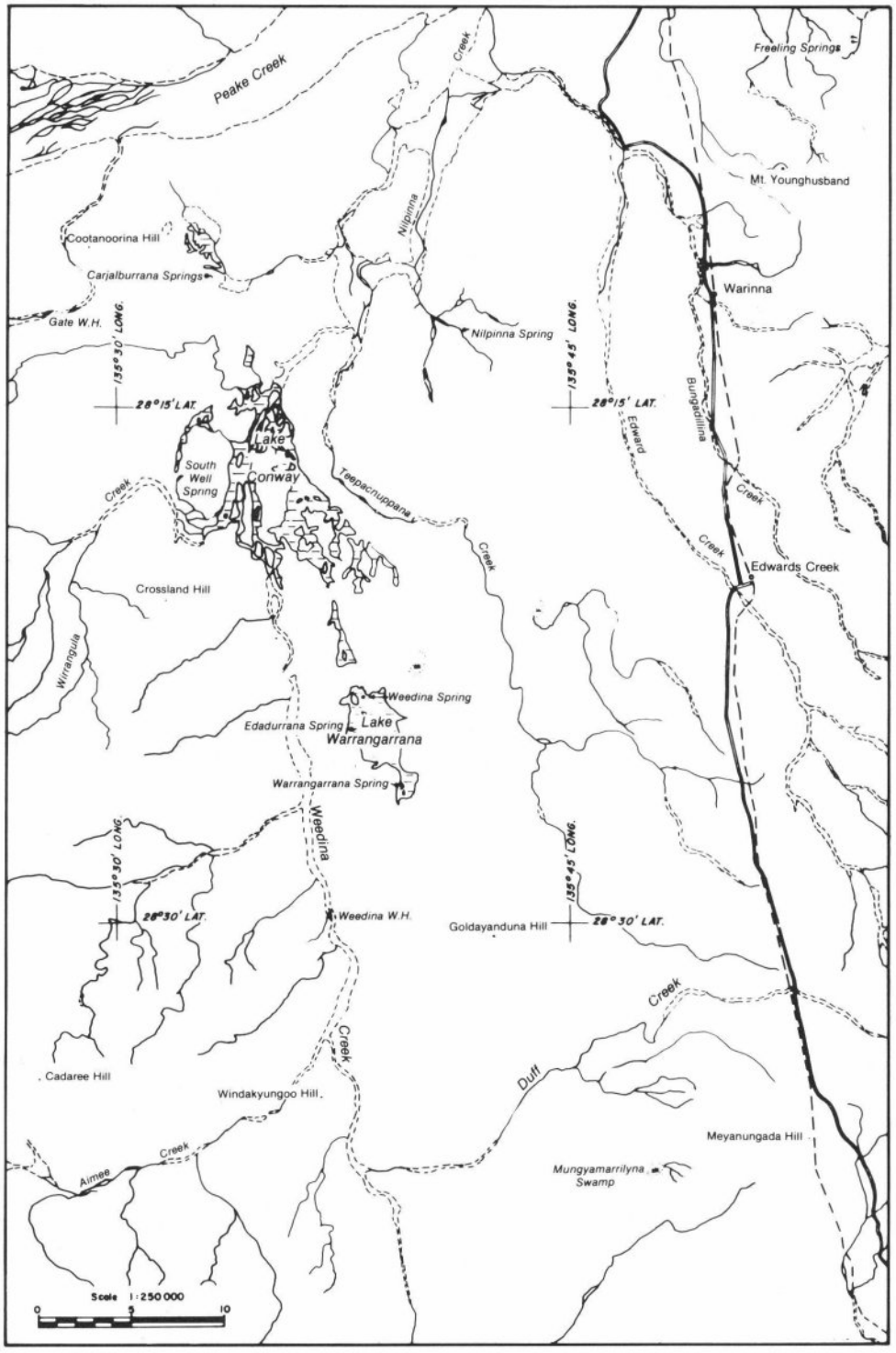

FIG. 58. The North Western Springs and Freeling Springs.

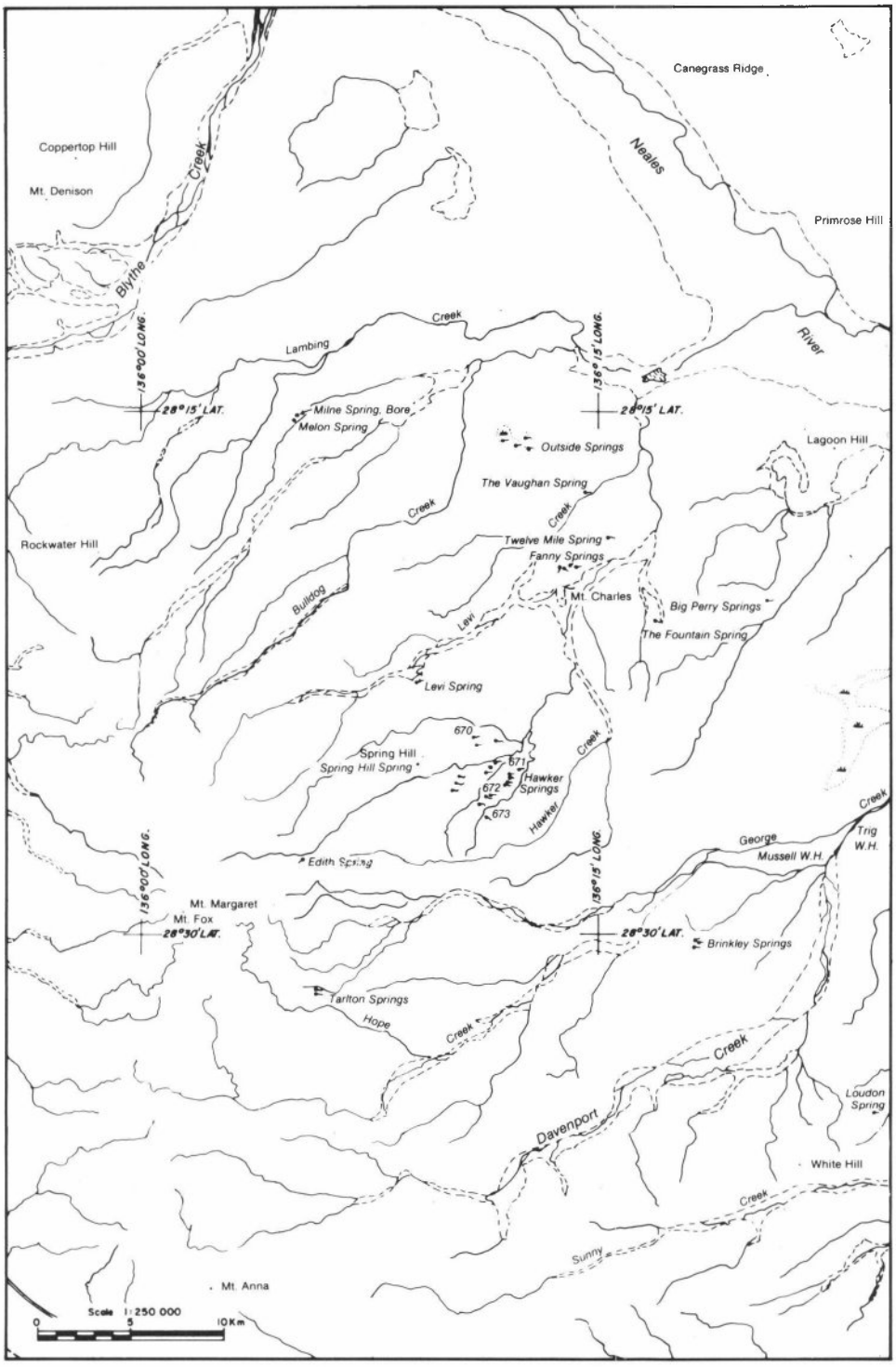

FIG. 59. The Northern Springs.

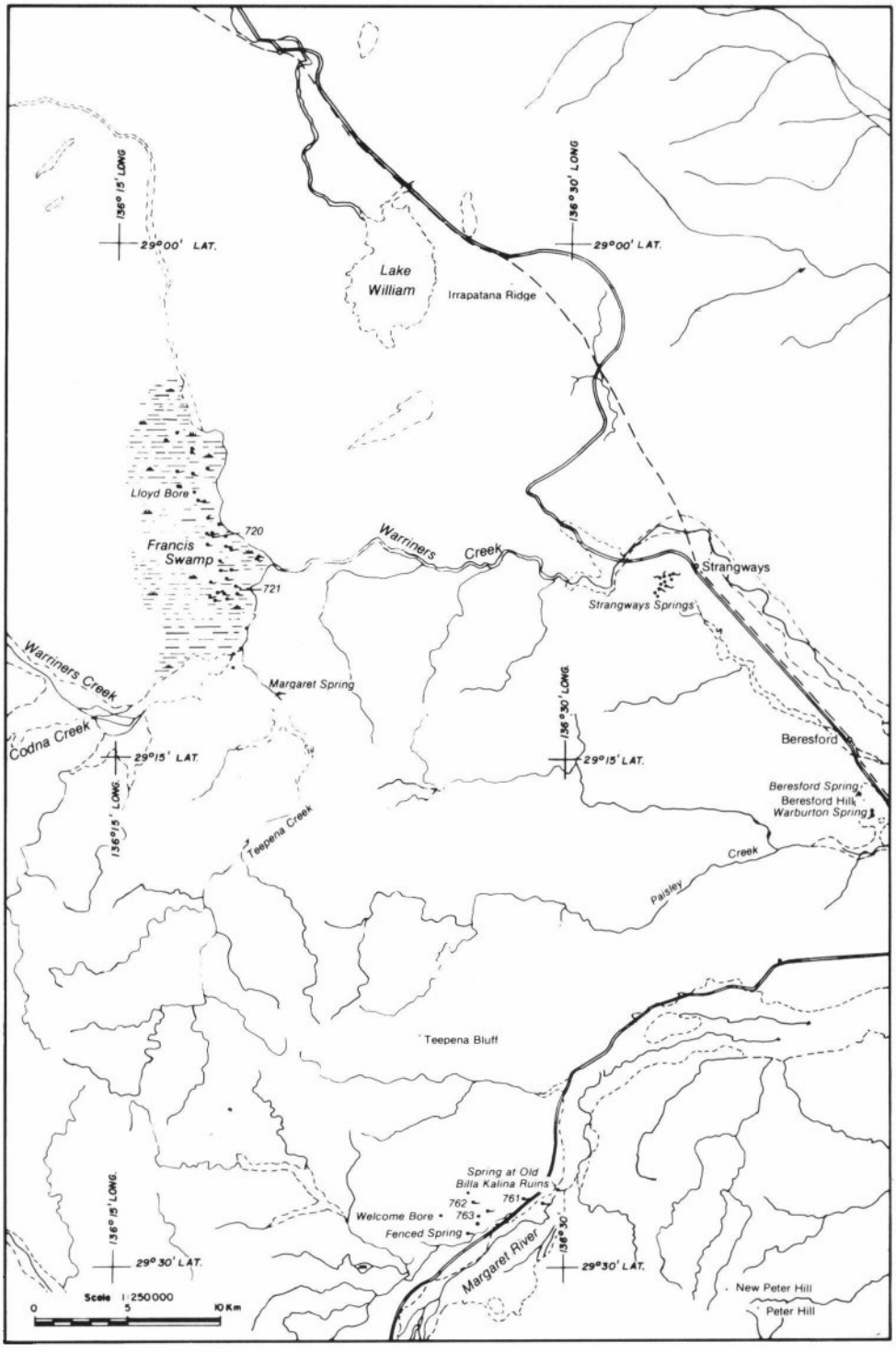

FIG. 60. The South Western Springs and the Beresford Spring Complex.

