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

By W.F. Ponder, R. Hershler*, and B. Jenkins,

The Australian Museum, Sydney South, NSW, 2000, Australia

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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 Ciénegas 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 Potamopsidae 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.

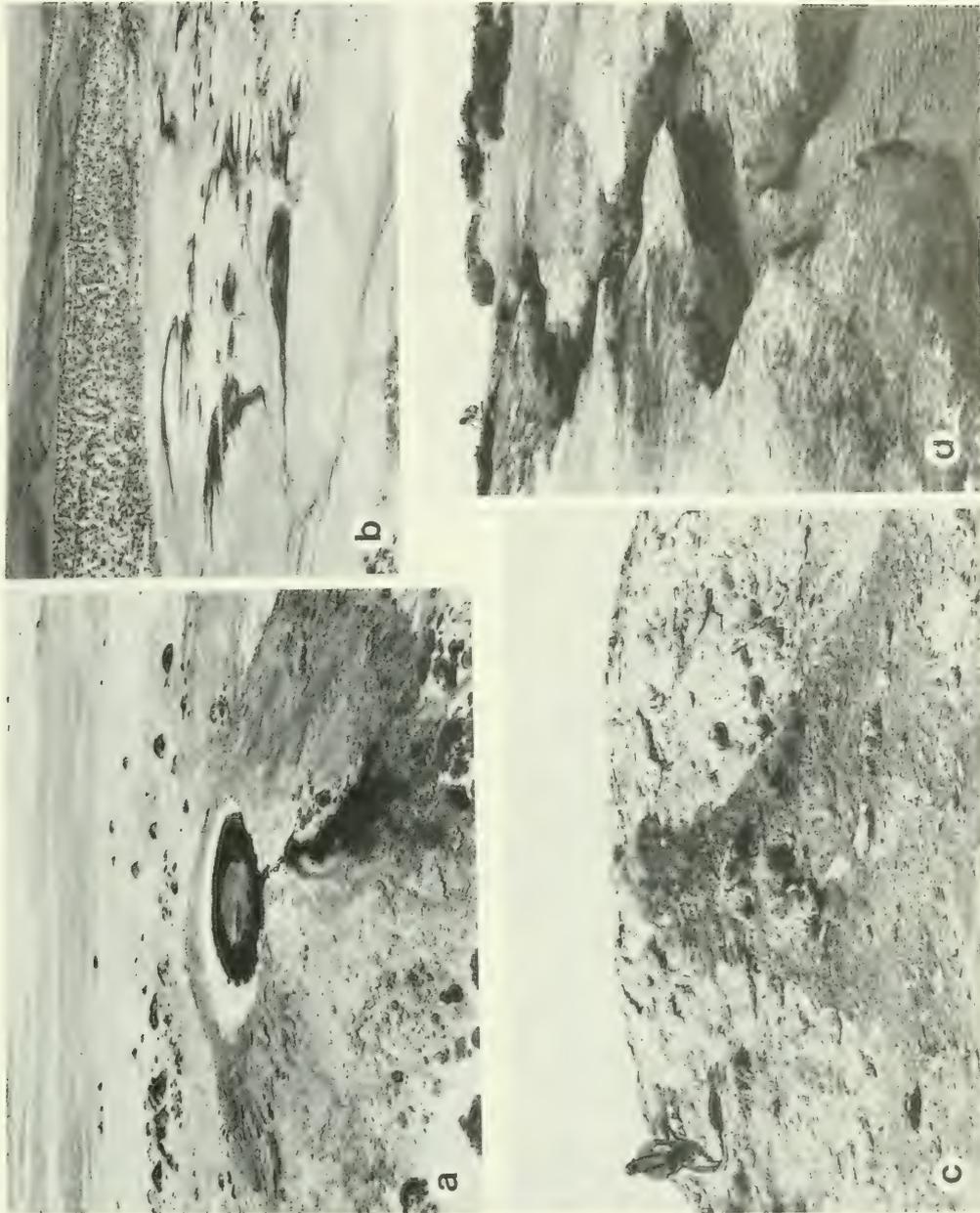


FIG. 1. Various springs in the Lake Eyre Supergroup showing some of the morphological diversity.
 A. Blanche Cup Spring (Stns 8–12), a conical, calcareous mound spring with a crater-like pool.
 B. Aerial view of part of Hermit Hill Spring Complex showing part of a spring group (Finniss Swamp West) composed 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.

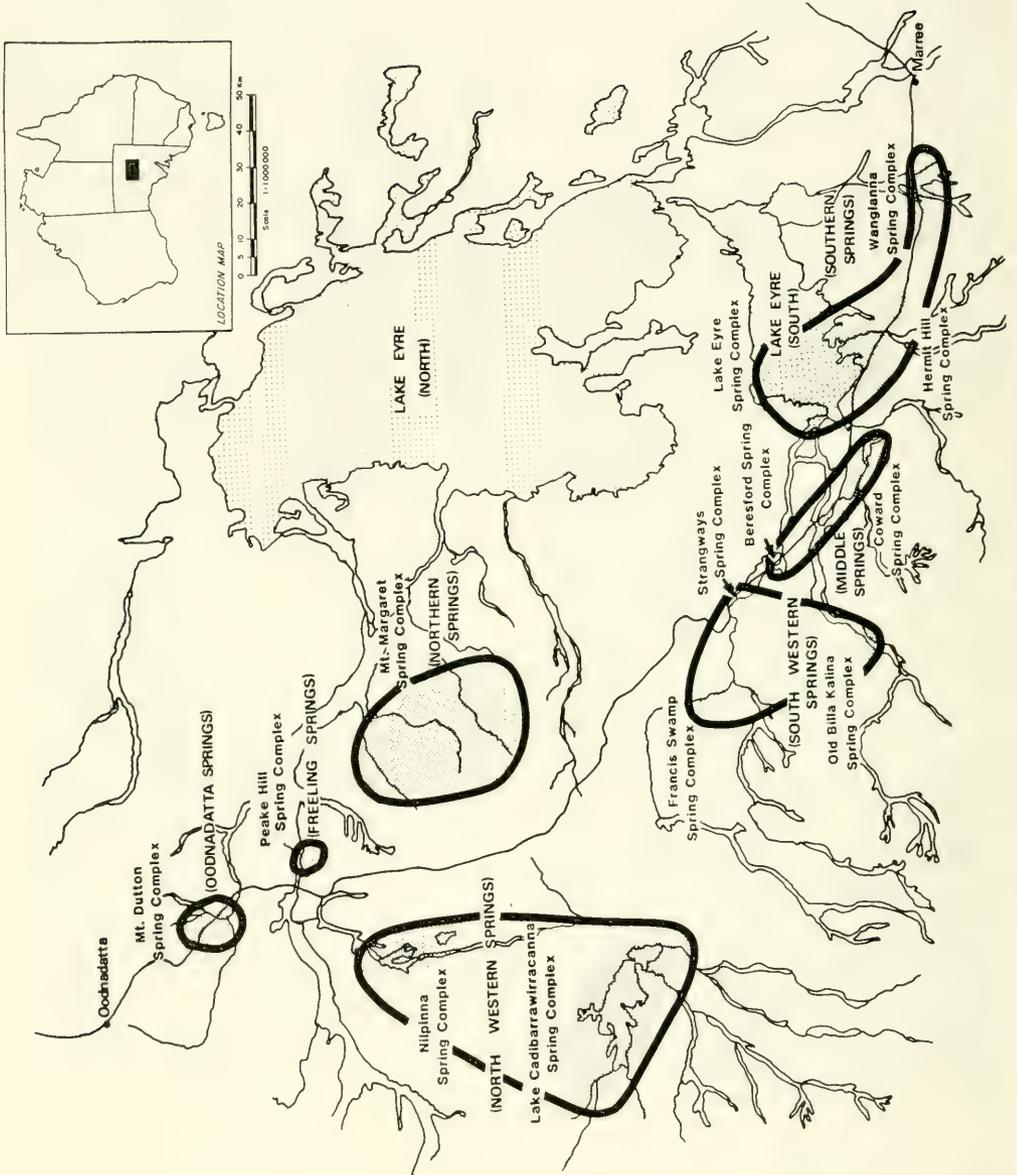


FIG. 2. The major spring complexes in the Lake Eyre Spring Group.

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. DeDecker (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 world-wide 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 Kerlatroaboorn-tallina 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., Finnis Swamp West (= West Finnis), 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	<i>F. zeidlerii</i> form A	<i>F. zeidlerii</i> form B	<i>F. aquatica</i> form A	<i>F. aquatica</i> form B	<i>F. accepta</i> form A	<i>F. accepta</i> form B	<i>F. accepta</i> form C	<i>F. variabilis</i> form A	<i>F. variabilis</i> form B	<i>F. variabilis</i> form C	<i>F. billakalina</i>	<i>F. conica</i>	<i>T. punicea</i>	<i>T. smithi</i>	<i>T. minuta</i>	<i>T. inflata</i>	SPRING COMPLEX
<u>Southern Springs</u>																	
Welcome group	x				x							x	x				Wangianna Spring Complex
Davenport group	x				x							x	x				
Old Woman group	x					x						x	x				
West Finnis group	x					x						s	x				
Hermit Springs group	x					x							x				
Old Finnis group	x					x							x				Hermit Hill Spring Complex
Dead Boy Spring						x							x				
Sulphuric group						x							x				
Bopeechee Spring						x							x				
Venable Spring	s					s						s	s				
Priscilla Spring	s					s						s	s				Lake Eyre Spring Complex
Centre Island Spring	s																
Emerald Spring							x										
<u>Middle Springs</u>																	
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 group (785, 787)	x	x										x	x				Blanche Cup Spring Complex
Blanche Cup Spring	x	x					x						x				
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 Complex
Julie group	x	x										x	x				
Elizabeth group	x	x										x	x				
Jersey group	x	x										x	x				
Warburton group	x	x										x	x				Beresford Spring Complex
Beresford group	x	x										x	x				
<u>South-Western Springs</u>																	
Strangways group	x	x									x		x				Strangways Spring Complex
Billa Kalina group	x	x									x		x				Old Billa Kalina Spring Complex
Fenced Spring	x	x									x		x				
Welcome Bore Spring	s										s						
Margaret Spring	s	s									s		s				Francis Swamp Spring Complex
Francis Swamp group	x	x									x		x				
Loyd Bore spring	x	x									x		x				
<u>Northern Springs</u>																	
Brinkley Spring	x	x												x			
Hawker group	x	x						x						x			
Twelve Mile group	x	x						x						x	x		Mt. Margaret Spring Complex
Outside group	x	x						x						x	x		
Fountain group	x	x						x						x	x		
Big Perry Spring	x	x						x						x	x		
Spring Hill Spring	s																
<u>Freeling Springs</u>																	
Freeling group	x		x							x				x	x		Peake Hill Spring Complex
North of Freeling Spring														x			
<u>Oodnadatta Springs</u>																	
Big Cadnaowie		x															Mt. Dutton Spring Complex

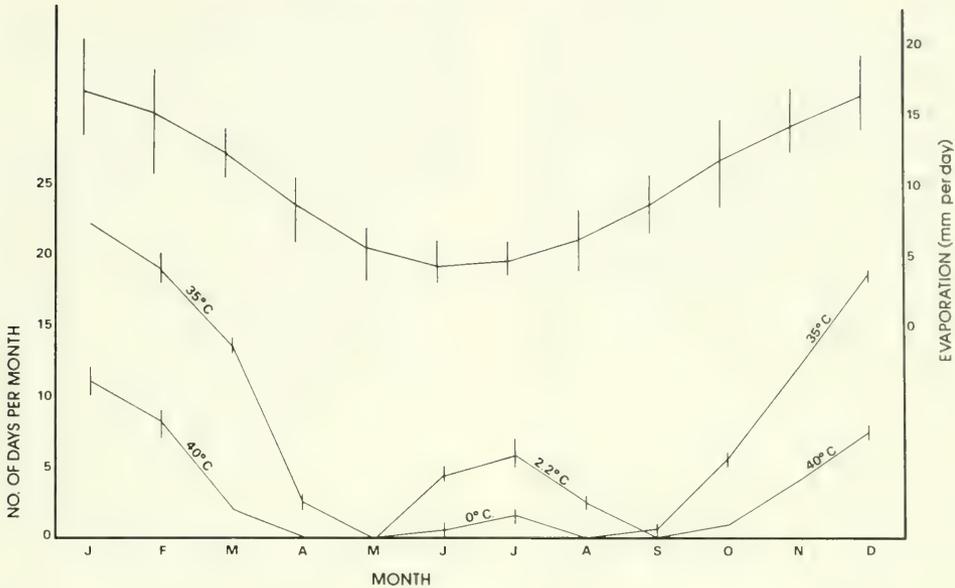


FIG. 3. Temperature and evaporation data for Marree and Oodnadatta. Mean daily evaporation, for each month, is given only for Oodnadatta, 1968–1982. The temperature data are for Marree, 1957–1982, and Oodnadatta, 1940–1982 together (with error bars indicating the range that the two encompass) and consists 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 $10\times$ eyepieces, and $12\times$ (large species) or $25\times$ (small species) magnification for all shell features except protoconch diameter ($50\times$). 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

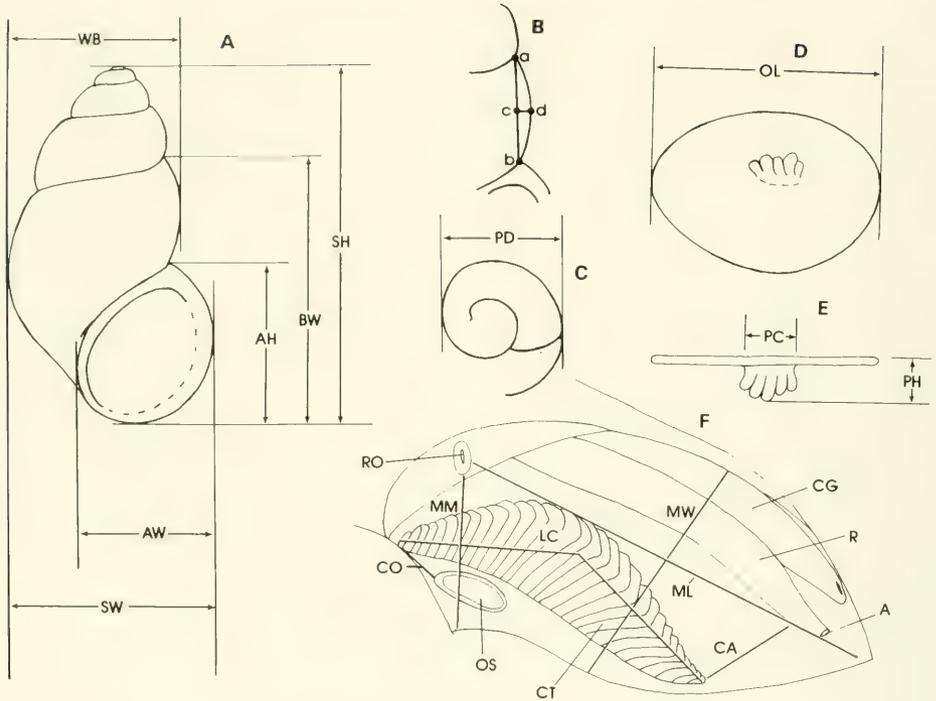


FIG. 4. Shell and operculum, showing various measurements.