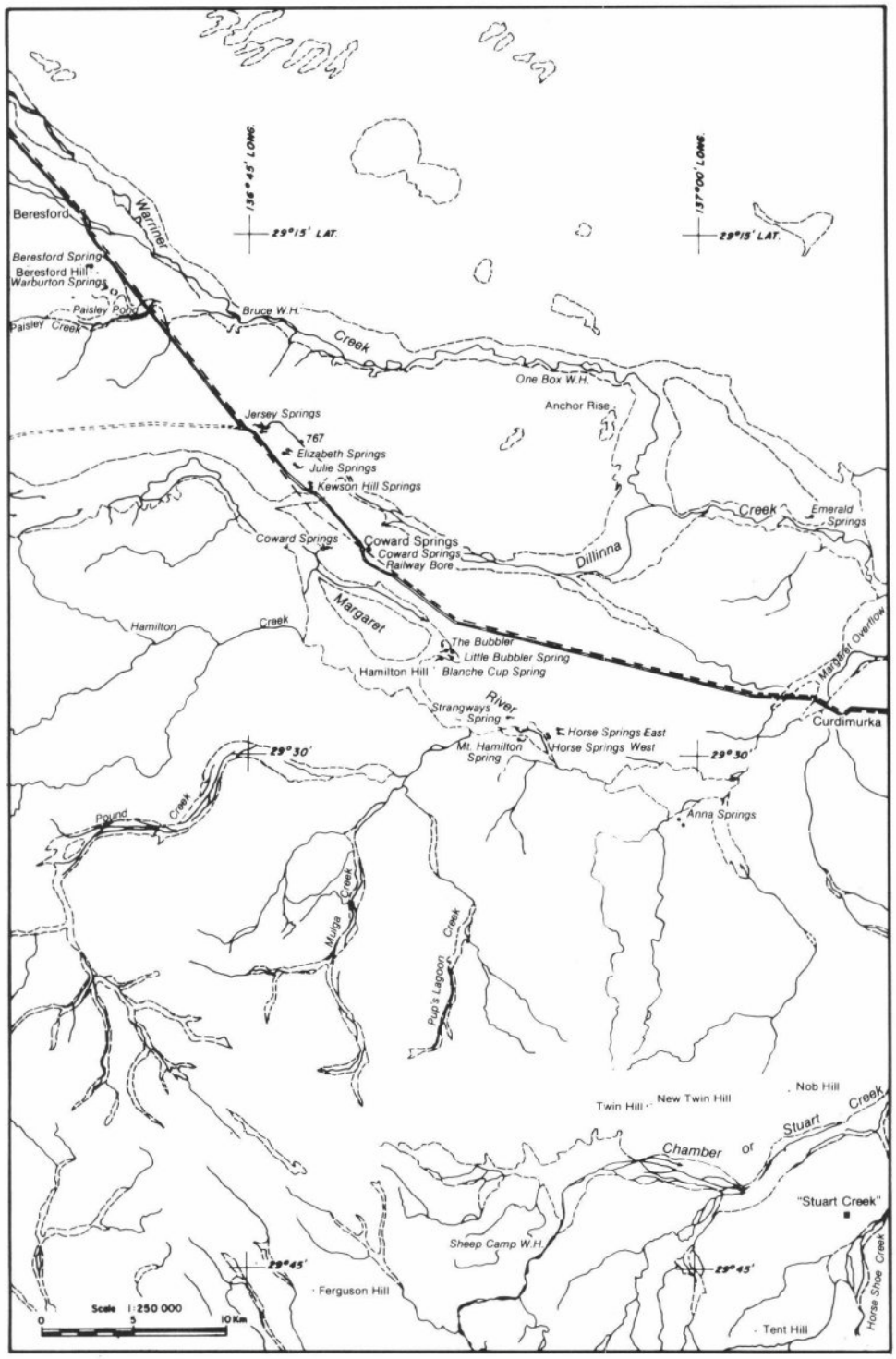

FIG. 61. The Middle Springs and Emerald Springs.

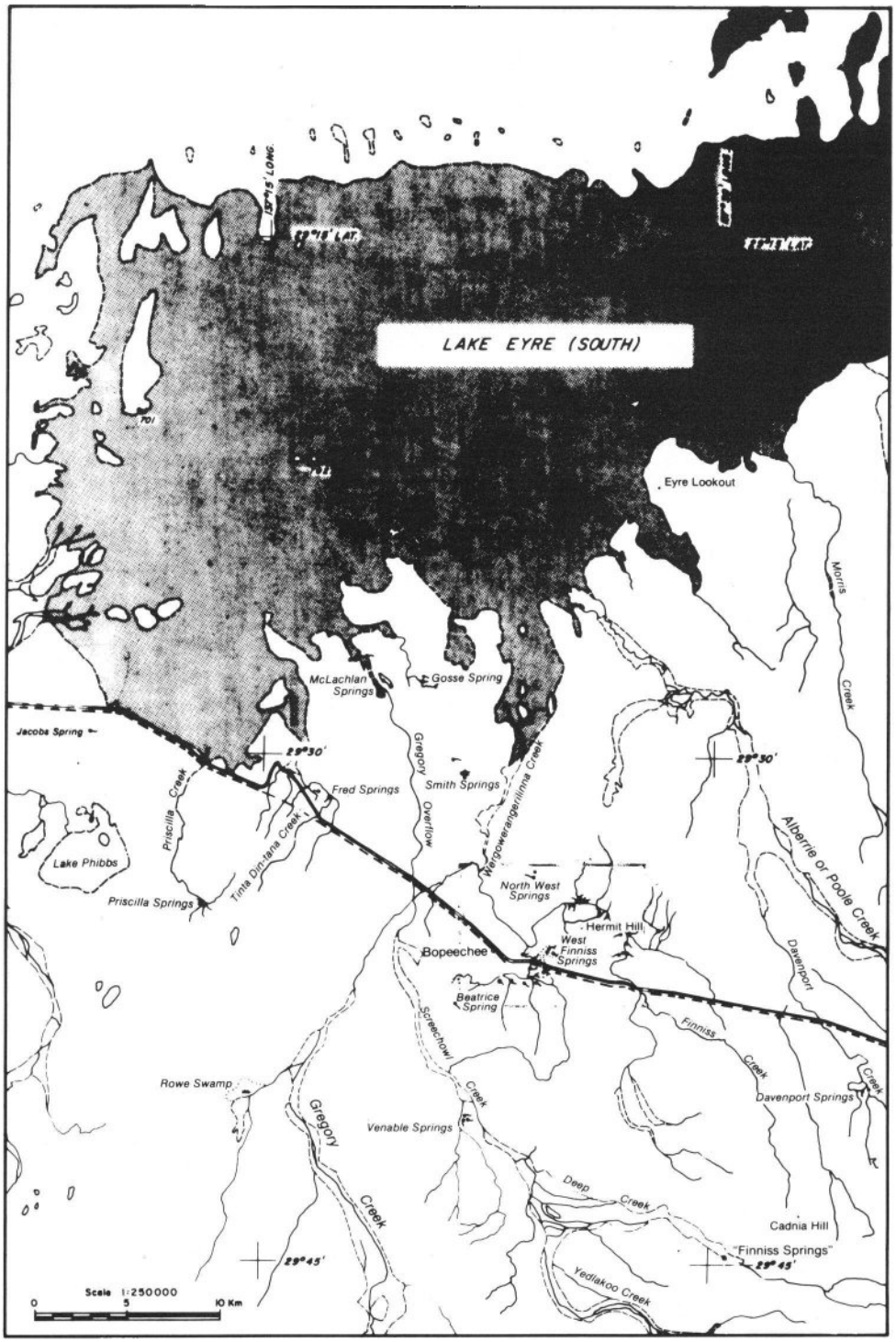

FIG. 62. The western Southern Springs.

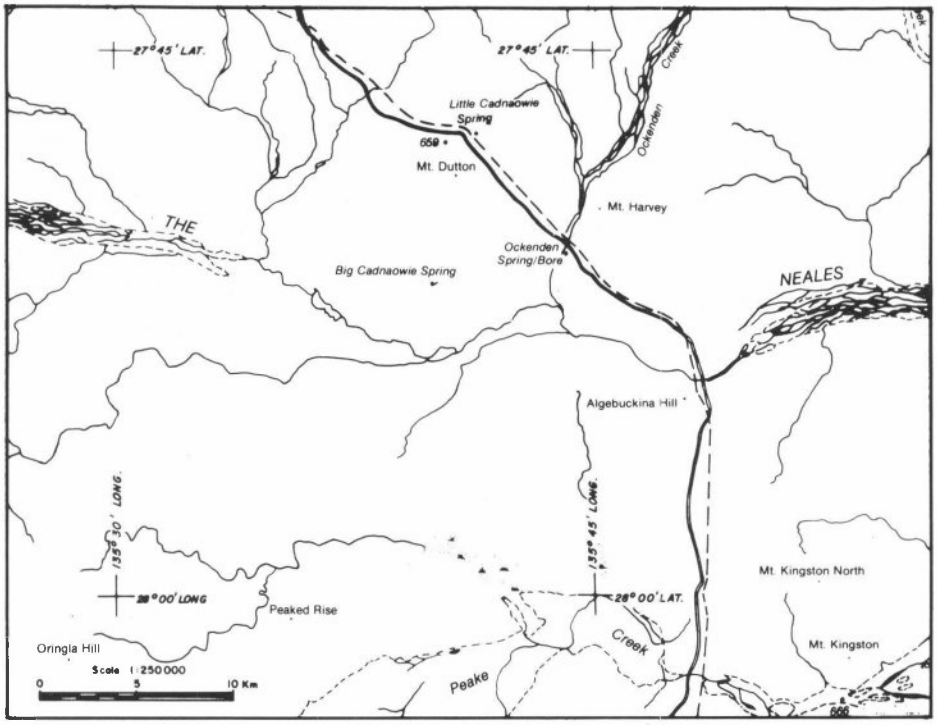

FIG. 63A. The Oodnadatta Springs and one of the Freeling Springs Group (station 666).