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 *Fanscochlea*. 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 anal-

yses (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. zeidlerii*): 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 rec-

tum (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 Finnis 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 Finnis 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 be-

ginning 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.

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

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.

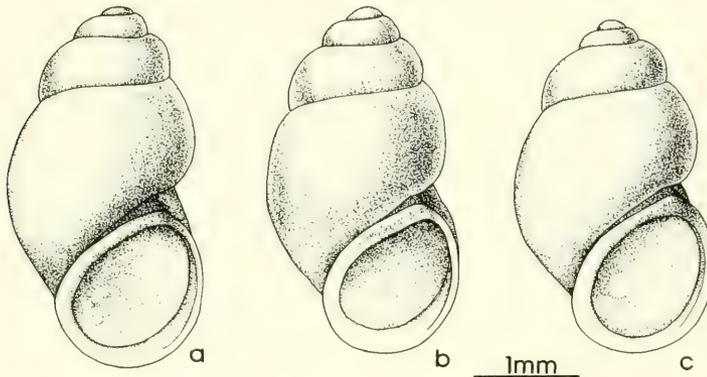


FIG. 5. Shells of *Fonscochlea accepta*.

- a. *Fonscochlea accepta* form A, holotype. Welcome Springs (003).
 b. *Fonscochlea accepta* form B. Old Finnis 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,

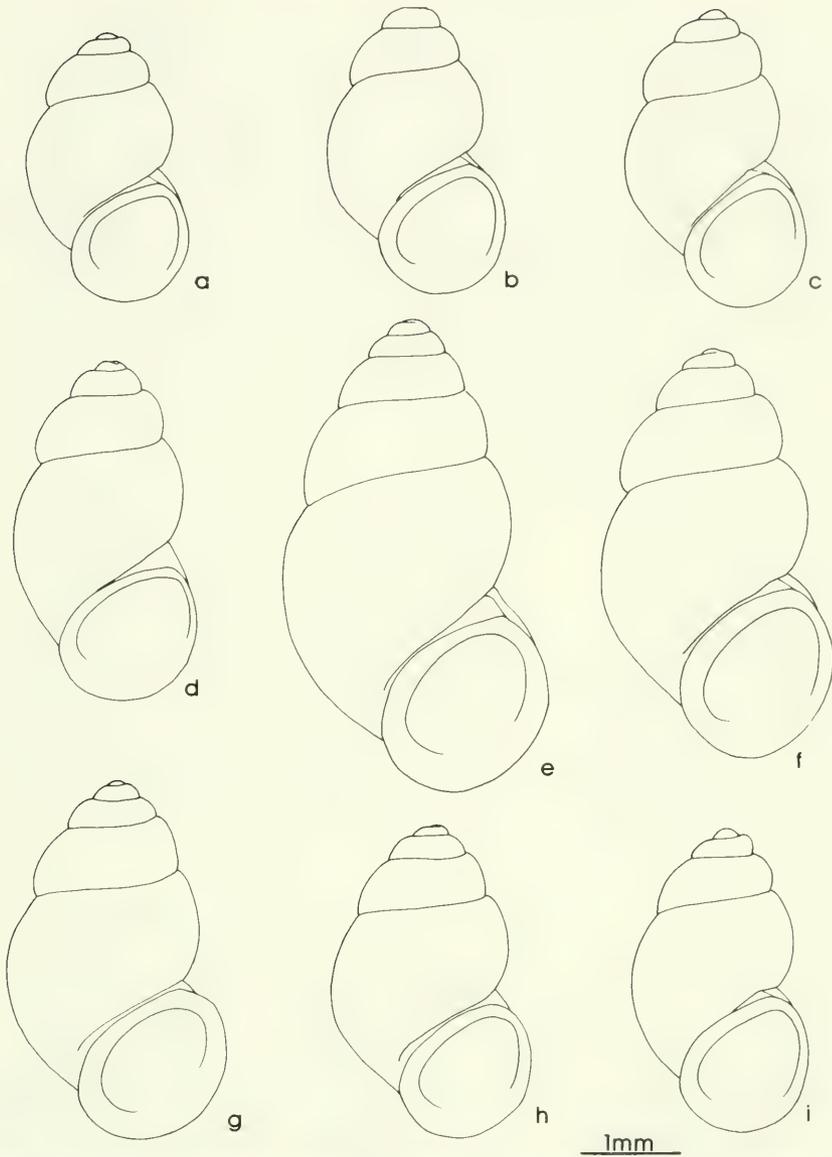


FIG. 6. Shells of species of *Fonscochlea*. a–d,i. *Fonscochlea accepta* form B. a. Finnis Swamp West (690)(AMS, C.152978). b. Sulphuric Springs (735) (AMS, C.152979). c. Hermit Hill Springs (711) (AMS, C.152980). d. Old Woman Spring (733) (AMS, C.152981). i. Old Finnis Springs (710) (AMS, C.152982). 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 ctenid-

ium. 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.

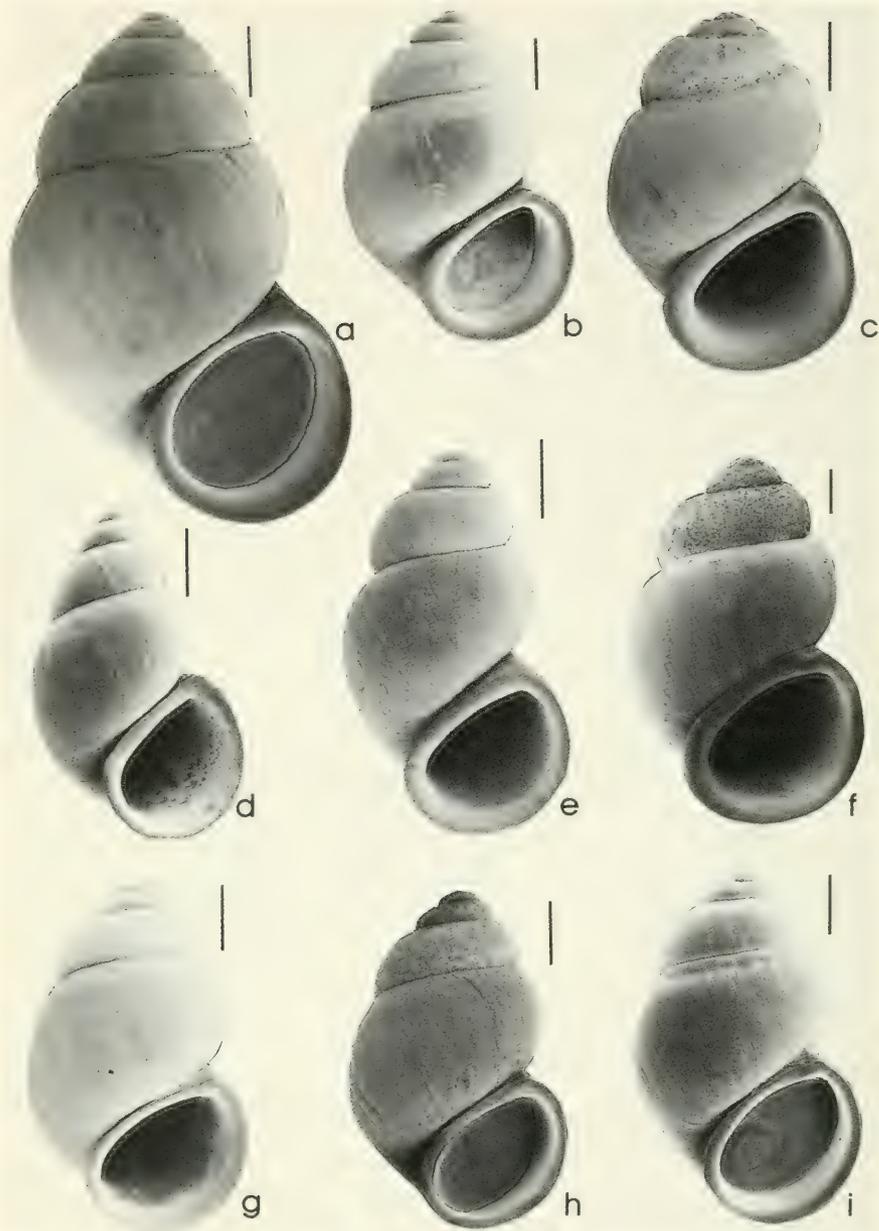


FIG. 7. Shells of species of *Fonscochlea*.

- 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.

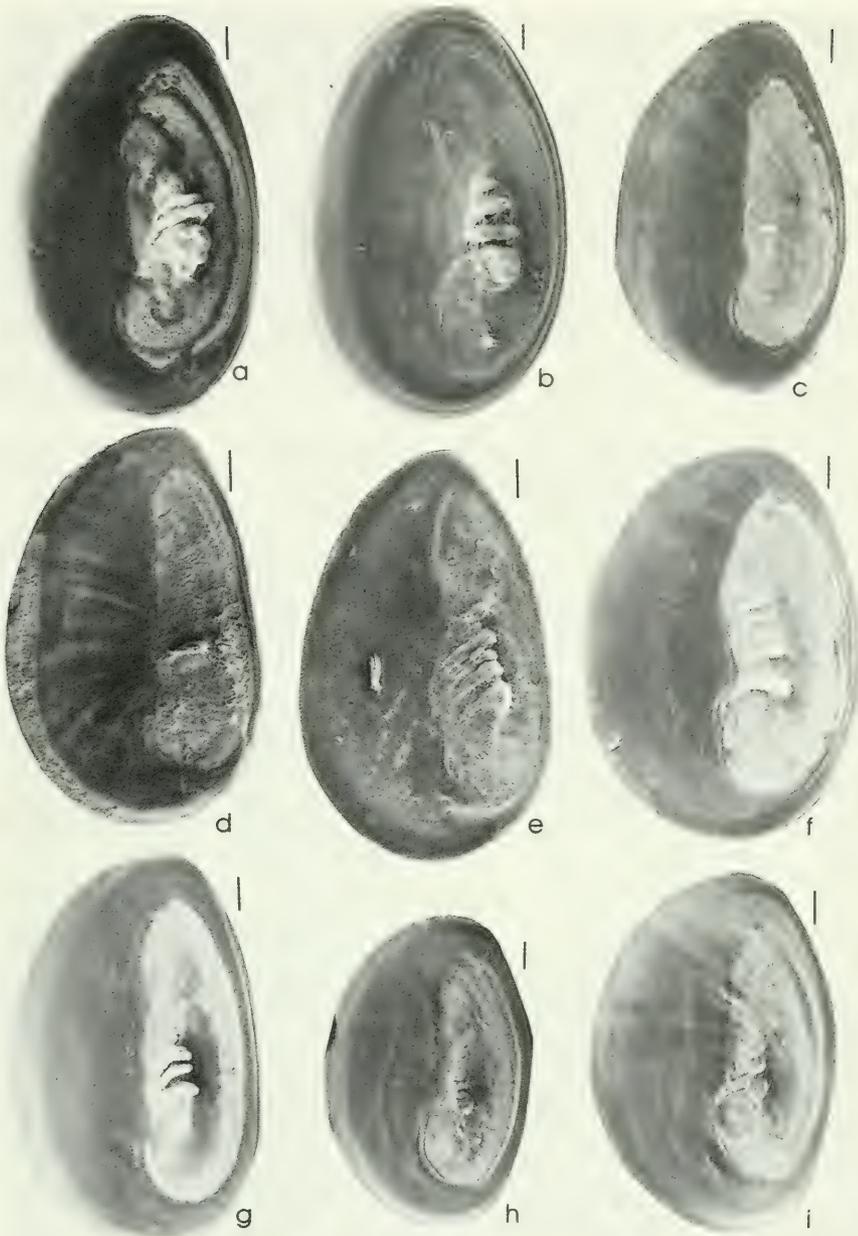


FIG. 8. Opercula of species of *Fonscochlea*.

- 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 Finniess Springs (694B).
 - h,i. *Fonscochlea accepta* form A, Welcome Springs (003).
- Scale: 0.1mm.

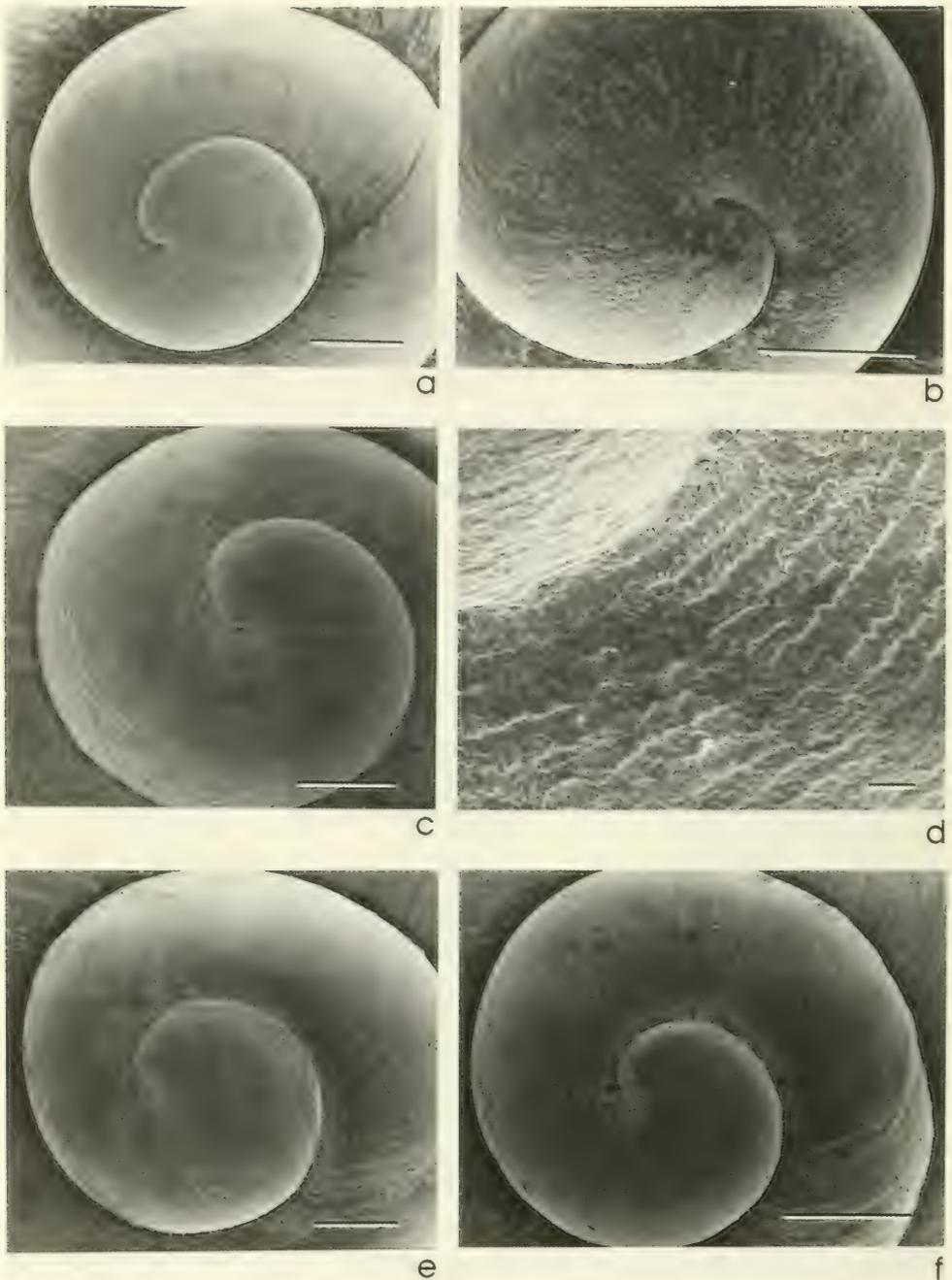


FIG. 9. Protoconchs of species of *Fonscochlea*.
 a. *Fonscochlea accepta* form A, Welcome Springs (003).
 b. *Fonscochlea accepta* form C, Emerald Springs (703).
 c-d. *Fonscochlea zeidleri* form A, Strangways Springs (030).
 e. *Fonscochlea aquatica* form A, Outside Springs (039).
 f. *Fonscochlea 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 Finnis 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

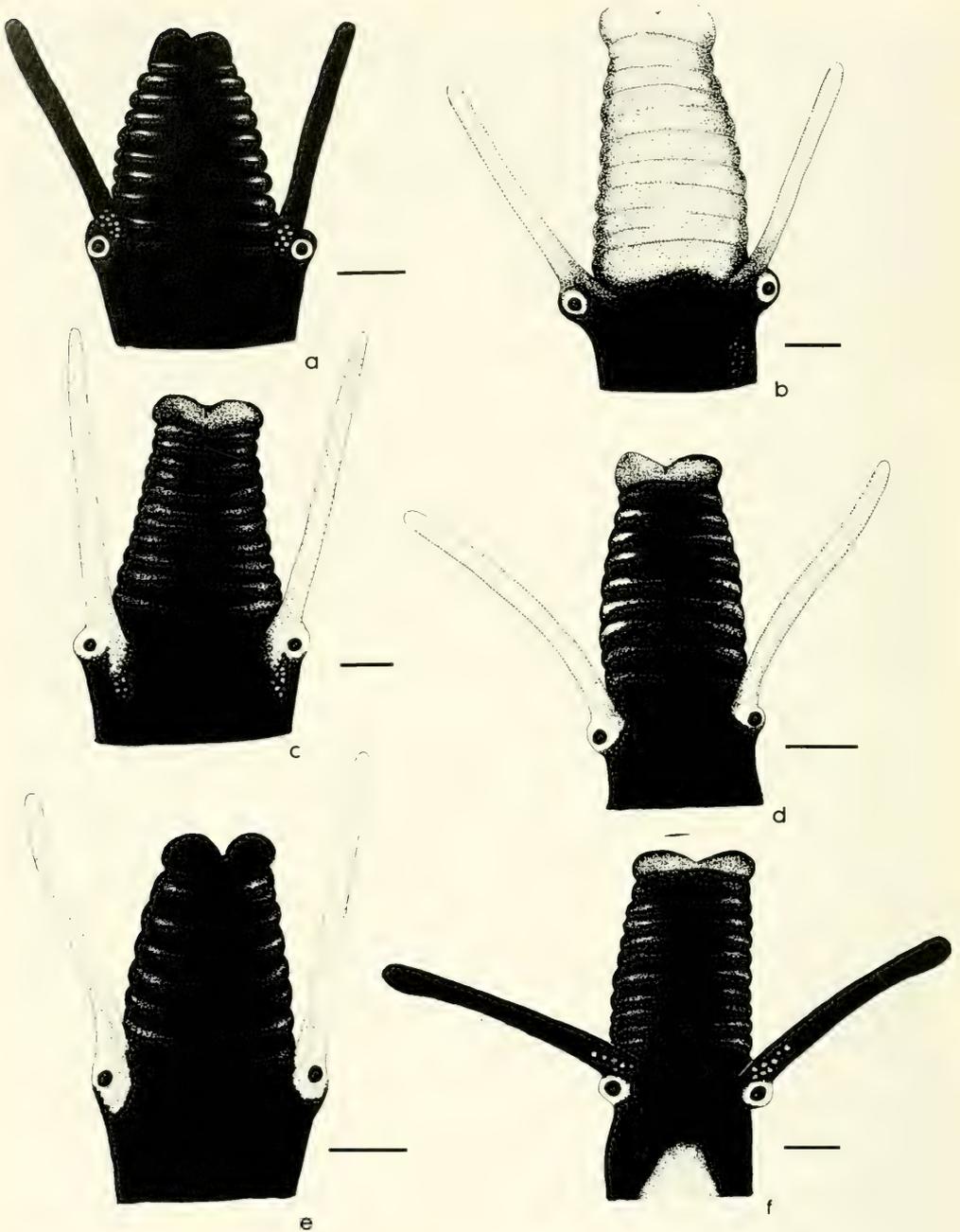


FIG. 11. Dorsal views of heads of large species of *Fonscochlea*; all from living material.
 a. *Fonscochlea zeidleri* form A, Kewson Hill Springs.
 b. *Fonscochlea zeidleri* form A, Welcome Springs.
 c. *Fonscochlea aquatica* form A, Blanche Cup Spring.
 d. *Fonscochlea accepta* form A, Welcome Springs.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

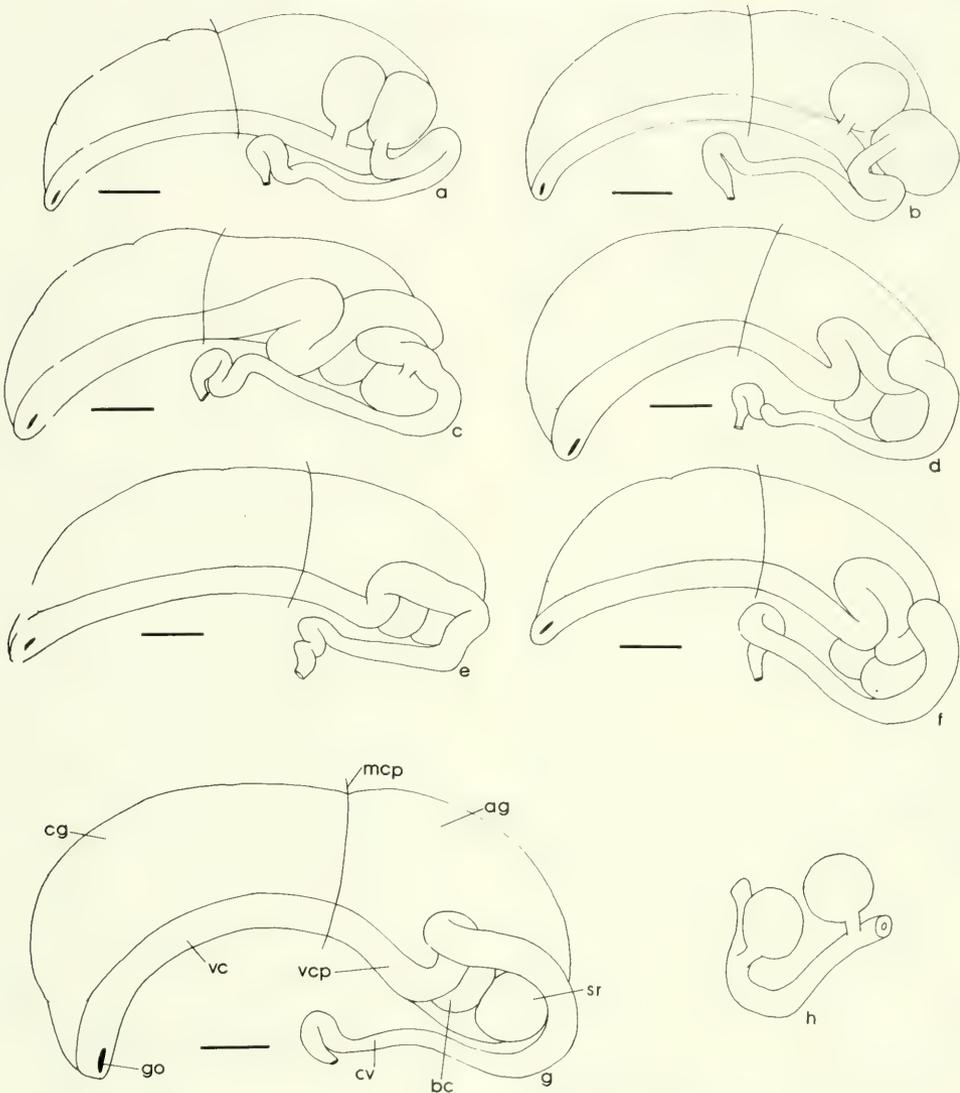


FIG. 12. Female genitalia of species of *Fonscochlea*.
 a. *Fonscochlea zeidleri* form B, Big Cadnaowie Spring.
 b. *Fonscochlea zeidleri* form A, Old Finnis Spring.
 c. *Fonscochlea aquatica* form A, Blanche Cup Spring.
 d. *Fonscochlea accepta* form A, Welcome Springs.
 e. *Fonscochlea accepta* form C, Emerald Springs.
 f. *Fonscochlea accepta* form B, Old Finnis 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 sub-terminal.

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 suboesophageal 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
<i>F. accepta</i> form A	3-4	1	3-4	3-4	9-10	24-25
<i>F. accepta</i> form B	3	1-2	2-3	3-4	9-12	—
<i>F. accepta</i> form C	4	1-2	3	3-4	10-13	—
<i>F. aquatica</i> form A	3-4	1	2-3	2-4	7-10	—
<i>F. aquatica</i> form B	2-3	1	3	3	8-9	21-25
<i>F. variabilis</i> form A	4-6	1-2	2-3	2-4	12-15	—
<i>F. variabilis</i> form B	3-4	1-2	2-3	2-3	9-12	—
<i>F. variabilis</i> form C	2-4	1-2	2	2-3	9-11	—
<i>F. billakalina</i>	3-4	1-2	2-3	2-4	10-12	—
<i>F. conica</i>	4-6	1-2	3	3-4	14-18	—
<i>F. zeidleri</i> form A	2-3	2	2-3	3	9-13	17-21
<i>F. zeidleri</i> form B	2-3	2	2-3	3	9-10	20-21
<i>T. punicea</i>	5-8	1-2	3-6	4-6	24-31	—
<i>T. smithi</i>	6-7	1	4-5	5-6	23-25	—
<i>T. minuta</i>	4-7	1-2	4-6	6-7	22-24	—
<i>T. inflata</i>	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,

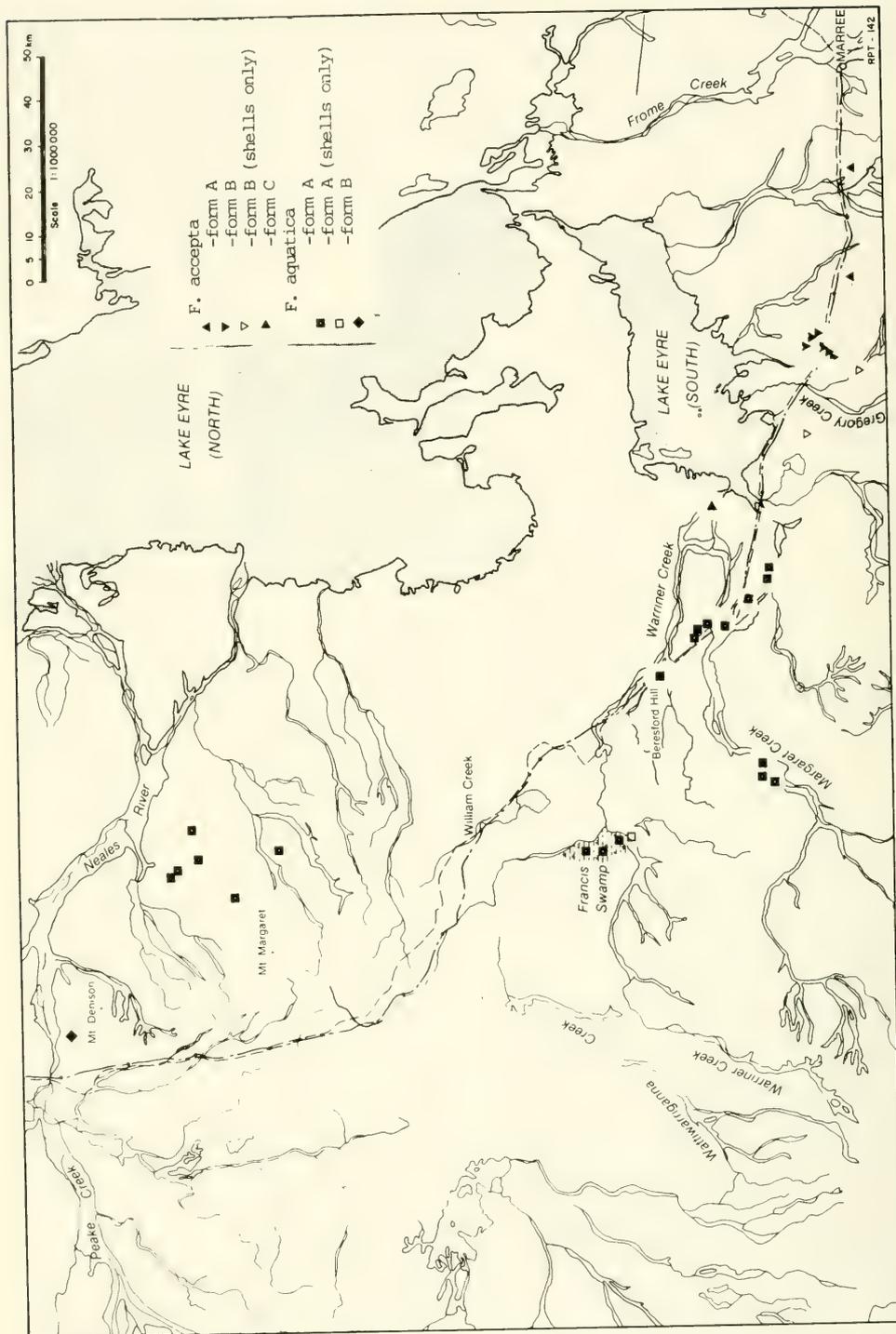


FIG. 13. Distribution of large aquatic species, *Fonscochlea accepta*, *F. aquatica*.

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 Finnis Springs (693A–C, 694A–C, 710); Old Woman Springs (733A–E); Finnis 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 ctenidial 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 behaviourally 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.