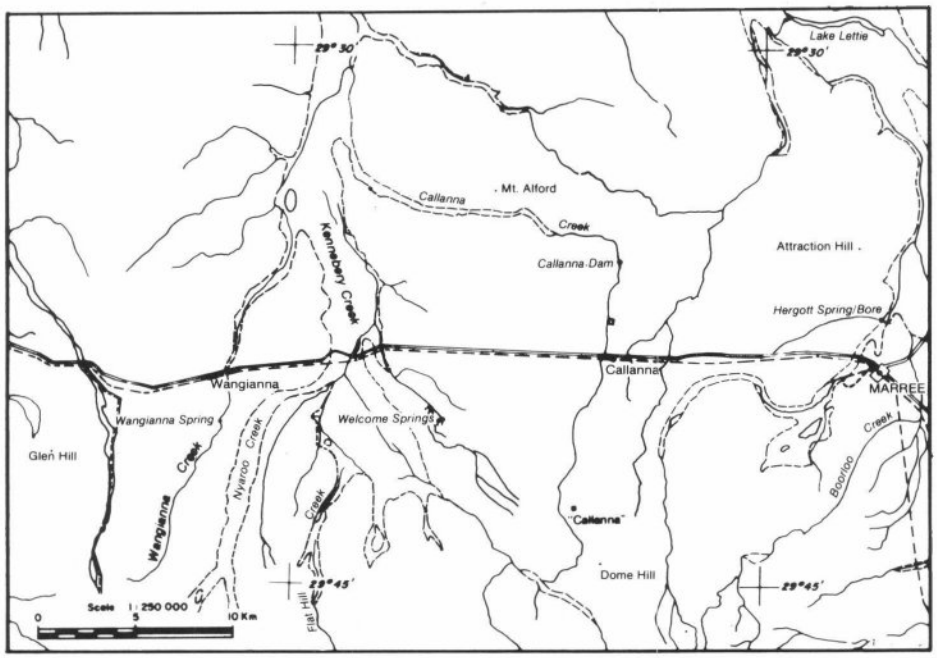

FIG. 63B. The easternmost Southern Springs.

APPENDIX 2

TABLES OF MEASUREMENTS

The following tables are a summary of the measurement data used in the statistical analyses. The original data set was analysed at the population level but the volume of these data is far too large for publication and, consequently, the data are presented only at the species level and for those infraspecific taxa recognised here as "forms". Copies of the full data set are housed in the Australian Museum and may be made available on request to the Senior author.

The means (top figure) and standard deviation (bottom figure) are given for each character for each species or form. The number of individuals measured is given in parenthesis in the first column, which also indicates the sex (F = female, M = male). Where the number of individuals measured for any one character is less than the number in the first column, this is indicated in parenthesis between the mean and SD. An explanation of the character codes and details concerning methods of measuring are given in the methods section.

TABLE 18A. *Fonscochlea accepta* and *F. aquatica,* shell and opercular measurements. AH, aperture height; AW, aperture width; BW, length of body whorl; CV, convexity of penultimate whorl; OL, length of operculum; PC, length of calcareous smear on operculum; PD, maximum diameter of protoconch; PH, height of tallest opercular peg; PN, number of opercular pegs; PW, number of protoconch whorls; SH, shell height; SW, shell width; TW, number of teleoconch whorls; WB, width of first half-whorl of body whorl.

Sex and No.		SH	SW	AH	AW	BW	WB	CV	PW	TW	PD	OL	PH	PC	PN
F. accepta form A (Stations 002, 003, 753, 755)															
F	$\bar{x}$	3.40	2.02	1.46	1.44	2.57	1.80 (26)	0.18 (26)	1.50 (33)	3.18	0.48 (33)	1.30 (31)	0.17 (31)	0.26 (31)	3.71 (31)
(39)	s	0.230	0.175	0.104	0.071	0.156	0.096	0.035	0.017	0.213	0.028	0.096	0.031	0.053	0.902
M	$\bar{x}$	3.30	1.96	1.43	1.43	2.51	1.77	0.17 (46)	1.50 (46)	3.12 (50)	0.48 (50)	1.30 (50)	0.17 (50)	0.25 (50)	3.74 (50)
(56)	s	0.225	0.166	0.097	0.074	0.149	0.083	0.033	0.034	0.227	0.042	0.094	0.027	0.054	1.121
F. accepta form B (Stations 689, 690, 691, 692, 693, 694A, 694B, 694C, 711, 712, 733, 735)															
F	$\bar{x}$	3.04	1.82	1.32	1.30	2.29	1.66 (138)	0.19 (138)	1.50 (133)	3.04 (157)	0.46 (131)	1.21 (135)	0.15 (135)	0.26 (135)	3.51 (135)
(158)	s	0.254	0.132	0.115	0.100	0.187	0.114	0.033	0.041	0.171	0.038	0.077	0.029	0.046	0.999
M	$\bar{x}$	2.97	1.79	1.31	1.29	2.25	1.65 (266)	0.18 (266)	1.48 (252)	3.01 (308)	0.46 (250)	1.20 (126)	0.15 (126)	0.26 (126)	3.49 (126)
(316)	s	0.259	0.133	0.112	0.109	0.201	0.125	0.032	0.058	0.165	0.038	0.082	0.029	0.042	1.002
F. accepta form C (Station 703)															
F	$\bar{x}$	3.26	1.97	1.51	1.45	2.45	1.77 (7)	0.19 (7)	1.44	3.09	0.44 (16)	1.26 (16)	0.17 (16)	0.25 (16)	3.13 (16)
(20)	s	0.150	0.097	0.095	0.049	0.096	0.037	0.022	0.064	0.143	0.031	0.041	0.020	0.050	0.806
M	$\bar{x}$	3.28	1.97	1.52 (3)	1.43 (3)	2.46	1.69	0.18	1.48	3.09	0.45	1.26 (11)	0.19 (11)	0.29 (11)	3.73 (11)
(15)	s	0.169	0.115	0.084	0.075	0.142	0.142	0.021	0.045	0.143	0.027	0.065	0.029	0.043	0.786
F. aquatica form A (Stations 006, 033, 039, 679, 683, 739, 741, 747, 764, 767)															
F	$\bar{x}$	4.19	2.37	1.86	1.70	3.06	2.09 (67)	0.18 (67)	1.50 (104)	3.23 (113)	0.55 (107)	1.49 (111)	0.10 (111)	0.20 (111)	2.55 (111)
(124)	s	0.386	0.201	0.145	0.131	0.218	0.170	0.029	0.050	0.238	0.055	0.127	0.051	0.106	1.419

(*continued*)

M	$\bar{x}$	3.95	2.28	1.78	1.64	2.91	1.97 (72)	0.17 (72)	1.49 (103)	3.20 (116)	0.53 (100)	1.52 (114)	0.10 (114)	0.20 (114)	2.44 (114)
(124)	s	0.432	0.241	0.170	0.155	0.239	0.190	0.030	0.042	0.250	0.051	0.134	0.051	0.105	1.337
F. aquatica form A (typical form: Stations 006, 033, 039, 679, 739, 747, 764)															
F	$\bar{x}$	4.33	2.45	1.90	1.75	3.12	2.17 (46)	0.19 (46)	1.51 (79)	3.30 (85)	0.55 (82)	1.58 (85)	0.13 (85)	0.25 (85)	2.85 (85)
(90)	s	0.255	0.158	0.113	0.105	0.159	0.114	0.030	0.053	0.155	0.052	0.079	0.038	0.064	1.200
M	$\bar{x}$	4.14	2.38	1.86	1.71	3.02	2.06 (47)	0.18 (47)	1.49 (75)	3.26 (87)	0.54 (72)	1.54 (84)	0.12 (84)	0.25 (84)	3.02 (84)
(89)	s	0.251	0.167	0.109	0.111	0.137	0.115	0.032	0.047	0.148	0.049	0.086	0.042	0.068	1.161
F. aquatica cf. form A (Stations 683, 741, 767)															
F	$\bar{x}$	3.84	2.17	1.74	1.57	2.91	1.91 (21)	0.17 (21)	1.49 (25)	3.02 (28)	0.55 (25)	1.36 (29)	0.04 (29)	0.06 (29)	1.24 (29)
(34)	s	0.445	0.155	0.157	0.099	0.276	0.142	0.022	0.034	0.313	0.067	0.137	0.023	0.057	0.951
M	$\bar{x}$	3.48	2.01	1.59	1.47	2.65	1.79 (25)	0.17 (25)	1.50 (28)	2.99 (29)	0.51 (28)	1.32 (27)	0.04 (27)	0.05 (27)	1.07 (27)
(35)	s	0.431	0.198	0.150	0.109	0.246	0.171	0.025	0.019	0.365	0.048	0.084	0.021	0.056	1.107
F. aquatica form B (Stations 046, 665)															
F	$\bar{x}$	4.14	2.32	1.82	1.61	2.85	2.13 (5)	0.23 (5)	1.54 (8)	3.33 (13)	0.54 (8)	1.52 (21)	0.14 (21)	0.39 (21)	3.15 (21)
(23)	s	0.223	0.112	0.129	0.132	0.140	0.103	0.016	0.106	0.205	0.023	0.064	0.038	0.089	0.801
M	$\bar{x}$	3.98	2.32	1.79	1.61	2.74	2.06 (5)	0.21 (5)	1.49 (13)	3.30 (18)	0.52 (13)	1.49 (25)	0.15 (25)	0.37 (25)	3.00 (25)
(29)	s	0.260	0.149	0.164	0.108	0.180	0.069	0.025	0.055	0.222	0.031	0.080	0.039	0.064	0.767

TABLE 18B. *Fonscochlea accepta* and *F. aquatica,* pallial measurements. AC, distance of gill apex from left side of filament; CO, distance between posterior end of ctenidium and posterior end of osphradium; DO, shortest distance between osphradium and edge of pallial cavity; FC, number of ctenidial filaments; HC, filament height; LC, length of ctenidium; LO, length of osphradium; ML, maximum length of pallial cavity; MM, minimum length of pallial cavity; MW, width of pallial cavity; WC, width of ctenidium; WO, width of osphradium.