	<i>F.ac.A</i>	<i>F.ac.B</i>	<i>F.ac.C</i>	<i>F.aq.A</i>	<i>F.aq.A(r)</i>	<i>F.aq.cf.A</i>	<i>F.aq.B</i>	
<i>F. accepta</i> form A	X	0.460	0.598	1.611	1.477	2.519	1.010	Right side: Female, shell & operculum Male, shell & operculum
		0.470	0.131	1.472	1.274	2.693	1.042	
<i>F. accepta</i> 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	
<i>F. accepta</i> 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	
<i>F. aquatica</i> form A (combined)	1.550	1.667	1.326	X	—	—	0.771	
	—	—	—	—	—	—	0.521	
<i>F. aquatica</i> form A (restricted)	1.384	1.630	1.272	—	X	1.842	0.507	
	9.365	9.533	6.756	—	—	2.119	0.372	
<i>F. aquatica</i> cf. form A	2.606	2.463	2.261	—	1.972	X	2.029	
	0.396	0.539	2.402	—	—	—	2.020	
<i>F. aquatica</i> 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 regarded 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 orthocone 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-

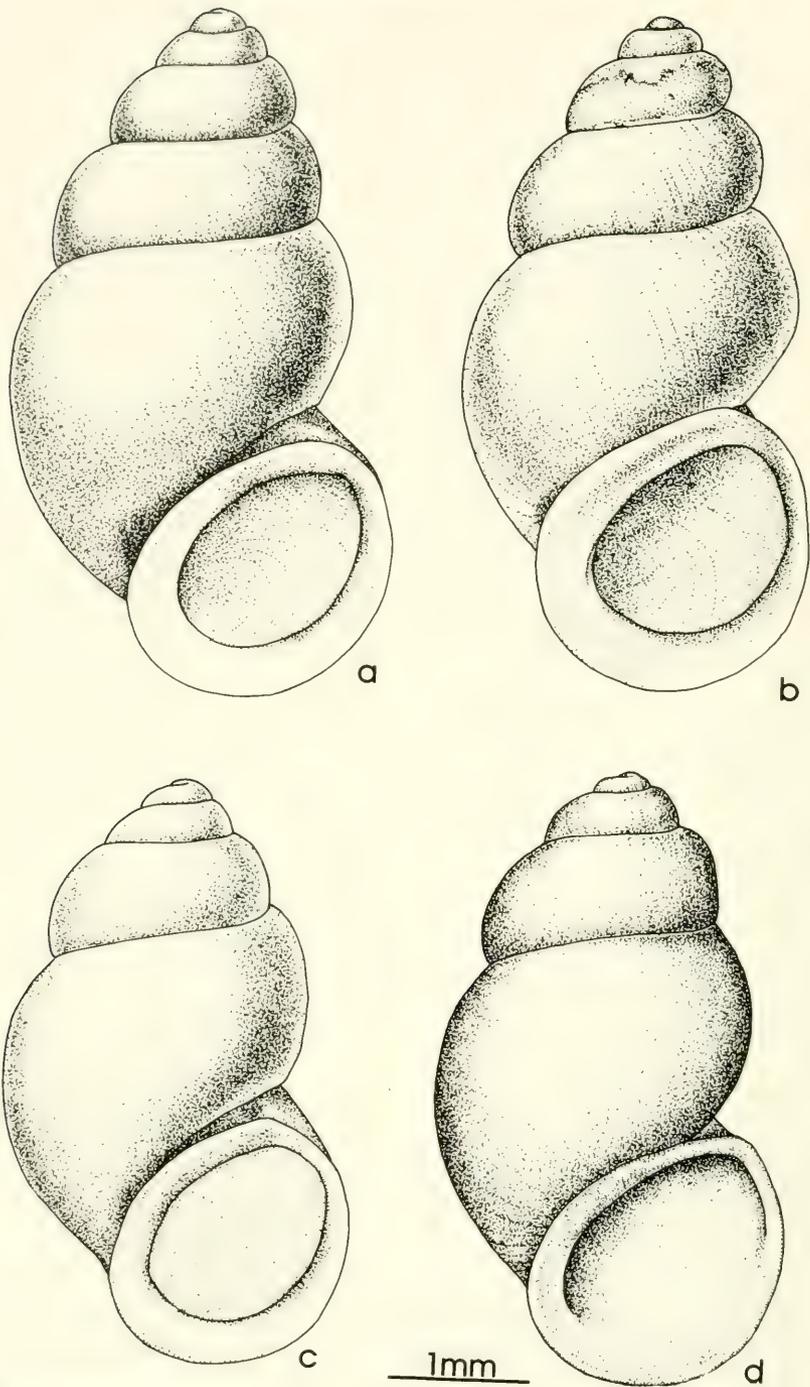


FIG. 14. Shells of species of *Fonscochlea*.

- 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).

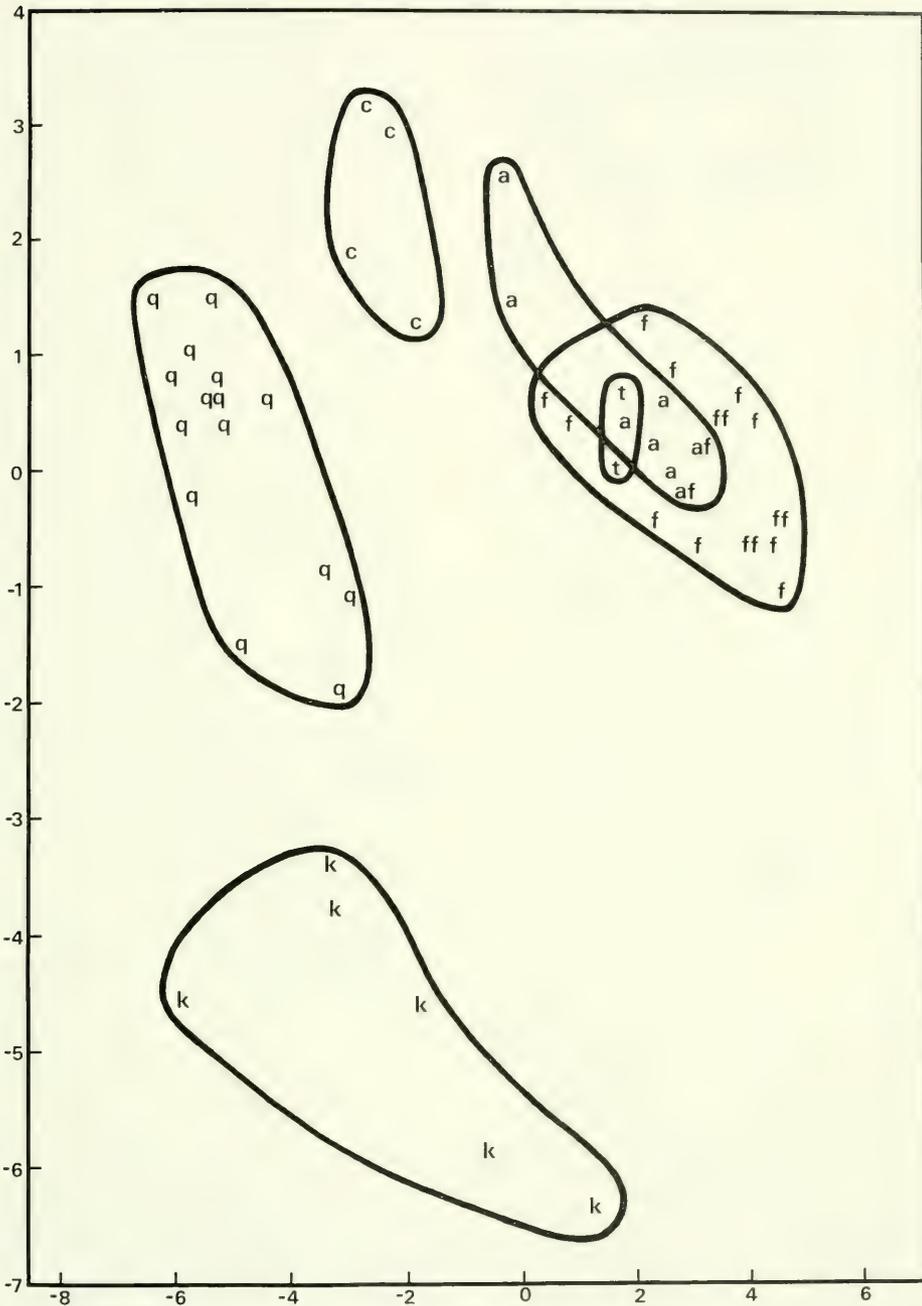


FIG. 15. Plot of group centroids, using the first two canonical axes, obtained from discriminate analysis of populations of large aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purposes of this analysis, treated as 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.

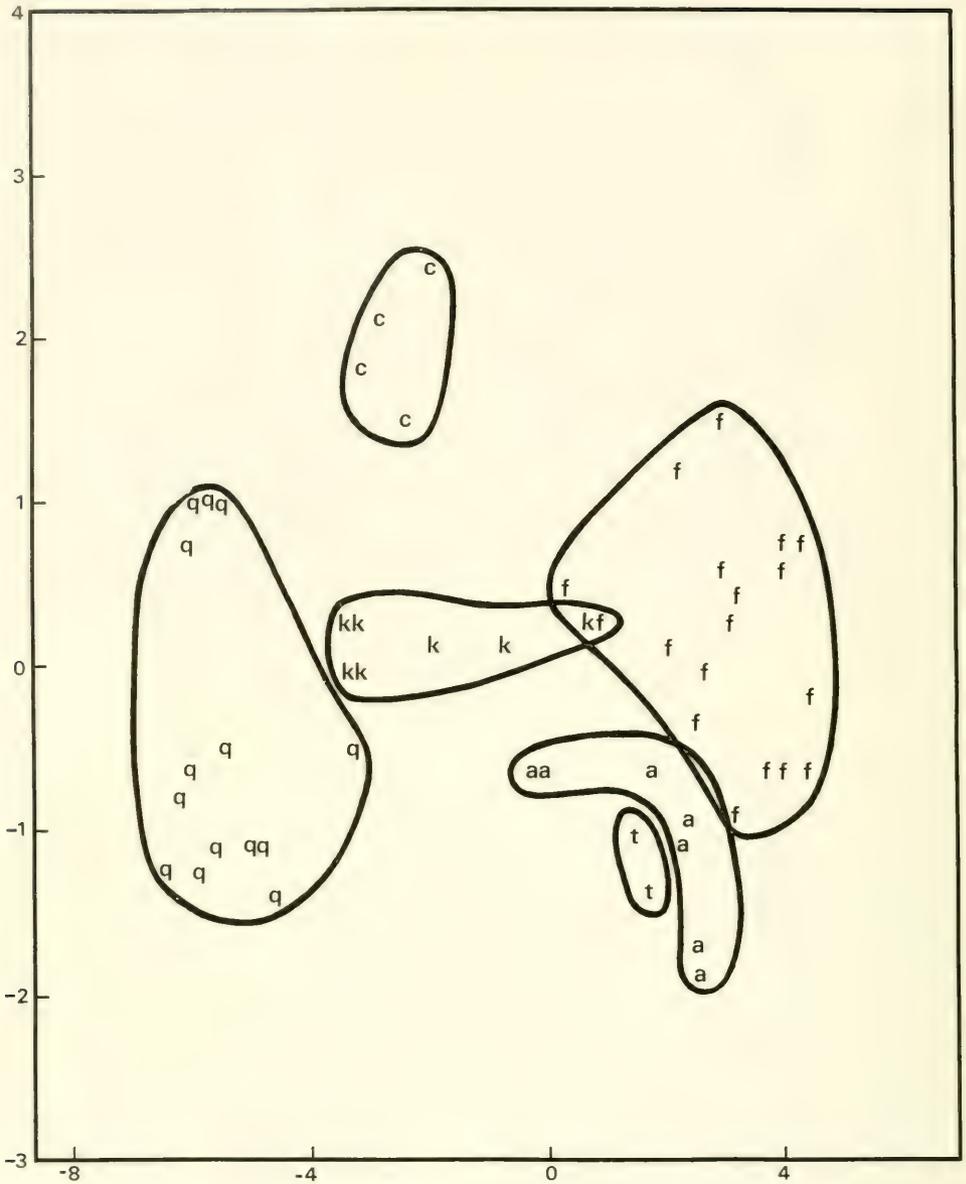


FIG. 16. Plot of group centroids, using first and third canonical axes, obtained from discriminate analysis of populations of large aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purpose of this analysis, treated as 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. Calcar-

eous 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*

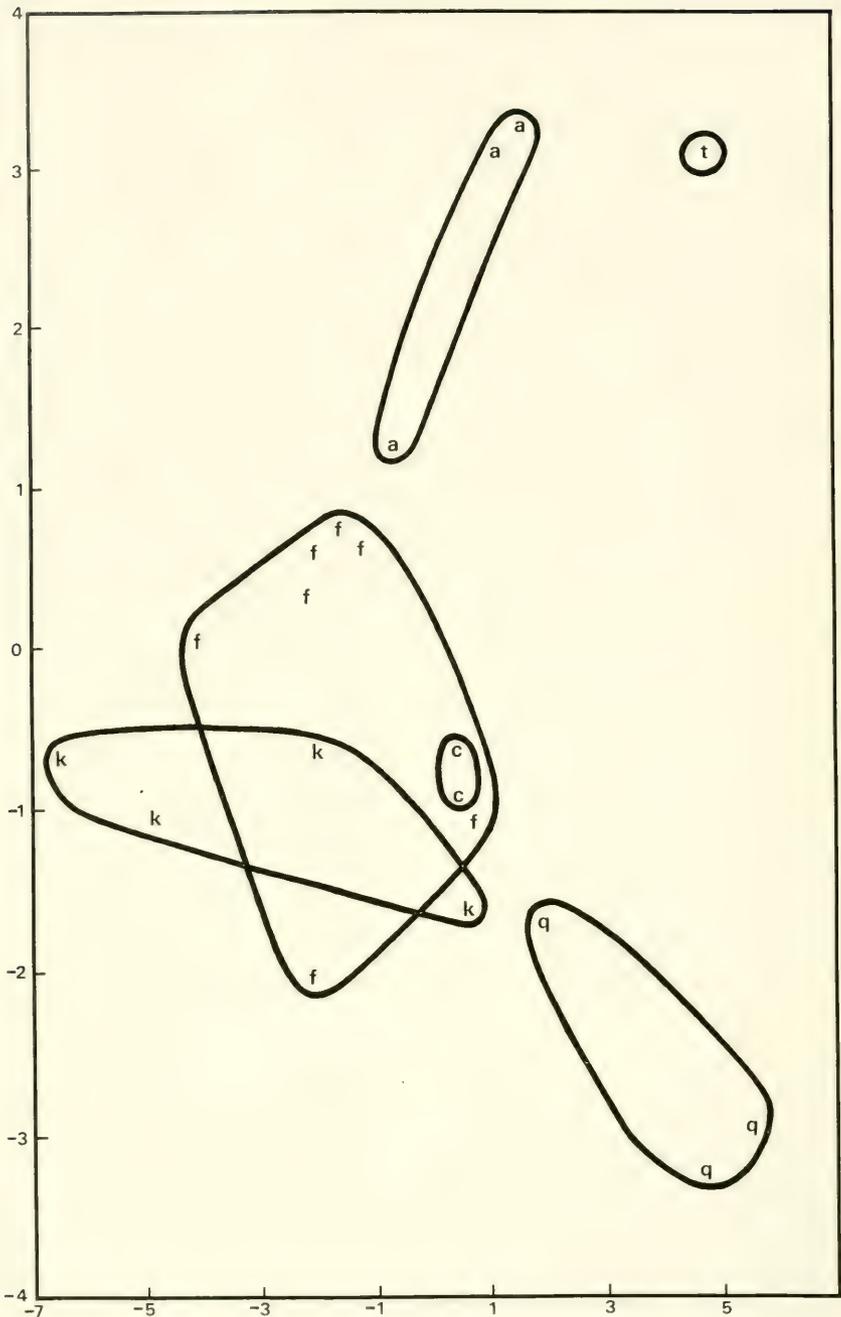


FIG. 17. Plot of group centroids, using first two canonical axes, obtained from discriminate analysis of populations, sexes combined, of large aquatic species and forms of *Fonsochlela* using pallial measurements. The axes contain the following percentages of the variance of the variables used: first (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.

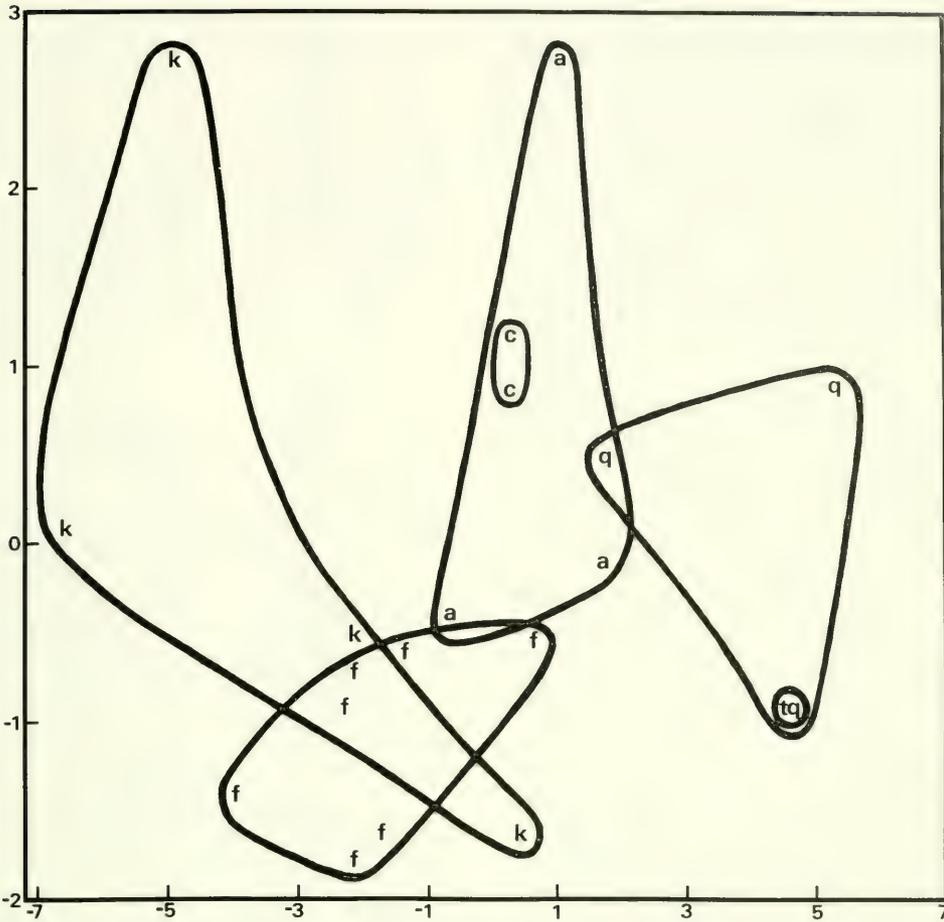


FIG. 18. Plot of group centroids, using first and third canonical axes, obtained from discriminate analysis of populations, sexes combined, of large aquatic species and forms of *Fonscochlea* using pallial measurements. The axes contain the following percentages of the variance of the variables used: 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.

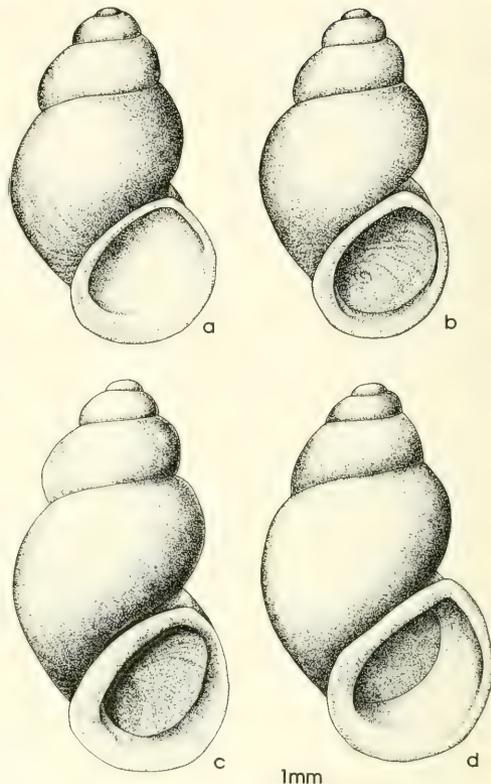


FIG. 19. Shells of species of *Fonscochlea*.

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

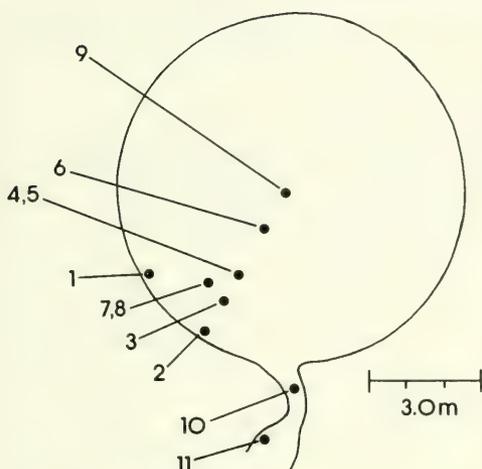


FIG. 20. Blanche Cup pool and upper outflow (Stn. 739), showing location of the 11 sampling sites for study of size-variation in *Fonscochlea variabilis*.

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).

Station	Shell Height (mm)					
	Males			Females		
	\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

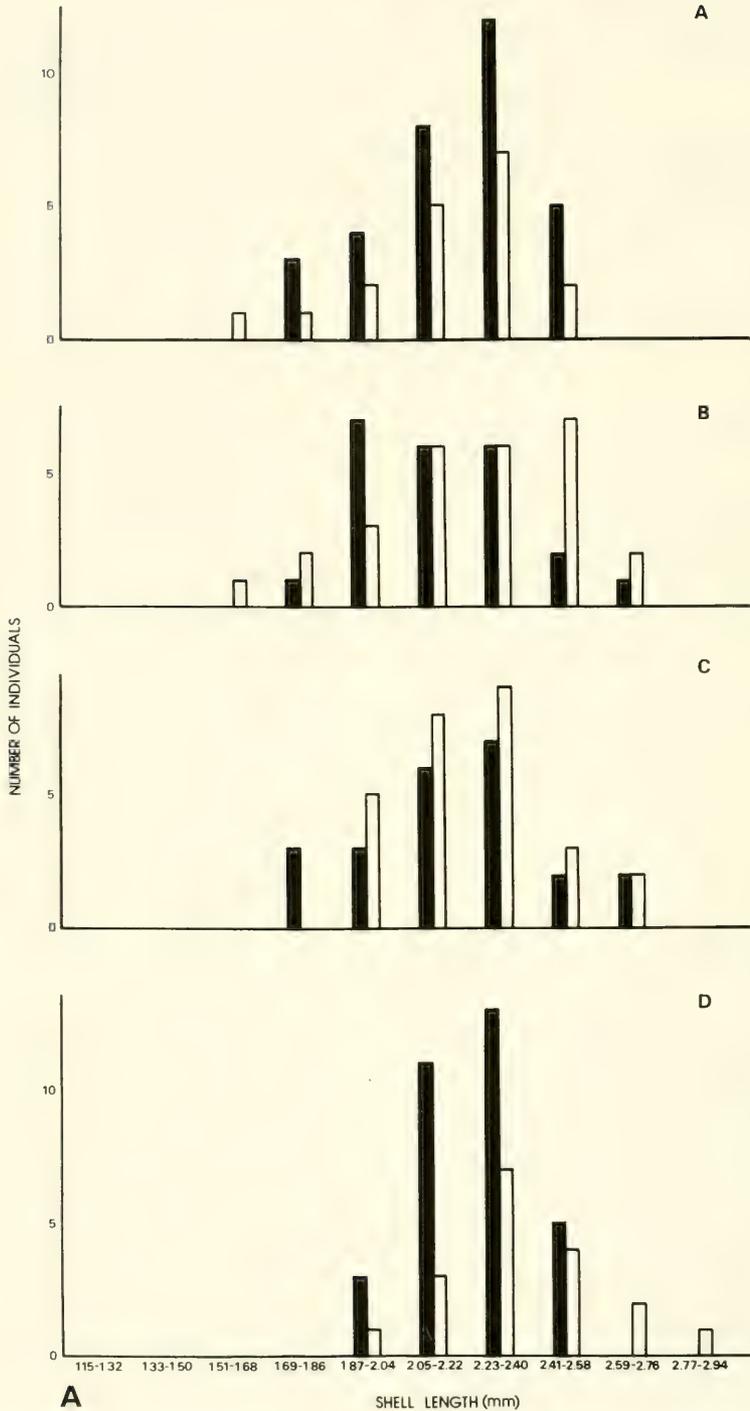


FIG. 21. Size-frequency histograms for *Fonscochlea variabilis* from eight stations at Blanche Cup (Stn. 739). Darkened columns, males; white columns, females.

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.

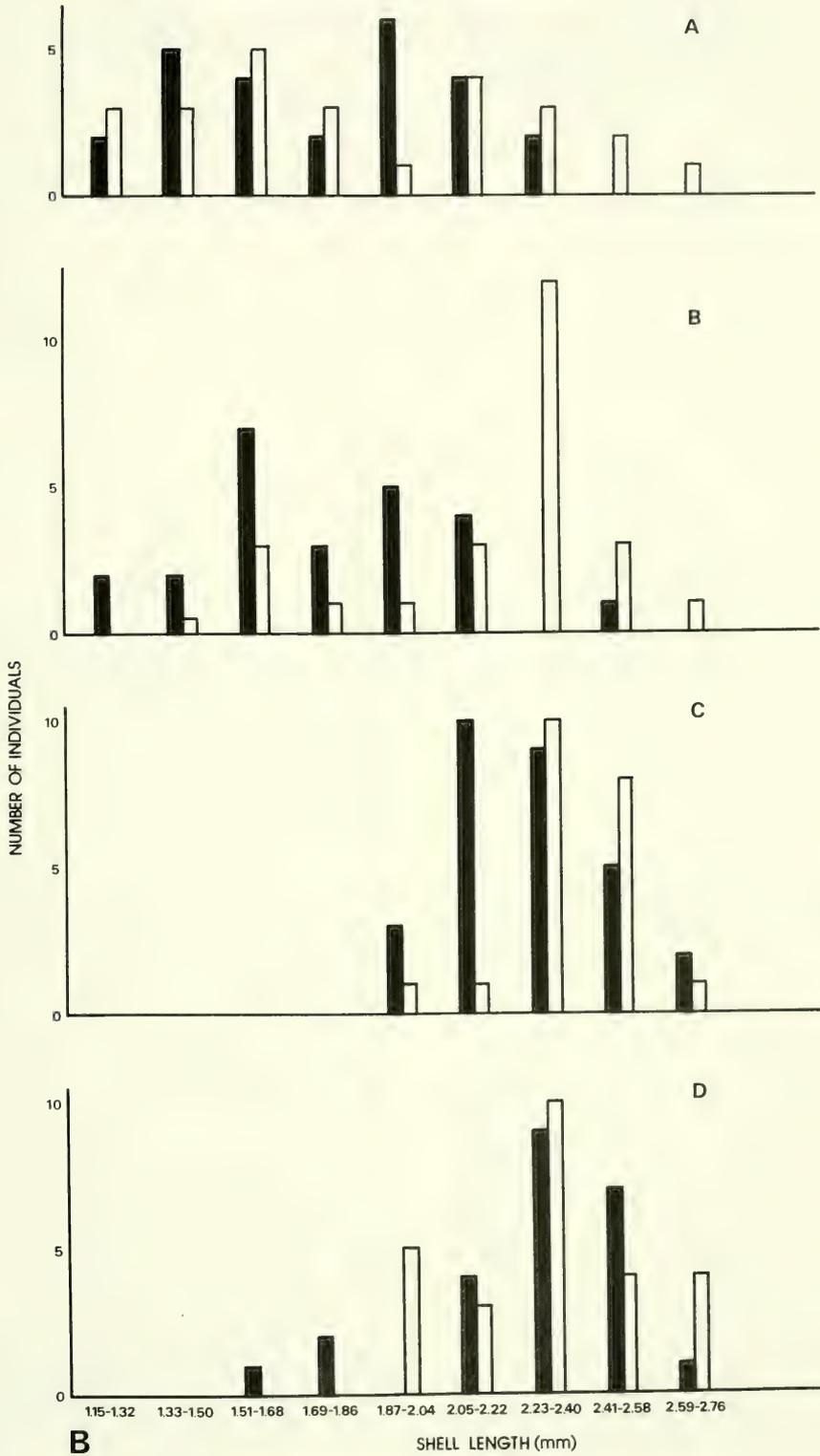


TABLE 7. Significant differences (SNK Test, $P \leq 0.01$) in shell height of *Fonscochlea variabilis* among stations at Blanche Cup (Stn. 739). Empty boxes indicate shell height for males or females does not differ significantly between that pair of stations.

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	—

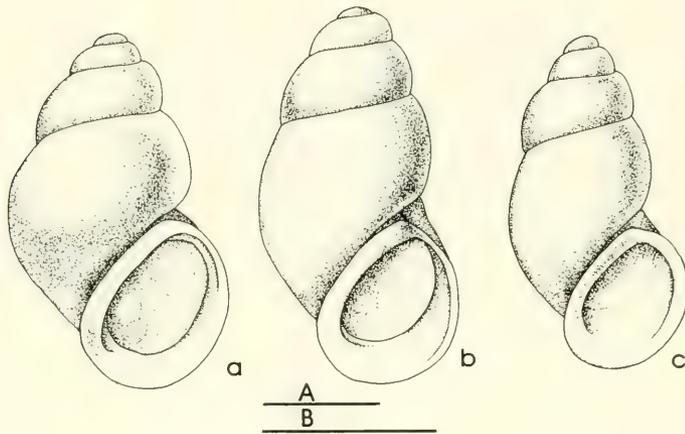


FIG. 22. Shells of species of *Fonscochlea*.

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 spec-

imens 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.