Sex and No.		LC	WC	FC	AC	HC	LO	WO	DO	CO	ML	MM	MW
F. accepta form A (Stations 002, 003, 752, 753)													
F	$\bar{x}$	1.59	0.50	31.54	0.21	0.20	0.45	0.11	0.34	0.28	1.88	1.09	1.31
					(9)	(10)					(12)	(12)	(10)
(13)	s	0.274	0.073	2.222	0.090	0.052	0.084	0.019	0.149	0.073	0.243	0.126	0.113
M	$\bar{x}$	1.46	0.52	30.85	0.23	0.20	0.41	0.12	0.33	0.27	1.84	1.09	1.24
(13)	s	0.224	0.069	2.911	0.063	0.027	0.083	0.026	0.150	0.060	0.328	0.122	0.093
F. accepta form B (Stations 689, 690, 692, 694, 711)													
F	$\bar{x}$	1.36	0.45	30.28	0.16	0.12	0.38	0.10	0.23	0.27	1.71	0.93	1.24
									(17)		(17)	(17)	
(18)	s	0.121	0.073	2.469	0.046	0.027	0.055	0.013	0.055	0.055	0.161	0.093	0.117
M	$\bar{x}$	1.30	0.47	28.83	0.16	0.12	0.37	0.11	0.23	0.23	1.59	0.88	1.20
(13)	s	0.124	0.058	2.368	0.044	0.029	0.033	0.014	0.049	0.064	0.120	0.095	0.099
F. accepta form C (Station 703)													
F	$\bar{x}$	1.69	0.49	32.50	0.13	0.26	0.43	0.10	0.12	1.39	1.96	1.01	1.48
		(4)		(4)	(4)								
(5)	s	0.193	0.034	2.380	0.041	0.023	0.026	0.011	0.006	0.126	0.256	0.073	0.149
M	$\bar{x}$	1.70	0.53	33.00	0.18	0.26	0.38	0.10	0.34	0.29	1.97	0.93	1.38
		(3)		(3)		(3)			(3)	(3)			
(4)	s	0.172	0.053	2.646	0.035	0.038	0.056	0.013	0.038	0.074	0.086	0.059	0.091
F. aquatica form A (Stations 028, 030, 039, 679, 683, 720, 723, 739, 741, 747, 767, 771)													
F	$\bar{x}$	1.59	0.45	34.49	0.22	0.15	0.39	0.12	0.35	0.27	1.97	1.07	1.49
		(33)		(33)	(34)	(24)	(33)	(33)	(28)	(29)	(34)	(33)	(32)
(35)	s	0.260	0.138	4.529	0.100	0.039	0.103	0.023	0.079	0.090	0.346	0.350	0.367
M	$\bar{x}$	1.42	0.43	34.05	0.22	0.14	0.36	0.12	0.32	0.24	1.81	0.97	1.41
		(20)	(20)	(20)	(20)	(15)	(20)	(20)	(20)	(21)	(19)	(19)	(20)
(22)	s	0.247	0.167	5.596	0.075	0.040	0.031	0.025	0.067	0.107	0.273	0.224	0.316
F. aquatica form A (typical form: Stations 028, 030, 039, 679, 720, 723, 739, 747, 771)													
F	$\bar{x}$	1.68	0.45	37.00	0.22	0.18	0.39	0.12	0.38	0.31	2.02	1.03	1.62
		(18)		(19)		(11)			(17)	(16)	(19)	(18)	(18)
(20)	s	0.223	0.173	3.844	0.109	0.030	0.128	0.024	0.073	0.067	0.317	0.291	0.399
M	$\bar{x}$	1.56	0.43	37.82	0.22	0.17	0.37	0.11	0.35	0.31	1.93	1.02	1.56
		(11)	(11)	(11)	(11)	(9)	(11)	(11)	(11)	(12)	(10)	(10)	(11)
(13)	s	0.193	0.220	3.710	0.080	0.028	0.027	0.016	0.060	0.052	0.310	0.283	0.317
F. aquatica cf. form A (Stations 683, 741, 767, 771)													
F	$\bar{x}$	1.49	0.45	31.07	0.21	0.12	0.40	0.12	0.31	0.23	1.91	1.12	1.31
				(14)	(14)	(13)	(13)	(13)	(11)	(13)			(14)
(15)	s	0.267	0.074	2.868	0.090	0.029	0.046	0.024	0.075	0.100	0.381	0.416	0.232
M	$\bar{x}$	1.25	0.42	29.44	0.21	0.11	0.35	0.12	0.27	0.15	1.67	0.91	1.20
						(8)							
(9)	s	0.196	0.073	3.712	0.071	0.027	0.033	0.033	0.045	0.094	0.143	0.128	0.145
F. aquatica form B (Stations 045, 046, 665)													
F	$\bar{x}$	1.56	0.49	33.25	0.18	0.16	0.37	0.12	0.29	0.35	1.82	1.10	1.33
				(8)					(8)				
(10)	s	0.037	0.025	1.581	0.031	0.015	0.008	0.035	0.071	0.054	0.110	0.057	0.139
M	$\bar{x}$	1.47	0.53	33.75	0.23	0.15	0.39	0.14	0.33	0.32	1.88	1.05	1.40
(8)	s	0.146	0.019	2.315	0.032	0.020	0.045	0.032	0.086	0.039	0.224	0.080	0.070

TABLE 18C. *Fonscochlea accepta* and *F. aquatica*, miscellaneous measurements. BM, length of buccal mass; CA, distance between ctenidium and anus; DG, length of digestive gland anterior to gonad; LD, length of digestive gland; LG, length of gonad; LS, length of snout; LT, length of cephalic tentacles; MA, shortest distance of anus from mantle edge; RS, length of radular sac behind buccal mass.

Sex and No.		LS	LT	LD	DG	LG	BM	RS	CA	MA
F. accepta form A (Stations 002, 003, 752, 753)										
F	$\bar{x}$	0.57	0.48	3.42	0.66	1.71	0.76	1.42	0.57	0.76
		(10)	(10)	(10)	(6)	(10)	(4)	(10)	(10)	
(13)	s	0.128	0.078	1.026	0.360	0.472	0.058	0.193	0.132	0.217
M	$\bar{x}$	0.59	0.47	3.56	0.34	2.44	0.58	1.42	0.56	0.79
		(10)	(10)	(10)	(5)	(10)	(7)	(10)	(10)	
(13)	s	0.118	0.072	0.687	0.142	0.411	0.232	0.144	0.096	0.171
F. accepta form B (Stations 689, 690, 692, 694, 711)										
F	$\bar{x}$	0.41	0.41	2.29	0.35	1.28	0.69	1.10	0.53	0.53
		(5)	(5)	(5)	(4)	(5)	(5)	(5)		(15)
(16)	s	0.053	0.090	0.401	0.092	0.119	0.104	0.124	0.102	0.090
M	$\bar{x}$	0.46	0.41	2.76	0.19	2.01	0.70	1.18	0.60	0.55
		(4)	(4)	(4)	(4)	(4)	(4)	(4)		
(11)	s	0.154	0.085	0.272	0.057	0.178	0.047	0.173	0.110	0.109
F. accepta form C (Station 703)										
F	$\bar{x}$	0.48	0.53	2.72	0.31	1.60	0.66	1.30	0.88	0.68
		(4)	(4)	(4)	(4)	(4)	(4)	(4)		
(5)	s	0.072	0.046	0.350	0.087	0.158	0.075	0.095	0.094	0.144
M	$\bar{x}$	0.47	0.57	3.20	0.33	2.23	0.65	1.26	0.83	0.82
(4)	s	0.078	0.078	0.304	0.047	0.209	0.063	0.279	0.138	0.142
F. aquatica form A (Stations 028, 030, 039, 679, 683, 720, 723, 739, 741, 747, 767, 771)										
F	$\bar{x}$	0.63	0.55	3.23	0.46	1.75	0.99	1.61	0.65	0.74
		(23)	(24)	(26)	(26)	(28)	(24)	(30)	(22)	(22)
(35)	s	0.108	0.160	0.631	0.138	0.660	0.067	0.244	0.163	0.180
M	$\bar{x}$	0.58	0.48	2.93	0.41	1.98	0.93	1.53	0.60	0.77
		(16)	(17)	(17)	(17)	(18)	(17)	(19)	(18)	(18)
(22)	s	0.095	0.109	0.723	0.100	0.649	0.079	0.193	0.185	0.222
F. aquatica form A (typical form: Stations 028, 030, 039, 679, 720, 723, 739, 747)										
F	$\bar{x}$	0.65	0.62	3.47	0.47	2.00	0.95	1.61	0.58	0.74
		(10)	(12)	(17)	(17)	(19)	(12)	(19)	(10)	(9)
(20)	s	0.143	0.180	0.498	0.109	0.642	0.042	0.235	0.105	0.103
M	$\bar{x}$	0.61	0.52	3.47	0.45	2.43	0.95	1.57	0.65	0.86
		(7)	(8)	(8)	(8)	(9)	(8)	(10)	(9)	(9)
(11)	s	0.099	0.099	0.476	0.099	0.518	0.031	0.199	0.209	0.269
F. aquatica cf. form A (Stations 683, 741, 767, 771)										
F	$\bar{x}$	0.61	0.49	2.79	0.45	1.23	1.03	1.61	0.71	0.75
		(13)	(12)	(9)	(9)	(9)	(12)	(12)	(12)	(13)
(15)	s	0.072	0.109	0.635	0.188	0.299	0.062	0.127	0.183	0.223
M	$\bar{x}$	0.56	0.43	2.45	0.38	1.53	0.91	1.49	0.55	0.69
(9)	s	0.092	0.106	0.546	0.096	0.412	0.104	0.189	0.153	0.125
F. aquatica form B (Stations 045, 046, 665)										
F	$\bar{x}$	0.55	0.56	3.19	0.60	1.29	0.89	1.71	0.74	0.59
		(8)	(8)	(8)	(6)	(6)				
(10)	s	0.075	0.117	0.408	0.036	0.165	0.052	0.188	0.056	0.084
M	$\bar{x}$	0.54	0.54	3.11	0.52	1.86	0.83	1.48	0.73	0.70
(8)	s	0.085	0.148	0.509	0.111	0.191	0.085	0.082	0.113	0.093

TABLE 18D. *Fonscochlea accepta* and *F. aquatica*, stomach and male genital measurements. AS, height of anterior stomach chamber; PL, length of penis; PP, length of pallial portion of prostate gland; PR, length of prostate gland; PS, height of posterior stomach chamber; PW, width of prostate gland; SL, length of stomach; SS, length of style sac.

Sex and No.		SL	SS	AS	PS	PL	PR	PW	PP
F. accepta form A (Stations 002, 003, 752)									
F	$\bar{x}$	1.05	0.61	0.72	0.63				
(10)	s	0.333	0.085	0.124	0.066				
M	$\bar{x}$	0.95	0.55	0.64	0.53	2.66	0.52	0.33 (7)	0.10
(10)	s	0.383	0.102	0.081	0.046	0.593	0.108	0.046	0.086
F. accepta form B (Stations 692, 711)									
F	$\bar{x}$	0.73	0.50	0.65	0.51				
(5)	s	0.073	0.024	0.085	0.060				
M	$\bar{x}$	0.69	0.47	0.61	0.53	1.73	0.46	0.29	0.08
(4)	s	0.082	0.061	0.094	0.095	0.311	0.079	0.054	0.021
F. accepta form C (Station 703)									
F	$\bar{x}$	0.98	0.49	0.66	0.65				
(4)	s	0.052	0.064	0.053	0.032				
M	$\bar{x}$	0.90	0.49 (3)	0.66	0.64	2.32	0.55	0.25 (3)	0.10
(4)	s	0.102	0.012	0.048	0.078	0.184	0.089	0.035	0.042
F. aquatica form A (Stations 028, 030, 039, 679, 683, 720, 723, 739, 741, 747, 767, 771)						(Stations 039, 683, 720, 723, 739, 741, 747, 767, 771)			
F	$\bar{x}$	1.14	0.69	0.85	0.69				
(31)	s	0.402	0.108	0.156	0.153				
M	$\bar{x}$	0.96 (16)	0.61	0.77	0.65 (18)	2.33 (13)	0.51 (14)	0.35 (12)	0.11 (12)
(18)	s	0.286	0.114	0.126	0.124	0.743	0.114	0.065	0.089
F. aquatica form A (typical form: Stations 028, 030, 039, 679, 720, 723, 739, 747, 771)						(Stations 039, 720, 723, 739, 747, 771)			
F	$\bar{x}$	1.32	0.74	0.91	0.75				
(18)	s	0.439	0.078	0.160	0.148				
M	$\bar{x}$	1.13	0.66	0.85 (7)	0.73	2.52 (8)	0.55 (9)	0.38 (7)	0.11 (8)
(15)	s	0.262	0.093	0.150	0.063	0.874	0.115	0.055	0.108
F. aquatica cf. form A (Stations 683, 741, 767)									
F	$\bar{x}$	0.89	0.61	0.77	0.60				
(13)	s	0.120	0.093	0.106	0.117				
M	$\bar{x}$	0.79	0.56	0.70	0.57	2.04 (5)	0.43 (5)	0.30 (5)	0.10 (4)
(9)	s	0.193	0.113	0.049	0.122	0.320	0.073	0.048	0.038
F. aquatica form B (Stations 045, 046, 665)									
F	$\bar{x}$	1.09	0.69	0.77	0.70				
(10)	s	0.111	0.052	0.072	0.068				
M	$\bar{x}$	1.12	0.70	0.79	0.74	2.87	0.56	0.34	0.11
(8)	s	0.044	0.034	0.013	0.051	0.178	0.019	0.071	0.012

TABLE 18E. *Fonscochlea accepta* and *F. aquatica,* female genital measurements. AG, length of albumen gland; BC, length of bursa copulatrix; BS, length of oviduct between "seminal receptacle" and bursa copulatrix; CG, length of capsule gland; CV, length of coiled portion of oviduct; DB, length of duct of bursa copulatrix; DR, length of duct of "seminal receptacle"; DV, maximal diameter of coiled portion of oviduct; GO, length of glandular oviduct; GP, length of female genital opening; MO, minimal diameter of coiled portion of oviduct; SR, length of "seminal receptacle"; VC, length of free portion of ventral channel; WB, width of bursa copulatrix; WR, width of "seminal receptacle".

No.		GO	CG	AG	BC	WB	DB	SR	WR	DR	CV	DV	MO	VC	BS	GP
F. accepta form A (Stations 002, 003, 752)																
	$\bar{x}$	1.82	1.03	0.78	0.21	0.19	0.03 (9)	0.26	0.21	0.06	1.15	0.12	0.06	0.31	0.63	0.04 (7)
(10)	s	0.322	0.202	0.140	0.042	0.030	0.009	0.090	0.033	0.025	0.542	0.016	0.009	0.222	0.099	0.010
F. accepta form B (Stations 692, 711)																
	$\bar{x}$	1.77 (4)	1.04 (4)	0.68 (3)	0.19	0.16	0.03	0.28	0.18	0.03	1.52	0.11 (4)	0.06 (4)	0.45	0.64	0.05 (2)
(5)	s	0.049	0.058	0.082	0.055	0.043	0.008	0.076	0.019	0.011	0.265	0.005	0.006	0.068	0.085	0
F. accepta form C (Station 703)																
	$\bar{x}$	1.79	1.12	0.67	0.18	0.15	0.03	0.29	0.19	0.03	1.39	0.12	0.05 (3)	0.32	0.49	0.05
(4)	s	0.071	0.068	0.080	0.033	0.022	0.015	0.065	0.024	0.015	0.126	0.006	0.006	0.073	0.015	0.008
F. aquatica form A (Stations 028, 030, 039, 679, 683, 720, 723, 739, 741, 747, 767, 771)																
	$\bar{x}$	1.75 (32)	0.95 (33)	0.81 (32)	0.21 (32)	0.21 (32)	0.04 (32)	0.25 (32)	0.23 (32)	0.05 (30)	1.85 (32)	0.11 (27)	0.06 (29)	0.88 (32)	0.40 (33)	0.06 (21)
(34)	s	0.292	0.166	0.158	0.053	0.046	0.028	0.053	0.038	0.029	0.305	0.019	0.011	0.243	0.133	0.017
F. aquatica form A (Typical form: Stations 028, 030, 039, 679, 720, 723, 739, 747, 767, 771)																
	$\bar{x}$	1.86 (19)	0.99 (19)	0.87 (19)	0.24 (19)	0.23 (19)	0.047 (19)	0.26 (19)	0.23 (19)	0.07 (17)	2.00	0.11 (15)	0.07 (17)	0.97 (19)	0.42	0.07 (11)
(20)	s	0.279	0.177	0.138	0.048	0.044	0.023	0.058	0.037	0.030	0.264	0.023	0.008	0.173	0.158	0.014
F. aquatica cf. form A (Stations 683, 741, 767, 771)																
	$\bar{x}$	1.60 (13)	0.90	0.71 (13)	0.17 (13)	0.17 (13)	0.04 (13)	0.25 (13)	0.22 (13)	0.04 (13)	1.59 (12)	0.11 (12)	0.05 (12)	0.75 (13)	0.36 (13)	0.06 (10)
(14)	s	0.240	0.140	0.135	0.021	0.023	0.033	0.045	0.040	0.015	0.167	0.012	0.010	0.280	0.072	0.016
F. aquatica form B (Station 046, 665)																
	$\bar{x}$	1.78 (6)	0.94 (6)	0.84 (6)	0.25 (8)	0.21 (8)	0.02 (7)	0.22 (8)	0.24 (8)	0.05 (8)	1.61 (8)	0.11	0.06 (8)	1.03	0.33 (8)	0.05 (6)
(10)	s	0.068	0.092	0.023	0.028	0.024	0	0.025	0.018	0.024	0.063	0.008	0	0.121	0.018	0

TABLE 19A. *Fonscochlea variabilis, F. billakalina* and *F. conica*, shell and opercular measurements. AH, aperture height; AW, aperture width; BW, length of body whorl; CV, convexity of penultimate whorl; OL, length of operculum; PC, length of calcareous deposit; PD, maximal length of protoconch; PH, height of tallest opercular peg; PN, number of opercular pegs; PW, number of protoconch whorls; SH, shell height; SW, shell width; TW, number of teleoconch whorls; WB, width of first half-whorl of body whorl.

Sex and No.		SH	SW	AH	AW	BW	WB	CV	PW	TW	PD	OL	PH	PC	PN
F. variabilis form A (Stations 014, 018, 739)															
F	$\bar{x}$	2.42	1.42	1.07	1.03	1.77	1.23 (31)	0.18 (31)	1.51 (48)	2.80 (48)	0.41 (48)	0.86	0.15	0.24	3.14
(49)	s	0.199	0.131	0.083	0.070	0.130	0.093	0.041	0.037	0.232	0.039	0.065	0.026	0.041	0.707
M	x	2.28	1.34	1.01	0.98	1.70	1.13 (25)	0.18 (25)	1.50 (46)	2.73 (46)	0.41 (46)	0.81 (46)	0.14 (46)	0.24 (46)	2.96 (46)
(48)	s	2.221	0.138	0.095	0.069	0.127	0.066	0.051	0.076	0.048	0.037	0.069	0.027	0.048	0.759
F. variabilis (small Blanche Cup form: Station 739)															
F	$\bar{x}$	1.44	0.93	0.68	0.65	1.176	0.89	0.17	0.30 (4)	1.98 (4)	0.41 (4)	0.57 (19)	0.08 (19)	0.10 (19)	1.42 (19)
(20)	s	0.145	0.071	0.053	0.082	0.118	0.081	0.049	0	0.065	0.053	0.052	0.029	0.048	0.607
M	$\bar{x}$	1.40	0.90	0.65	0.66	1.13	0.85	0.19	1.35 (2)	2.15 (2)	0.38 (2)	0.54 (32)	0.09 (32)	0.1 (32)	1.75 (32)
(35)	s	0.148	0.073	0.062	0.068	0.104	0.077	0.049	0.071	0.071	0.014	0.045	0.021	0.038	0.508
F. variabilis form B (Stations 032, 034, 037, 673)															
F	$\bar{x}$	2.79	1.64	1.19	1.15	2.01	1.39 (17)	0.19 (17)	1.50 (13)	2.98	0.41 (15)	0.95	0.11	0.31	4.85
(40)	s	0.357	0.186	0.141	0.130	0.220	0.193	0.032	0	0.184	0.041	0.104	0.024	0.072	1.442
M	$\bar{x}$	2.58	1.53	1.12	1.08	1.87	1.26 (11)	0.16 (11)	1.50 (14)	2.89	0.41 (15)	0.88	0.10	0.28	3.88
(32)	s	0.184	0.138	0.091	0.071	0.113	0.106	0.047	0	0.193	0.021	0.059	0.022	0.054	0.907