	<i>F.va.A</i>	<i>f.va</i> (small)	<i>F.va.B</i>	<i>F.va.C</i>	<i>F.conica</i>	<i>F.bill.</i>	
<i>F. variabilis</i> 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
<i>F. variabilis</i> (small form)	3.421	X	3.953 2.727	3.662 3.139	1.577 1.127	1.684 1.714	
<i>F. variabilis</i> form B	1.480	3.382	X	0.446 0.502	2.440 1.661	3.283 2.492	
<i>F. variabilis</i> form C	1.506	3.421	0.162	X	2.139 2.978	2.899 2.978	
<i>F. conica</i>	0.660	1.376	2.073	2.115	X	1.283 1.395	
<i>F. billakalina</i>	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 discriminant 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

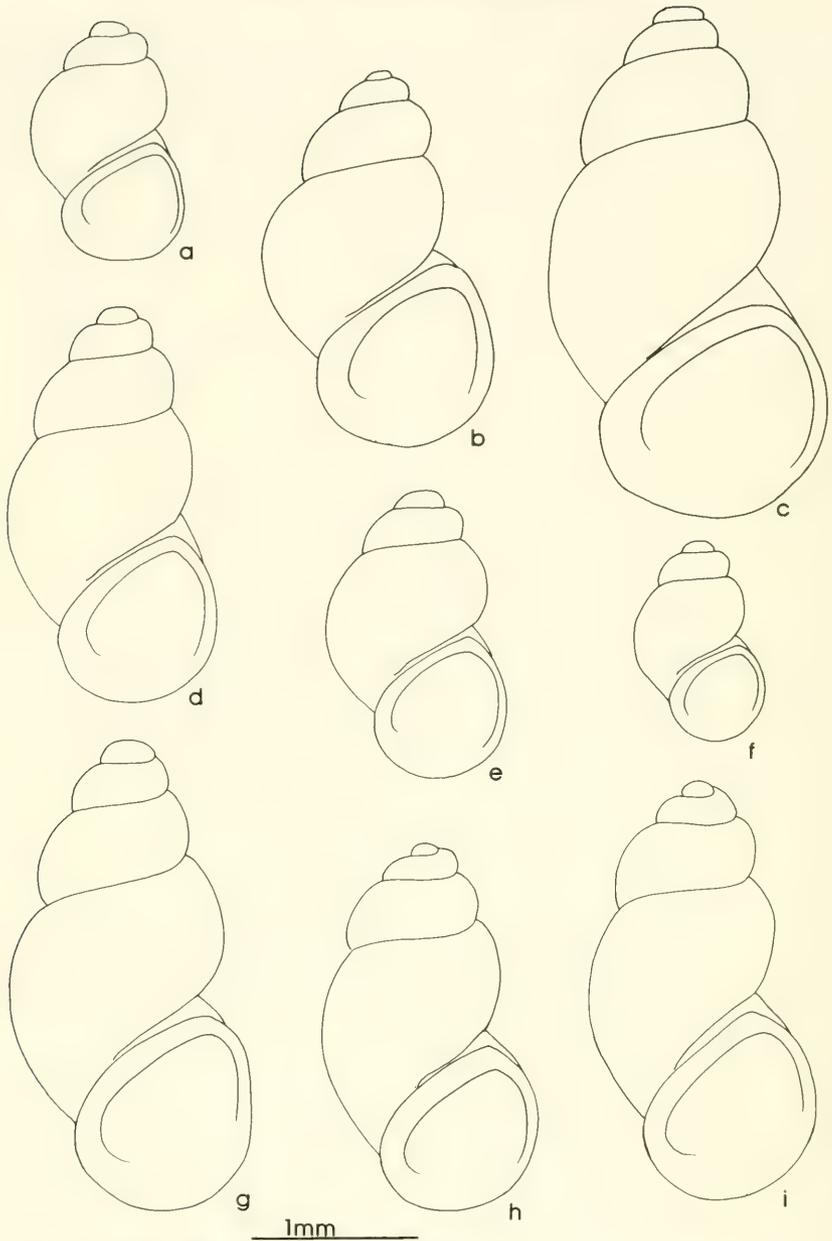


FIG. 23. Shells of *Fonscochlea billakalina* and *F. variabilis*.

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 Fin-

niss 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.

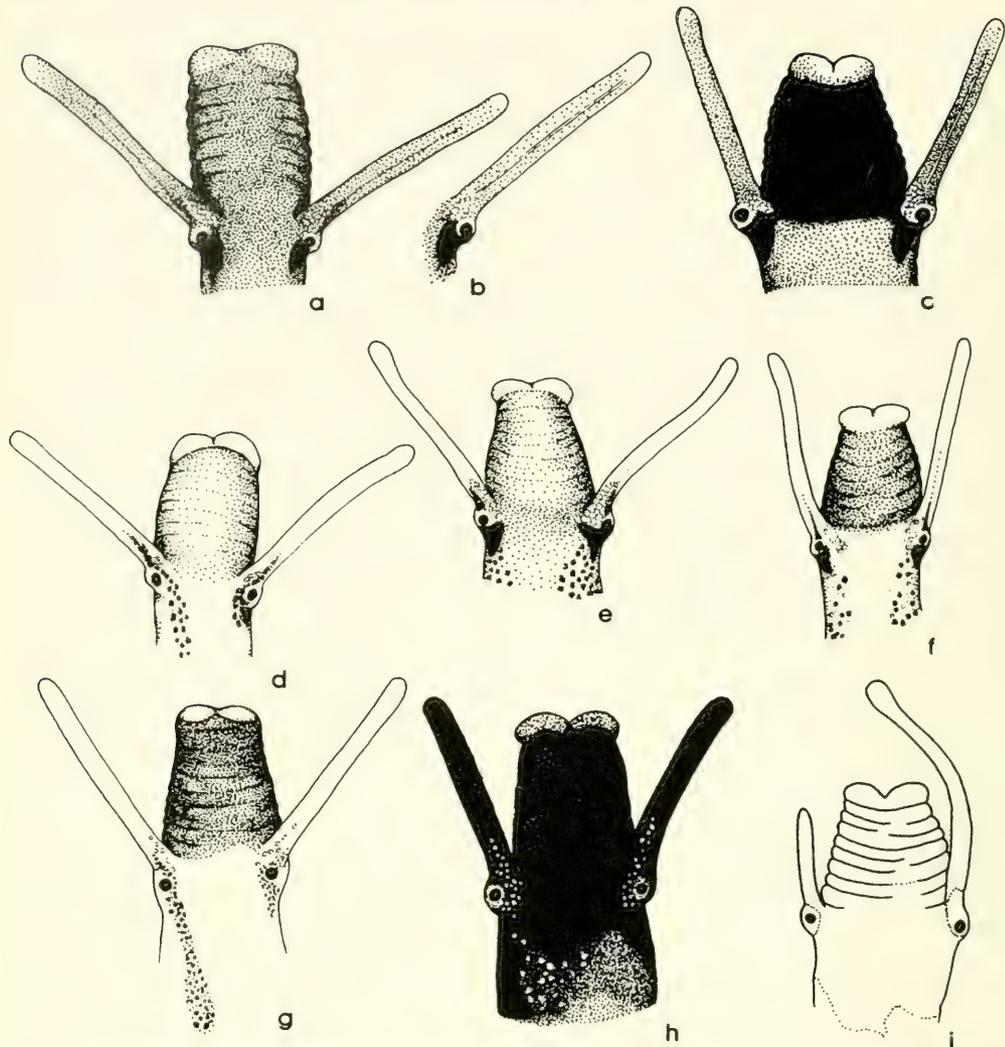


FIG. 24. Dorsal views of heads of species of *Fonscochlea* and *Trochidrobia punicea*. All figures except i from living material.

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

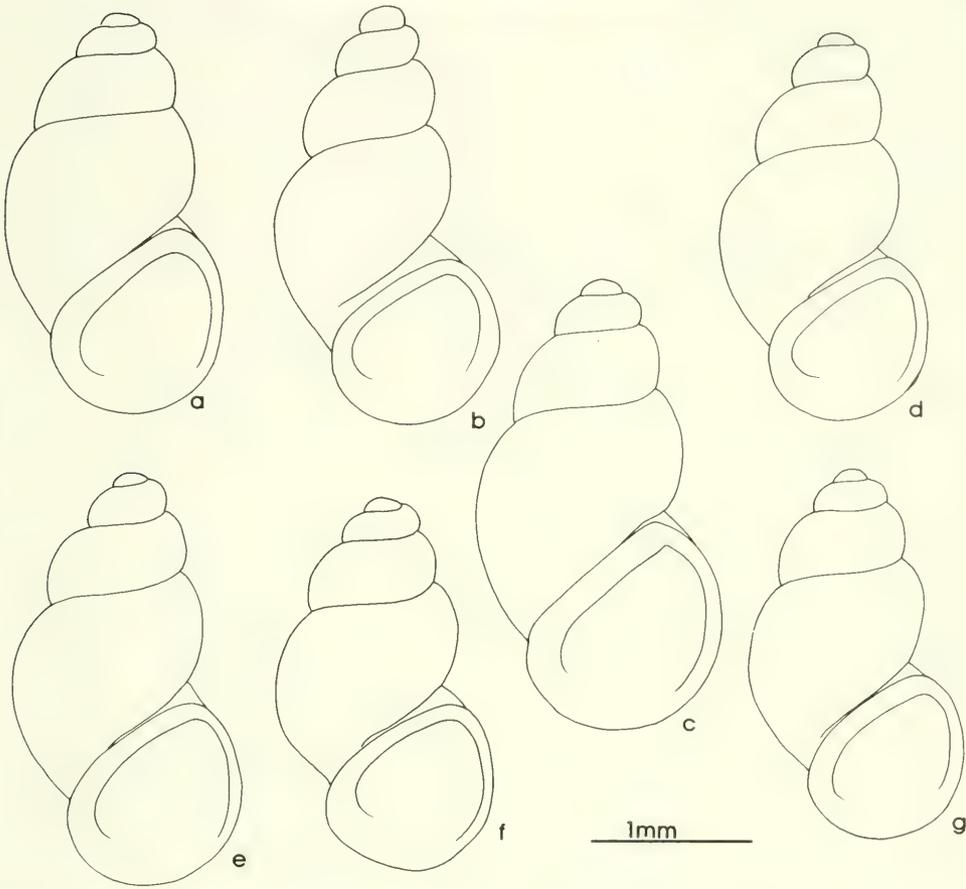


FIG. 25. Shells of *Fonscochlea billakalina* and *F. variabilis* form B.

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,

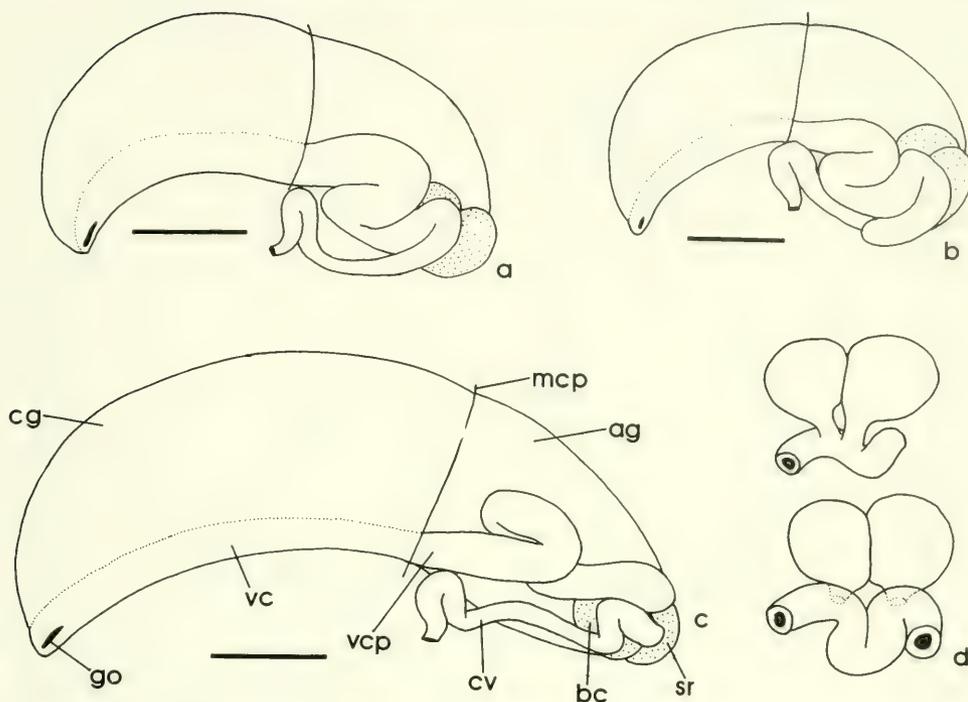


FIG. 27. Female genitalia of species of *Fonscochlea*.

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-

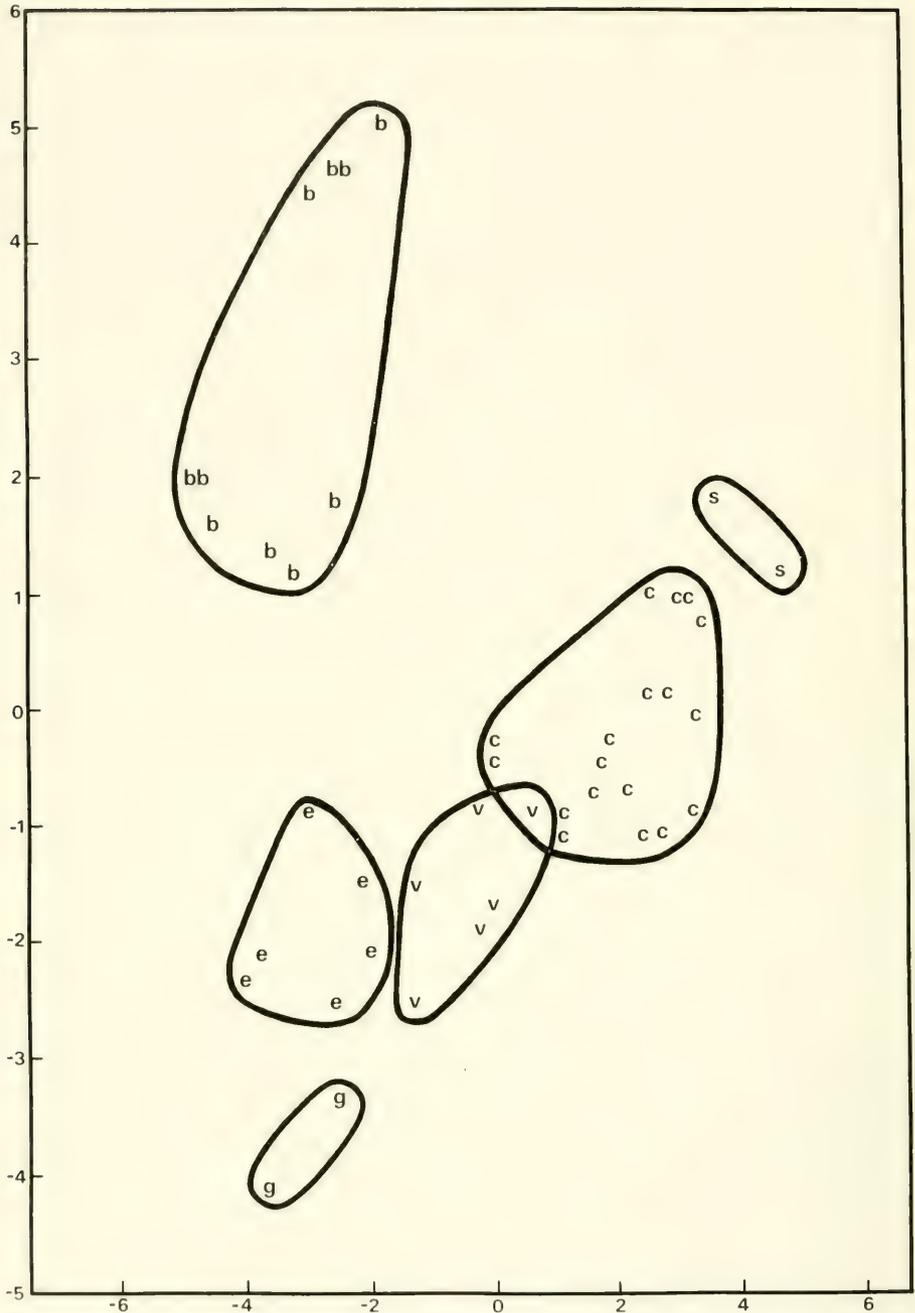


FIG. 28. Plot of group centroids, using first two canonical axes, obtained from discriminant analysis of populations of small aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct 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.