(*continued*)

F. variabilis form C (Stations 045, 665)															
F	$\bar{x}$	2.84	1.72	1.24	1.26	2.10	1.49	0.20 (7)	1.50 (7)	2.96 (11)	0.42	1.03	0.16	0.43	4.44
(18)	s	0.013	0.157	0.112	0.098	0.152	0.030	0.032	0	0.234	0.026	0.013	0.017	0.062	1.097
M	$\bar{x}$	2.60	1.61	1.16	1.15	1.95	1.35 (3)	0.23 (3)	1.50 (11)	2.84	0.40 (11)	0.91	0.13	0.37	4.36
(14)	s	0.248	0.120	0.092	0.076	0.144	0.047	0.006	0	0.220	0.022	0.021	0.030	0.048	0.477
F. billakalina (Stations 026, 029, 679, 721, 723, 763)															
F	$\bar{x}$	2.64	1.55	1.17	1.14	1.94	1.29 (59)	0.14 (59)	1.51 (16)	2.77	0.44 (25)	0.94 (70)	0.07 (70)	0.13 (70)	1.59 (70)
(83)	s	0.273	0.149	0.111	0.115	0.174	0.095	0.047	0.077	0.246	0.029	0.093	0.030	0.089	1.056
M	$\bar{x}$	2.60	1.51	1.15	1.13	1.92	1.27 (47)	0.15 (47)	1.51 (13)	2.75	0.43 (21)	0.93 (56)	0.07 (56)	0.13 (56)	1.39 (56)
(67)	s	0.289	0.161	0.125	0.118	0.188	0.102	0.048	0.028	0.273	0.028	0.102	0.028	0.080	1.021
F. conica (Stations 003, 007, 019, 020, 021, 023, 024, 681, 755, 766, 769)															
F	$\bar{x}$	2.07	1.20	0.86	0.85	1.52	1.02 (54)	0.16 (54)	1.50 (110)	2.67	0.40 (112)	0.71	0.10	0.18	2.64
(127)	s	0.237	0.130	0.090	0.088	0.150	0.119	0.044	0.038	0.231	0.040	0.068	0.024	0.045	0.906
M	$\bar{x}$	1.95	1.14	0.82	0.80	1.44	1.00 (46)	0.13 (46)	1.49 (104)	2.57	0.39 (105)	0.67	0.10	0.17	2.48
(114)	s	0.224	0.119	0.091	0.088	0.156	0.113	0.040	0.073	0.224	0.036	0.071	0.020	0.046	0.924

TABLE 19B. *Fonscochlea variabilis, F. billakalina* and *F. conica,* miscellaneous, pallial and stomach measurements. AC, width of ctenidium; AS, height of anterior stomach chamber; CO, distance between posterior tip of osphradium and posterior tip of ctenidium; DG, length of digestive gland anterior to gonad; DO, shortest distance between osphradium and edge of pallial cavity; FC, number of ctenidial filaments; LC, length of ctenidium; LD, length of digestive gland; LG, length of gonad; LO, length of osphradium; ML, maximal length of pallial cavity; MM, minimal length of pallial cavity; MW, width of pallial cavity; PS, height of posterior stomach chamber; RS, length of radular sac behind buccal mass; SL, length of stomach + style sac; SS, length of style sac; WC, width of ctenidium; WO, width of osphradium.

Sex & No.		LD	LG	DG	RS	LC	WC	FC	AC	LO	WO	DO	CO	ML	MM	MW	SL	SS	AS	PS
F. variabilis form A (Stations 008, 014)																				
F	$\bar{x}$	1.72	0.80	0.16 (1)	—	0.74	0.19	17.00	0.21 (2)	0.20	0.15	0.16 (2)	—	—	—	1.04	0.90	0.44	0.51 (2)	0.40 (2)
(3)	s	0.387	0.229	—	—	0.133	0.058	2.646	0.071	0.012	0.023	0.042	—	—	—	0.323	0.169	0.166	0.113	0.092
M	$\bar{x}$	1.71	1.31	0.14	—	0.76	0.20	20.50	0.20	0.27	0.10	0.19	—	1.13	0.68	1.25	0.73	0.30	0.53	—
(2)	s	0.537	0.453	0.071	—	0.099	0.057	0.707	0.057	0.014	0.014	0.064	—	0.283	0.212	0.191	0.141	0.127	0.049	—
F. variabilis form B (Station 031)																				
F (1)		1.33	0.63	0.19	0.86	0.86	0.23	27.00	0.23	0.29	0.11	0.33	0.26	0.99	0.53	1.33	1.03	0.33	0.66	0.36
M (1)		2.76	1.66	0.26	1.06	0.93	0.16	21.00	0.16	0.26	0.09	0.23	0.09	0.96	0.29	1.06	1.16	0.53	0.59	0.46
F. variabilis form C (Station 042)																				
F (1)		1.83	0.89	0.26	1.03	0.96	0.29	24.00	0.29	0.28	0.09	0.26	0.13	1.33	0.49	—	1.03	0.46	0.59	0.41
M (1)		1.49	0.96	0.33	1.33	0.93	0.28	24.00	0.28	0.26	0.10	—	0.23	1.49	0.59	0.43	0.93	0.36	0.66	0.44
F. billakalina (Stations 026, 029)																				
F	$\bar{x}$	2.28	0.94 (4)	0.33 (2)	0.90 (4)	1.07	0.33	27.00	0.27 (4)	0.33 (4)	0.11 (4)	0.23 (4)	0.32 (4)	1.53	0.49 (4)	1.28 (4)	0.91 (4)	0.36 (4)	0.52 (4)	0.32 (3)
(5)	s	0.663	0.387	0.050	0.184	0.277	0.135	5.958	0.029	0.112	0.019	0.091	0.160	0.421	0.136	0.230	0.099	0.025	0.062	0.051
M	$\bar{x}$	2.23 (2)	2.18 (2)	0.05 (2)	1.09	1.48	0.29	25.67	0.24	0.29	0.11	0.22	0.22	1.45	0.33 (1)	1.35	0.75	0.30	0.49	0.33
(3)	s	0.141	0.162	0.021	0.152	0.166	0.055	0.577	0.040	0.035	0.019	0.023	0.098	0.215	—	2.201	0.051	0.060	0.065	0
F. conica (Stations 005, 007, 020, 024, 748)																				
F	$\bar{x}$	1.29 (7)	0.39 (8)	0.29 (7)	0.80 (7)	0.72	0.18	20.40	0.17	0.19 (9)	0.08 (9)	0.12 (9)	0.12 (9)	0.83 (9)	0.38 (8)	0.84 (8)	0.54 (6)	0.24 (6)	0.37 (6)	0.23 (6)
(10)	s	0.364	0.128	0.110	0.071	0.157	0.045	2.270	0.040	0.053	0.009	0.036	0.044	0.157	0.111	0.131	0.149	0.042	0.038	0.021
M	$\bar{x}$	1.13 (9)	0.65 (8)	0.21 (7)	0.56 (9)	0.63	0.16	17.55	0.13 (10)	0.14	0.07	0.13 (10)	0.11 (9)	0.78	0.33 (10)	0.68 (9)	0.40 (10)	0.21 (9)	0.30 (10)	0.21 (9)
(11)	s	0.275	0.316	0.137	0.165	0.161	0.064	3.446	0.055	0.045	0.014	0.044	0.034	0.197	0.110	0.198	0.161	0.061	0.053	0.045

TABLE 19C. *Fonscochlea variabilis, F. billakalina* and *F. conica,* female and male genital measurements. AG, length of albumen gland; BC, length of bursa copulatrix; BS, length of oviduct between "seminal receptacle" and bursa copulatrix; CG, length of capsule gland; CV, length of coiled portion of oviduct; DB, length of duct of bursa copulatrix; DR, length of duct of "seminal receptacle"; DV, maximal diameter of coiled portion of oviduct; GO, length of glandular oviduct; MO, minimal diameter of coiled portion of oviduct; PL, length of penis; PP, length of pallial portion of prostate gland; PR, length of prostate gland; SR, length of "seminal receptacle"; VC, length of free portion of ventral channel; WB, width of bursa copulatrix; WR, width of "seminal receptacle."

Sex & No.		GO	CG	AG	BC	WB	DB	SR	WR	DR	CV	DV	MO	VC	BS	Sex & No.	PL	PR	PP
F. variabilis form A (Stations 008, 014)																(Station 014)			
F	$\bar{x}$	1.16	0.71	0.44	0.20	0.15	—	0.19	0.17	0.04	0.81	0.11	0.07	0.50	0.31	M	1.10	0.53	0.31
		(2)	(2)	(2)						(3)		(3)	(2)	(2)	(2)				
(5)	s	0	0.071	0.071	0.029	0.030	—	0.046	0.016	0.005	0.134	0.043	0.007	0.233	0.113	(2)	0.191	0.092	0.028
F. variabilis form B (Station 031)																			
F		1.46	0.83	0.63	0.13	0.16	0.09	0.13	0.16	0.01	0.93	0.07	0.04	1.23	0.19	M	3.06	0.53	0.19
(1)																(1)			
F. variabilis form C (Station 042)																			
F		1.39	0.83	0.56	0.23	0.16	0.04	0.23	0.16	0.01	0.24	—	0.04	0.99	0.19	M	1.36	0.49	0.39
(1)																(1)			
F. billakalina (Stations 026, 029)																(station 26)			
F	$\bar{x}$	1.48	0.92	0.55	0.20	0.14	0.07	0.18	0.15	0.06	1.19	0.07	0.04	0.58	0.13	M	1.11	0.44	0.14
					(4)	(4)	(4)	(4)	(4)	(2)					(4)				
(5)	s	0.382	0.266	0.158	0.049	0.025	0.024	0.024	0.022	—	0.259	0.013	0.006	0.368	0.097	(3)	0.040	0.075	0.015
F. conica (Stations 005, 007, 020, 024, 748)																(Stations 005,748)			
F	$\bar{x}$	0.75	0.43	0.32	0.12	0.11	0.04	0.11	0.11	0.05	0.59	0.05	0.03	0.43	0.16	M	0.87	0.29	0.09
					(8)	(8)	(8)	(8)	(8)	(4)	(8)	(7)	(7)	(8)				(7)	
(9)	s	0.166	0.104	0.088	0.021	0.030	0.028	0.027	0.037	0.019	0.100	0.005	0.007	0.143	0.134	(9)	0.327	0.121	0.066

TABLE 20A. *Fonscochlea zeidleri,* shell and opercular measurements. AH, aperture height; AW, aperture width; BW, length of body whorl; CV, convexity of penultimate whorl; OL, length of operculum; PC, length of calcareous deposit; PD, maximal length of protoconch; PH, height of tallest opercular peg; PN, number of opercular pegs; PW, number of protoconch whorls; SH, shell height; SW, shell width; TW, number of teleoconch whorls; WB, width of first half-whorl of body whorl.

Sex and No.		SH	SW	AH	AW	BW	WB	CV	PW	TW	PD	OL	PH	PC	PN
F. zeidleri form A (Stations 011, 018, 024, 025, 028, 030, 664, 671, 694, 741, 755, 771)															
F	$\bar{x}$	3.69	2.32	1.55	1.45	2.58	2.02	0.18	1.52	3.55	0.53	1.35	0.31	0.39	4.02
							(30)	(30)	(119)	(119)	(119)	(100)	(100)	(100)	(100)
(132)	s	0.538	0.287	0.156	0.189	0.256	0.161	0.035	0.069	0.291	0.044	0.118	0.046	0.065	0.791
M	$\bar{x}$	3.66	2.26	1.53	1.46	2.55	2.05	0.16	1.51	3.52	0.52	1.33	0.32	0.39	4.02
							(46)	(46)	(112)	(116)	(112)	(102)	(102)	(102)	(102)
(121)	s	0.447	0.295	0.148	0.160	0.228	0.188	0.044	0.062	0.315	0.042	0.118	0.047	0.074	1.015
F. zeidleri form B (Station 661)															
F	$\bar{x}$	3.46	2.23	1.62	1.37	2.62	1.96	0.17	1.51	3.09	—	1.31	0.30	0.34	3.40
							(5)	(5)	(10)	(10)		(20)	(20)	(20)	(20)
(21)	s	0.177	0.016	0.095	0.107	0.109	0.059	0.033	0.016	0.166	—	0.066	0.029	0.034	0.754
M	$\bar{x}$	3.37	2.21	1.58	1.37	2.58	1.93	0.18	1.50	3.00	0.55	1.31	0.29	0.35	3.85
							(5)	(5)	(7)	(7)	(1)	(13)	(13)	(13)	(13)
(15)	s	0.189	0.130	0.089	0.112	0.122	0.049	0.026	0	0.057	0	0.063	0.037	0.036	0.987

TABLE 20B. *Fonscochlea zeidleri,* pallial measurements. AC, width of ctenidium from left side to position of filament apex; CO, distance between posterior tip of osphradium and posterior tip of ctenidium; DO, shortest distance between osphradium and edge of pallial cavity; FC, number of ctenidial filaments; HC, filament height; LC, length of ctenidium; LO, length of osphradium; ML, maximal length of pallial cavity; MM, minimal length of pallial cavity; MW, width of pallial cavity; WC, width of ctenidium; WO, width of osphradium.

Sex and No.		LC	WC	FC	AC	HC	LO	WO	DO	CO	ML	MM	MW
F. zeidleri form A (Stations 011, 013, 018, 024, 026, 028, 030, 034, 039, 046, 694, 742, 766, 771)													
F	$\bar{x}$	1.43	0.43	26.68	0.19	0.11	0.44	0.12	0.28	0.30	2.05	1.02	1.49
		(32)	(33)		(31)	(16)	(31)	(32)	(26)	(23)	(25)	(29)	(27)
(34)	s	0.365	0.136	3.042	0.088	0.039	0.125	0.034	0.088	0.094	0.427	0.364	0.438
M	$\bar{x}$	1.28	0.43	25.42	0.20	0.08	0.38	0.13	0.27	0.29	1.66	0.93	1.47
		(23)	(23)	(24)	(23)	(12)	(22)	(22)	(18)	(22)	(21)	(19)	(21)
(25)	s	0.355	0.164	3.175	0.105	0.023	0.139	0.086	0.095	0.124	0.414	0.223	0.368
F. zeidleri form B (Station 661)													
F	$\bar{x}$	1.26	0.37	23.20	0.14	0.12	0.36	0.09	0.31	0.28	1.59	0.91	1.29
(5)	s	0.171	0.069	0.837	0.048	0.038	0.038	0.007	0.082	0.024	0.225	0.084	0.142
M	$\bar{x}$	1.23	0.33	24.00	0.15	0.14	0.35	0.11	0.30	0.28	1.51	0.95	1.31
(4)	s	0.115	0.039	1.633	0.012	0.035	0.021	0.025	0.030	0.057	0.183	0.197	0.138

TABLE 20C. *Fonscochlea zeidleri,* miscellaneous measurements. BM, length of buccal mass; CA, distance between ctenidium and anus; DG, length of digestive gland anterior to gonad; LD, length of digestive gland; LG, length of gonad; LS, length of snout; LT, length of tentacles; MA, distance of anus from mantle edge; RS, length of radular sac behind buccal mass.

Sex and No.		LS	LT	LD	DG	LG	BM	RS	CA	MA
F. zeidleri zeidleri (Stations 011, 013, 018, 024, 026, 028, 030, 034, 039, 046, 694, 742, 766, 771)										
F	$\bar{x}$	0.53	0.38	3.27	0.45	1.50	0.74	0.87	0.47	0.40
		(18)	(18)	(27)	(24)	(26)	(18)	(27)	(16)	(15)
(34)	s	0.100	0.076	1.050	0.123	0.640	0.105	0.136	0.137	0.150
M	$\bar{x}$	0.48	0.35	3.52	0.33	2.46	0.63	0.83	0.57	0.33
		(13)	(13)	(22)	(22)	(22)	(13)	(21)	(17)	(12)
(27)	s	0.078	0.080	0.771	0.100	0.852	0.124	0.164	0.234	0.083
F. zeidleri form B (Station 661)										
F	$\bar{x}$	0.45	0.41	3.00	0.38	1.55	0.63	0.84	0.49	0.43
(5)	s	0.065	0.075	0.245	0.065	0.136	0.046	0.061	0.080	0.071
M	$\bar{x}$	0.45	0.38	2.51	0.32	1.48	0.63	0.90	0.48	0.40
(4)	s	0.021	0.055	0.255	0.116	0.219	0.067	0.104	0.118	0.096

TABLE 20D. *Fonscochlea zeidleri,* stomach and male genital measurements. AS, height of anterior stomach chamber; PL, length of penis; PP, length of pallial portion of prostate gland; PR, length of prostate gland; PS, height of posterior stomach chamber; PW, width of prostate gland; SL, length of stomach + style sac; SS, length of style sac.

Sex and No.		SL	SS	AS	PS	PL	PR	PW	PP
F. zeidleri form A		(Stations 011, 013, 018, 024, 026, 030, 034, 039, 046, 694, 742, 766, 771)				(Stations 011, 018, 024, 034, 039, 694, 742, 766, 771)			
F	$\bar{x}$	1.02	0.71	0.81	0.68				
		(17)	(27)	(20)	(25)				
(28)	s	0.320	0.151	0.143	0.138				
M	$\bar{x}$	0.93	0.70	0.74	0.64	1.83	0.65	0.37	0.14
		(14)	(22)	(19)	(19)	(23)	(24)	(17)	(23)
(24)	s	0.377	0.168	0.177	0.133	0.537	0.290	0.129	0.119
F. zeidleri form B (Station 661)									
F	$\bar{x}$	0.83	0.69	0.68	0.64				
(5)	s	0.040	0.072	0.050	0.028				
M	$\bar{x}$	0.82	0.69	0.68	0.63	1.59	0.56	0.32	0.14
									(3)
(4)	s	0.025	0.064	0.062	0.044	0.113	0.047	0.060	0.082

TABLE 20E. *Fonscochlea zeidleri,* female genital measurements. AG, length of albumen gland; BC, length of bursa copulatrix; BS, length of oviduct between "seminal receptacle" and bursa copulatrix; CG, length of capsule gland; CV, length of coiled portion of oviduct; DB, length of duct of bursa copulatrix; DR, length of duct of "seminal receptacle"; DV, maximal diameter of coiled portion of oviduct; GO, length of glandular oviduct; GP, length of genital opening; MO, minimal diameter of coiled portion of oviduct; SR, length of "seminal receptacle"; VC, length of free portion of ventral channel; WB, width of bursa copulatrix; WR, width of "seminal receptacle".

Sex and No.		GO	CG	AG	BC	WB	DB	SR	WR	DR	CV	DV	MO	VC	BS	GP
F. zeidleri form A (Stations 011, 013, 018, 024, 026, 030, 046, 694, 742, 766, 771)																
F	$\bar{x}$	1.55	0.86	0.72	0.24	0.22	0.099	0.31	0.24	0.10	1.56	0.11	0.06	0.47	0.15	0.07
		(25)	(25)	(26)			(27)	(27)	(27)	(26)	(22)	(25)	(27)	(27)	(26)	(17)
(28)	s	0.467	0.246	0.220	0.071	0.048	0.031	0.122	0.079	0.057	0.261	0.022	0.011	0.104	0.053	0.020
F. zeidleri form B (Station 661)																
F	$\bar{x}$	1.49	0.80	0.68	0.20	0.18	0.04	0.23	0.24	0.09	1.26	0.09	0.05	0.40	0.15	0.05
					(4)	(4)										(4)
(5)	s	0.132	0.082	0.055	0.017	0.006	0.011	0.023	0.041	0.020	0.071	0.011	0.005	0.028	0.023	0.005

TABLE 21A. *Trochidrobia* species, shell measurements. AH, aperture height; AW, aperture width; BW, length of body whorl; PD, maximal length of protoconch; PW, number of protoconch whorls; SH, shell height; SW, shell width; TW, number of teleoconch whorls.