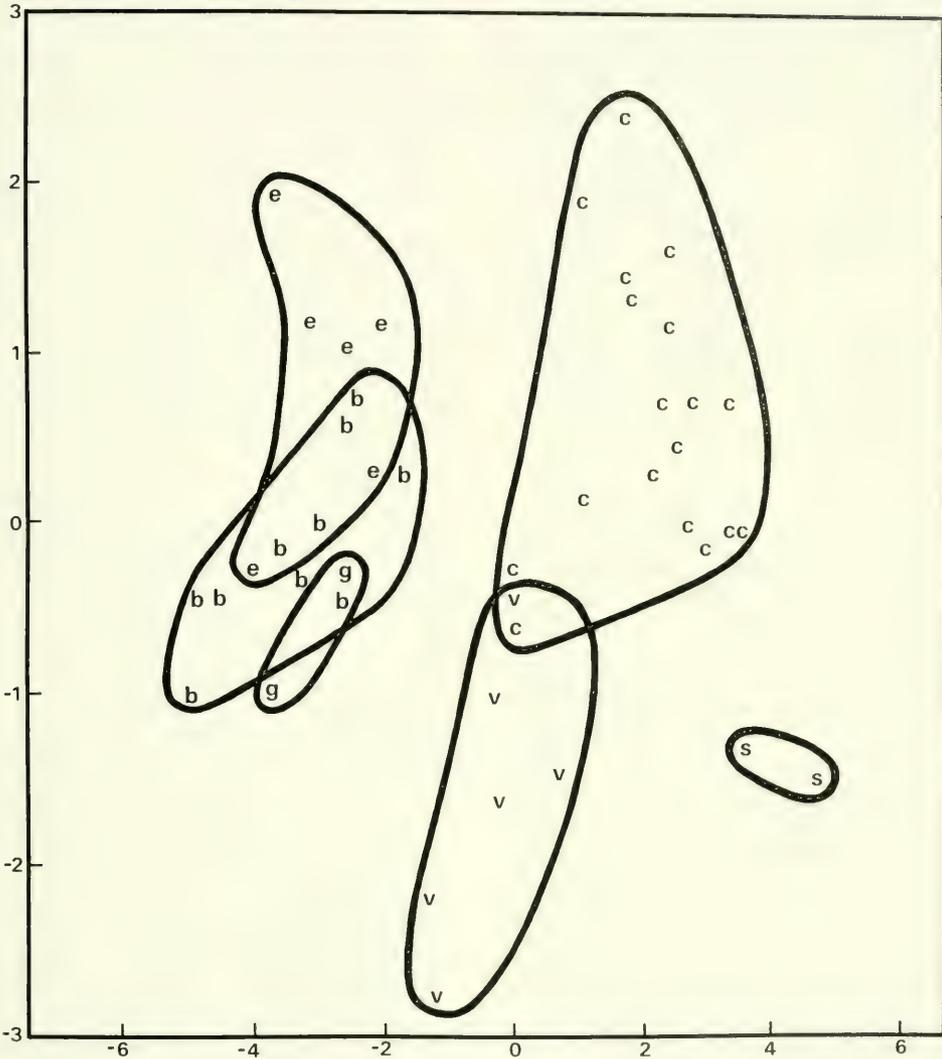


FIG. 29. Plot of group centroids, using first and third canonical axes, obtained from discriminate analysis of populations of small aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purposes of this analysis, treated as 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-*

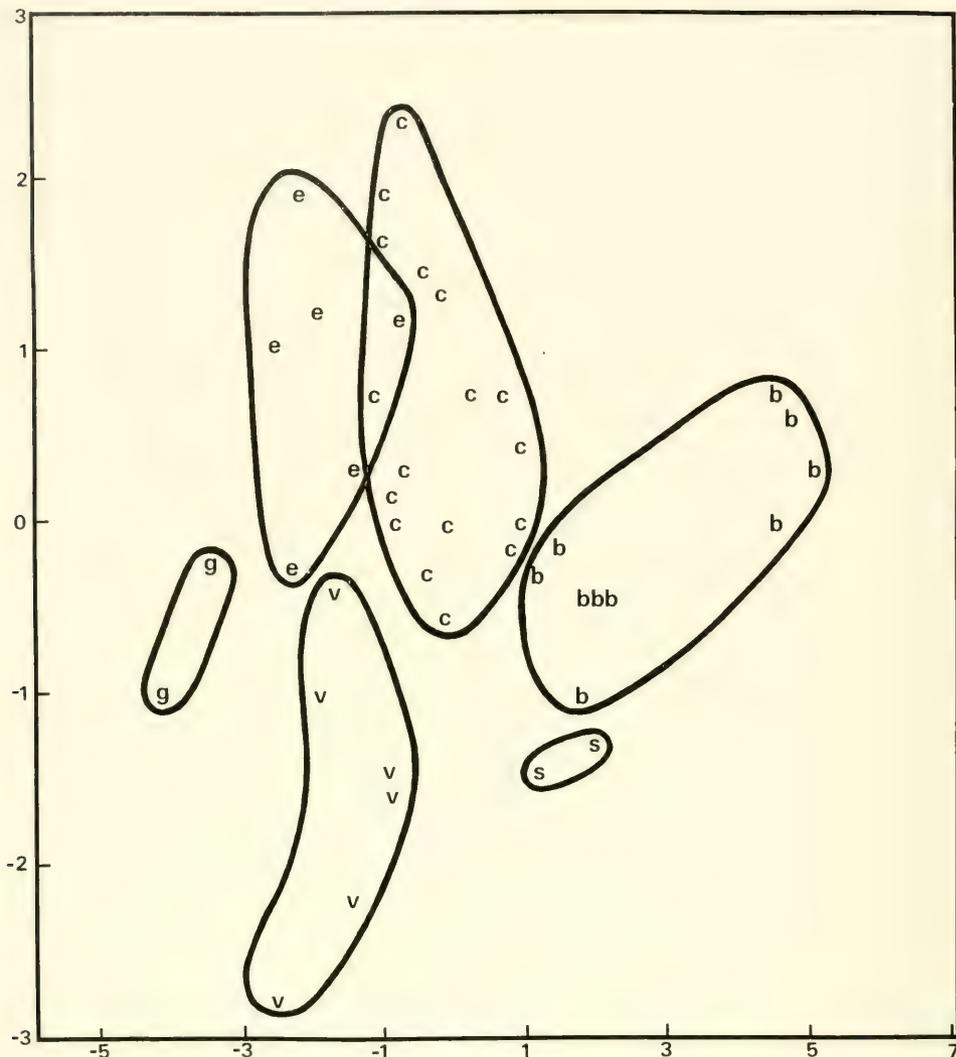


FIG. 30. Plot of group centroids, using second and third canonical axes, obtained from discriminate analysis of populations of small aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purposes of this analysis, treated 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 differ-

ent 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 subgenerally 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

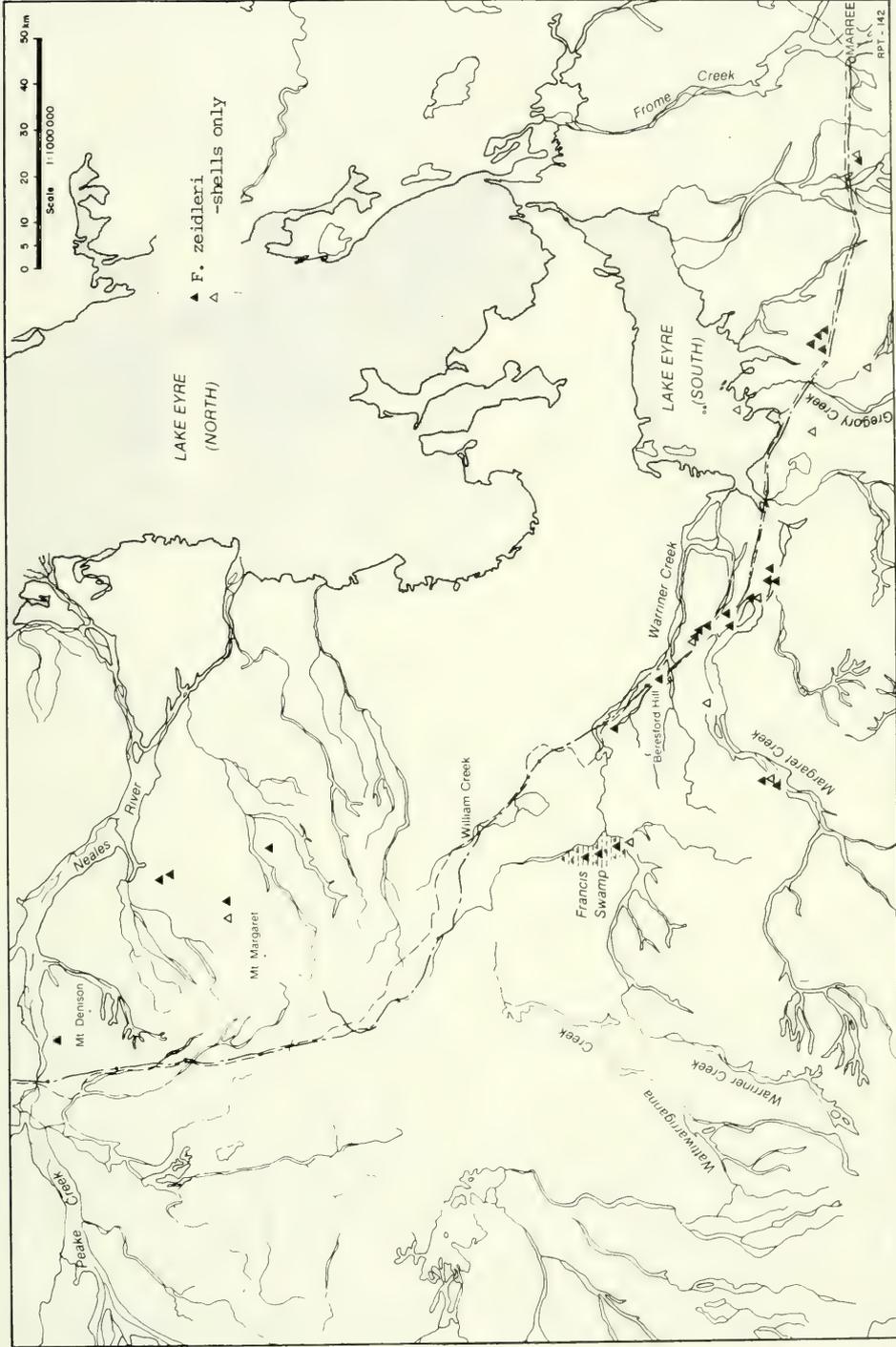


FIG. 31. Distribution of *Fonscochlea zeidlerii* form A.

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 discriminant analysis on a subset of shell measurements.

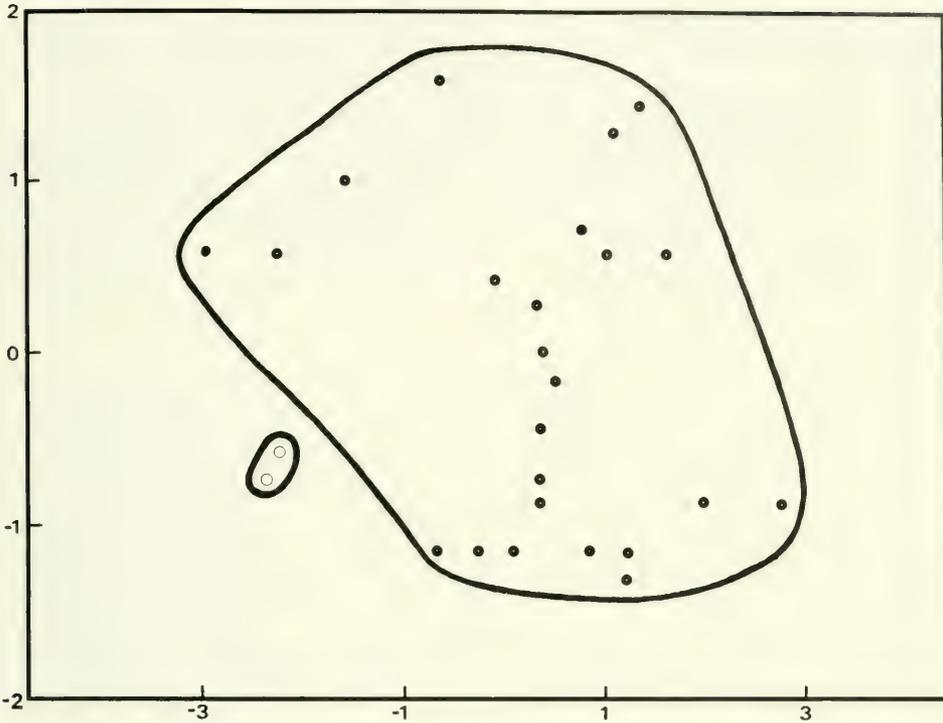


FIG. 32. Plot of group centroids, using first two canonical axes, obtained from discriminate analysis of populations of *Fonsochlea zeidleri* using shell measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct populations. The axes contain the following 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 (*Tro-*

chus), 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.

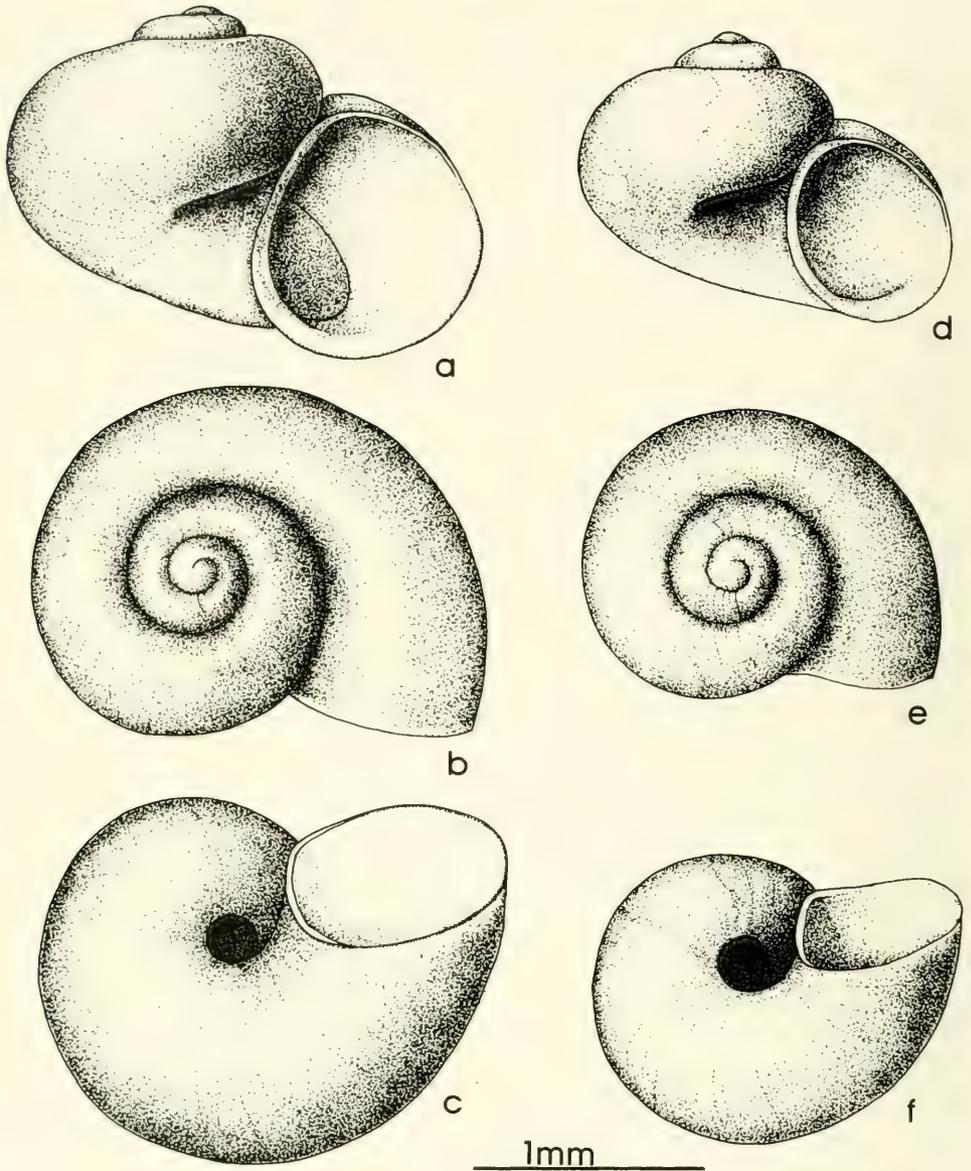


FIG. 33. Shells of *Trochidrobia*.