Sex and No.		SH	SW	AH	AW	BW	PW	TW	PD
T. punicea (Stations 002, 007, 008, 022, 025, 027)									
F	$\bar{x}$	1.43	1.74	0.80	0.80	1.26	1.48 (83)	1.97	0.37 (90)
(95)	s	0.136	0.263	0.085	0.068	0.136	0.073	0.145	0.038
M	$\bar{x}$	1.35	1.64	0.77	0.75	1.18	1.48 (34)	1.86	0.36
(36)	s	0.145	0.104	0.068	0.059	0.128	0.059	0.143	0.041
T. smithi (Stations 033, 038)									
F	$\bar{x}$	1.48	1.80	0.86	0.85	1.30	1.50	1.92	0.41
(26)	s	0.167	0.145	0.062	0.061	0.165	0.072	0.117	0.035
M	$\bar{x}$	1.48	1.80	0.85	0.83	1.30	1.50	1.92	0.40
(19)	s	0.153	0.122	0.058	0.056	0.113	0.046	0.119	0.030
T. minuta (Station 045)									
F	$\bar{x}$	0.69	1.11	0.44	0.47	0.61	1.46	1.43	0.33
(11)	s	0.061	0.052	0.036	0.026	0.054	0.081	0.085	0.029
M	$\bar{x}$	0.72	1.10	0.44	0.47	0.64	1.43	1.47	0.34
(12)	s	0.092	0.070	0.035	0.033	0.077	0.098	0.054	0.033
T. inflata (Station 043)									
F	$\bar{x}$	1.51	1.53	0.86	0.81	1.26	1.50	1.95	0.41
(11)	s	0.172	0.170	0.105	0.084	0.155	0	0.204	0.017
M	$\bar{x}$	1.43	1.45	0.80	0.75	1.18	1.53	1.89	0.42
(11)	s	0.140	0.140	0.056	0.064	0.128	0.090	0.140	0.024

TABLE 21B. *Trochidrobia* species, pallial, miscellaneous and stomach measurements. AC, width of ctenidium; AS, height of anterior stomach chamber; CA, distance between ctenidium and anus; CO, distance between posterior tip of osphradium and posterior tip of ctenidium; DG, length of digestive gland anterior to gonad; DO, shortest distance between osphradium and edge of pallial cavity; FC, number of ctenidial filaments; LC, length of ctenidium; LD, length of digestive gland; LG, length of gonad; LO, length of osphradium; ML, maximal length of pallial cavity; MM, minimal length of pallial cavity; MW, width of pallial cavity; PS, height of posterior stomach chamber; RS, length of radular sac behind buccal mass; SL, length of stomach + style sac; SS, length of style sac; WC, width of ctenidium; WO, width of osphradium.

Sex & No.		LD	LG	DG	RS	CA	LC	WC	FC	AC	LO	WO	DO	CO	ML	MM	MW	SL	SS	AS	PS
T. punicea (Stations 002, 007, 009, 020, 024, 693, 748)																					
F	$\bar{x}$	2.00	0.80	0.43	0.32	0.29	0.85	0.24	19.50	0.21	0.26	0.09	0.16	0.14	0.80	0.45	1.03	1.04	0.45	0.48	0.32
		(7)	(8)	(5)	(3)	(9)	(9)			(4)	(9)		(9)	(7)	(7)	(7)	(9)	(7)	(7)	(7)	(7)
(10)	s	0.551	0.357	0.127	0.052	0.091	0.197	0.047	2.369	0.027	0.071	0.030	0.056	0.050	0.104	0.144	0.149	0.115	0.060	0.060	0.058
M	$\bar{x}$	1.45	0.82	0.25	0.31	0.27	0.72	0.21	18.63	0.17	0.25	0.08	0.15	0.10	0.87	0.38	0.93	0.78	0.33	0.40	0.24
		(6)	(6)	(6)	(5)	(7)	(6)	(7)		(4)	(7)	(6)	(7)	(6)	(7)	(6)	(7)	(7)	(6)	(7)	(4)
(8)	s	0.429	0.349	0.089	0.047	0.106	0.131	0.055	3.292	0.061	0.059	0.021	0.044	0.029	0.218	0.049	0.111	0.119	0.090	0.093	0.013
T. smithi (Stations 027, 029, 033, 037, 038, 039, 679, 681, 721)																					
F	$\bar{x}$	1.69	0.59	0.41	0.20	0.34	0.98	0.28	19.93	0.25	0.24	0.08	0.16	0.18	0.95	0.51	1.19	0.91	0.34	0.46	0.32
		(9)	(10)	(10)	(9)	(12)	(13)	(13)		(7)	(13)		(13)	(12)	(12)	(10)	(11)	(10)	(10)	(10)	(9)
(14)	s	0.459	0.130	0.096	0.049	0.071	0.385	0.048	1.328	0.051	0.040	0.013	0.053	0.047	0.248	0.061	0.227	0.103	0.058	0.047	0.048
M	$\bar{x}$	1.94	1.54	0.20	0.16	0.32	0.91	0.26	20.00	0.24	0.24	0.08	0.16	0.18	0.93	0.50	1.18	0.88	0.33	0.47	0.35
		(4)	(4)	(4)	(4)	(4)	(7)	(7)		(2)	(7)	(7)	(6)	(6)	(5)	(5)	(4)	(4)	(4)	(4)	(4)
(8)	s	0.578	0.649	0.032	0.030	0.103	0.152	0.043	1.414	0.014	0.034	0.015	0.034	0.046	0.262	0.089	0.228	0.098	0.047	0.048	0.115
T. minuta (Stations 043, 045)																					
F	$\bar{x}$	1.02	0.25	0.23	0.17	0.08	0.58	0.14	15.00	—	0.16	0.08	0.13	0.17	0.64	0.31	0.70	0.57	0.24	0.26	0.23
		(2)	(3)	(2)	(2)	(2)	(2)	(2)	(2)		(2)	(2)	(2)	(2)	(2)	(1)	(2)			(2)	
(3)	s	0.289	0.045	0.035	0.028	0.071	0.078	0.057	2.828	—	0	0.021	0.042	0.092	0.078	—	0.057	0.023	0.015	0.042	0.055
M	$\bar{x}$	1.22	0.88	0.14	0.17	0.10	0.56	0.15	17.20	—	0.17	0.08	0.14	0.12	0.67	0.36	0.67	0.59	0.25	0.30	0.21
		(2)		(2)	(2)	(4)								(3)	(4)	(3)	(4)	(3)	(3)	(3)	(3)
(5)	s	0.247	0.216	0.042	0.014	0.053	0.175	0.054	2.387	—	0.044	0.015	0.043	0.040	0.262	0.091	0.075	0.070	0.075	0.078	0.050
T. inflata (Stations 043, 044)																					
F	$\bar{x}$	2.13	0.47	0.30	0.20	0.25	0.94	0.26	20.00	—	0.25	0.10	0.22	0.28	1.05	0.66	1.17	0.89	0.35	0.50	0.40
		(1)		(3)	(2)	(2)	(3)	(3)	(3)		(3)	(3)	(2)	(3)	(2)	(3)	(3)	(3)			
(4)	s	—	0.150	0.040	0	0.127	0.086	0.025	2.646	—	0.015	0.010	0.064	0.080	0.021	0.123	0.170	0.123	0.018	0.043	0.085
M	$\bar{x}$	1.87	1.43	0.29	0.22	0.26	1.00	0.21	20.00	—	0.21	0.08	0.19	0.19	1.01	0.49	1.11	0.84	0.37	0.48	0.34
		(2)	(2)	(2)	(2)	(2)										(2)		(2)	(2)	(2)	(2)
(3)	s	0.176	0.106	0.077	0.021	0.049	0.078	0.027	1.000	—	0.040	0.021	0.031	0.035	0.167	0.035	0.111	0.120	0.042	0.106	0.042

TABLE 21C. *Trochidrobia* species, female and male genital measurements. AG, length of albumen gland; BC, length of bursa copulatrix; CG, length of capsule gland; CV, length of coiled portion of oviduct; DB, length of duct of bursa copulatrix; DV, maximal diameter of coiled portion of oviduct; GO, length of glandular oviduct; MO, minimal diameter of coiled portion of oviduct; PL, length of penis; PP, length of pallial portion of prostate gland; PR, length of prostate gland; PW, width of prostate gland; VC, length of free portion of ventral channel; WB, width of bursa copulatrix.

Sex & No.		GO	CG	AG	BC	WB	DB	CV	DV	MO	VC	Sex & No.	PL	PR	PW	PP
T. punicea (Stations 002, 007, 009, 020, 693)												(Stations 007, 009, 024, 693, 748)				
F	$\bar{x}$	1.13	0.53	0.61	0.28	0.20	0.27	1.43	0.13	0.05	0.34	M	1.06	0.51	0.26	0.19
		(9)		(9)			(9)	(8)	(8)	(7)	(6)		(7)		(4)	(7)
(10)	s	0.240	0.180	0.230	0.106	0.087	0.194	0.253	0.034	0.014	0.160	(10)	0.126	0.095	0.060	0.031
T. smithi (Stations 027, 033, 036, 037, 038, 039, 681, 721)												(Stations 033, 037, 038, 039, 679)				
F	$\bar{x}$	0.99	0.48	0.52	0.16	0.14	0.03	0.79	0.06	0.04	0.06	M	0.68	0.29	0.11	0.16
					(14)	(14)	(14)		(11)	(10)	(9)		(4)		(2)	(6)
(15)	s	0.196	0.153	0.108	0.027	0.025	0.014	0.085	0.011	0.003	0.039	(8)	0.099	0.075	0	0.059
T. minuta (Stations 043, 045)																
F	$\bar{x}$	0.63	0.32	0.30	0.17	0.09	0.02	0.51	0.04	0.03	0.24	M	0.56	0.27	—	0.11
							(2)				(2)		(2)			(2)
(3)	s	0.092	0.066	0.055	0.012	0.006	0.007	0.104	0.006	0	0.070	(4)	0.106	0.063	—	0.007
T. inflata (Stations 043, 044)																
F	$\bar{x}$	1.03	0.55	0.42	0.18	0.14	0.02	0.50	0.06	0.04	0.10	M	0.87	0.25	—	0.10
		(3)	(3)				(2)		(3)	(2)	(2)		(2)			(2)
(4)	s	0.078	0.118	0.165	0.025	0.023	0	0.190	0.015	0	0.014	(3)	0	0.051	—	0.021