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

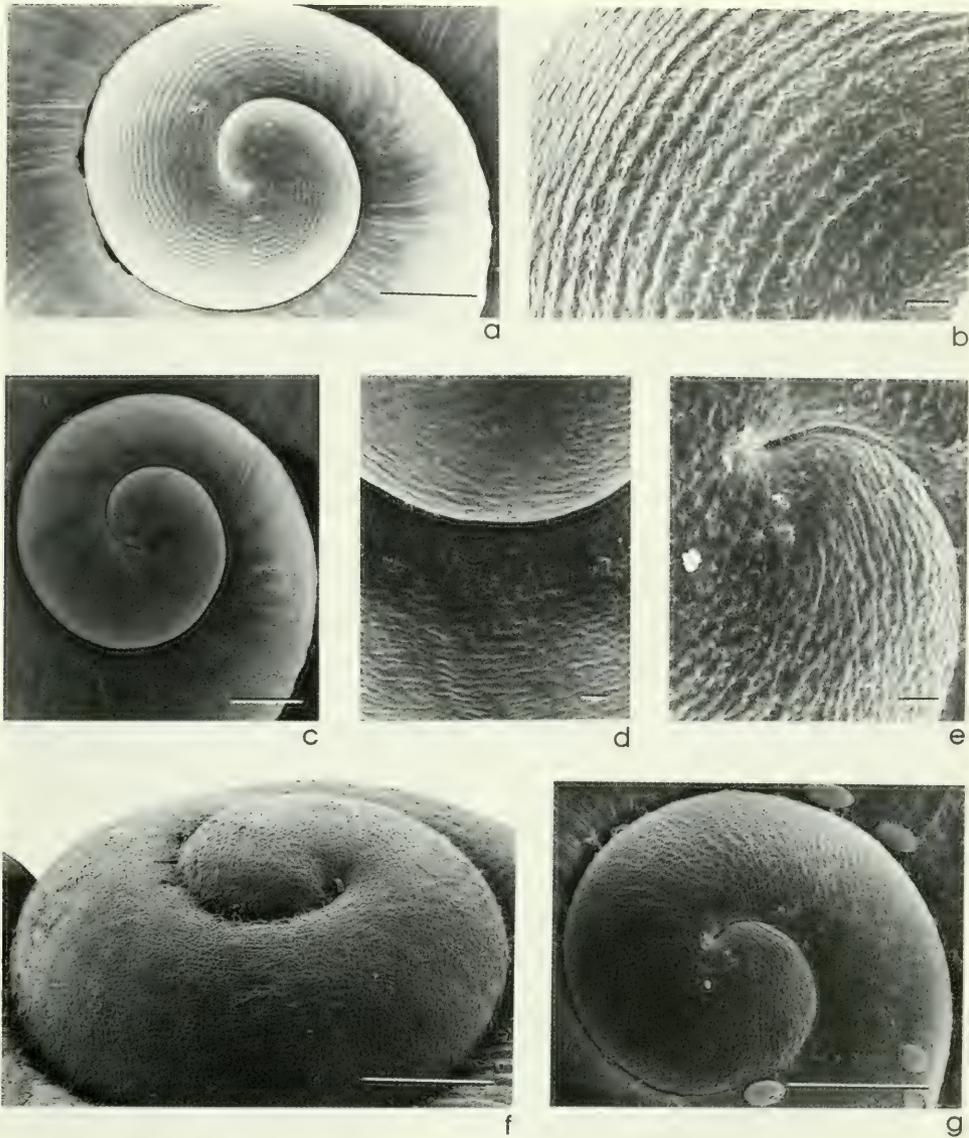


FIG. 34. Protoconchs of species of *Trochidrobia*.
 a,b. *Trochidrobia punicea*, Coward Springs (020).
 c,d. *Trochidrobia smithi*, The Fountain Spring (032).
 e,g. *Trochidrobia minuta*, Freeling Springs (045).
 f. *Trochidrobia inflata*, Freeling Springs (043).
 Scale: a,c,f,g = 0.1mm; b,d,e = 0.01mm.

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

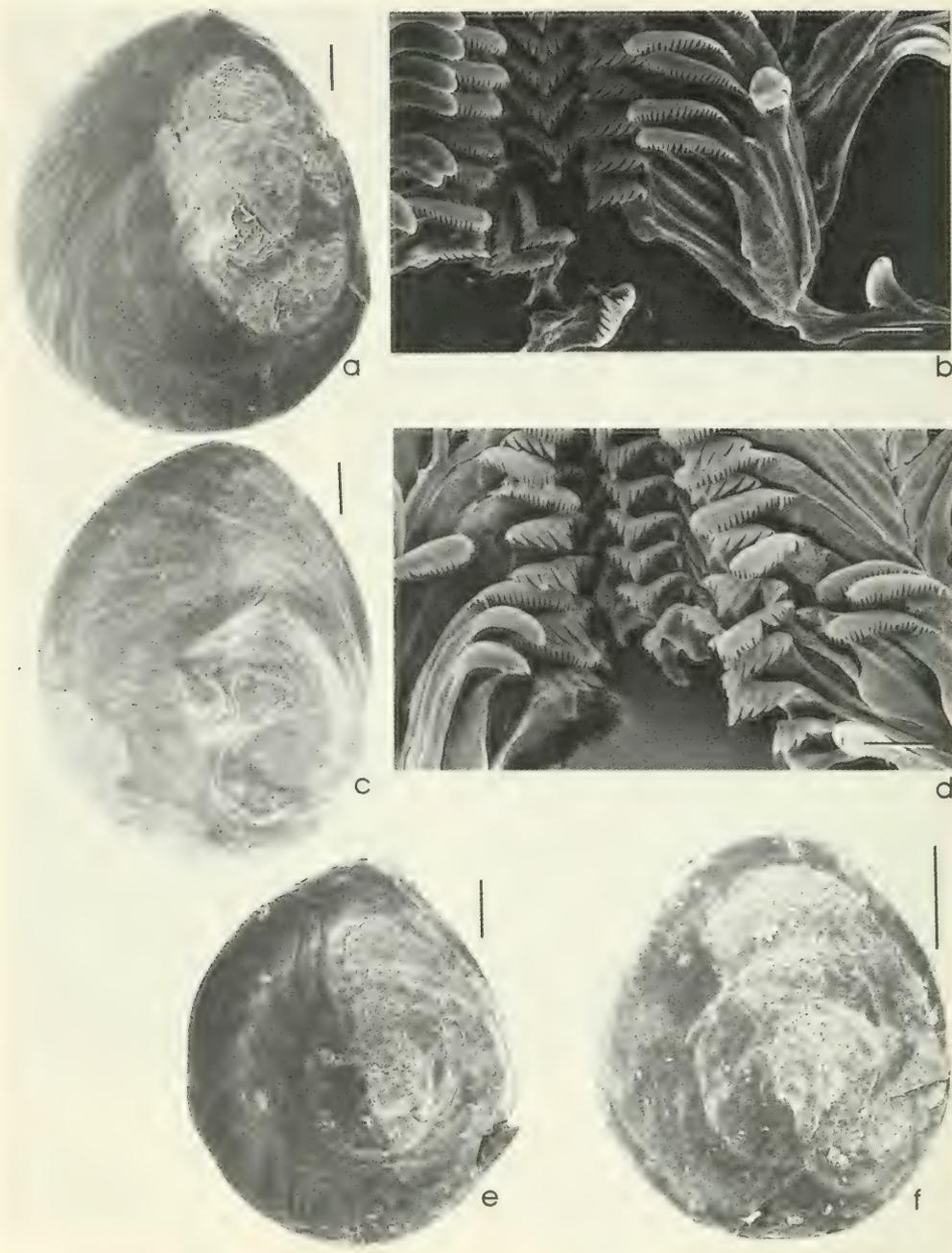


FIG. 35. Radulae and opercula of *Trochidrobia*.

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.

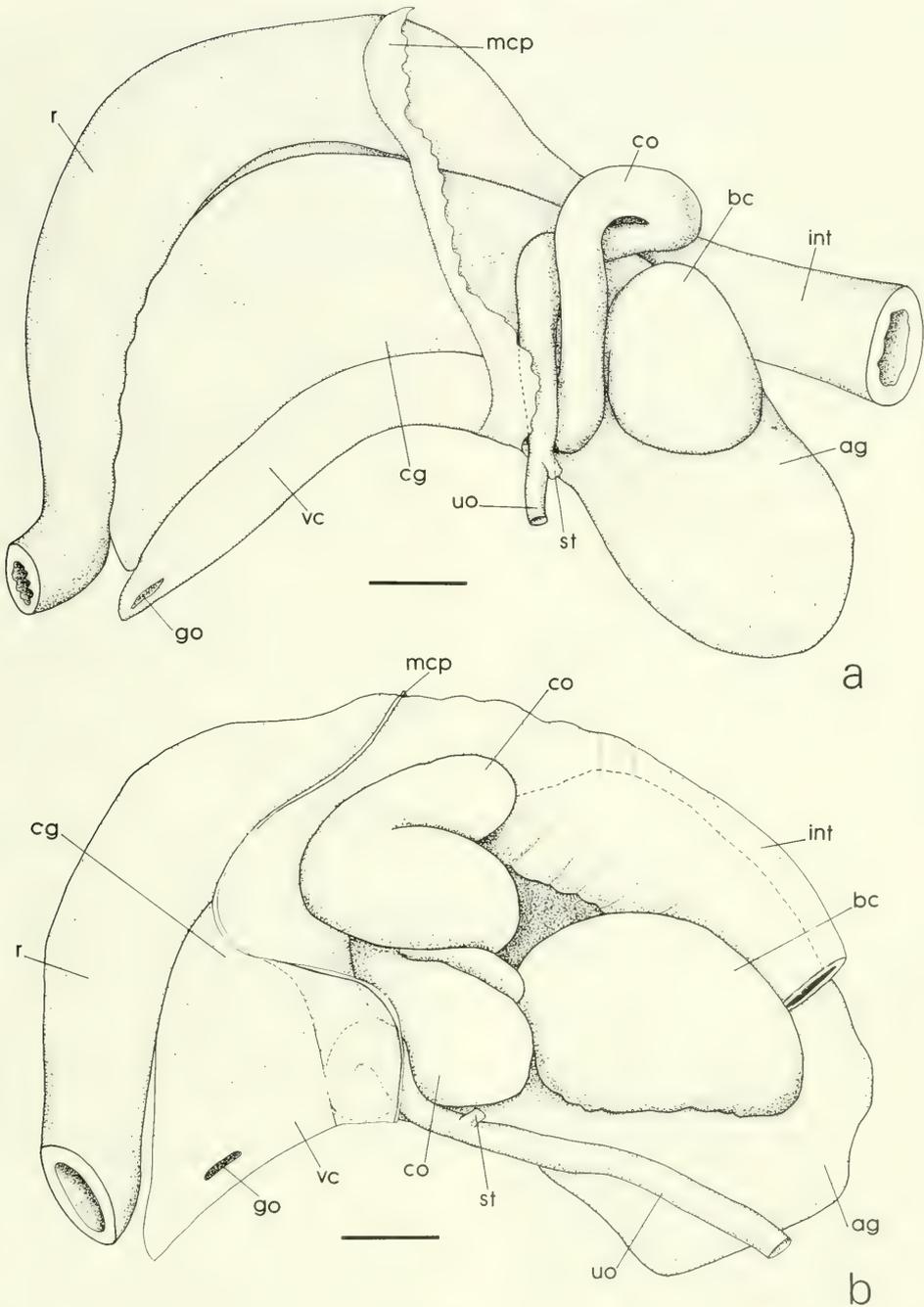


FIG. 36. Female genitalia of species of *Trochidrobia*.

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-spined 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), Finnis Swamp West (690A–C, 691), Bopeechee Springs (692A,B), Old Finnis 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).

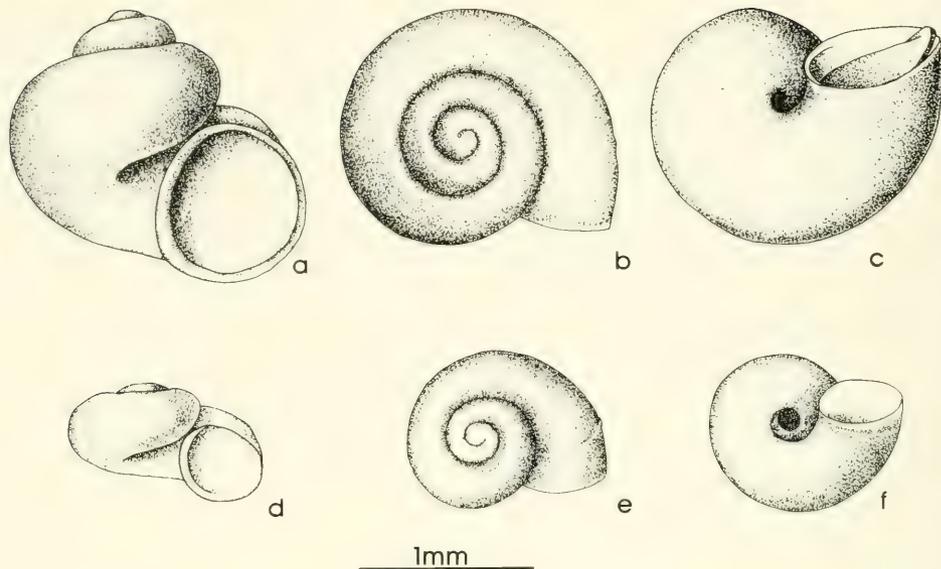


FIG. 37. Shells of species of *Trochidrobia*.

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 ap-

pears 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-

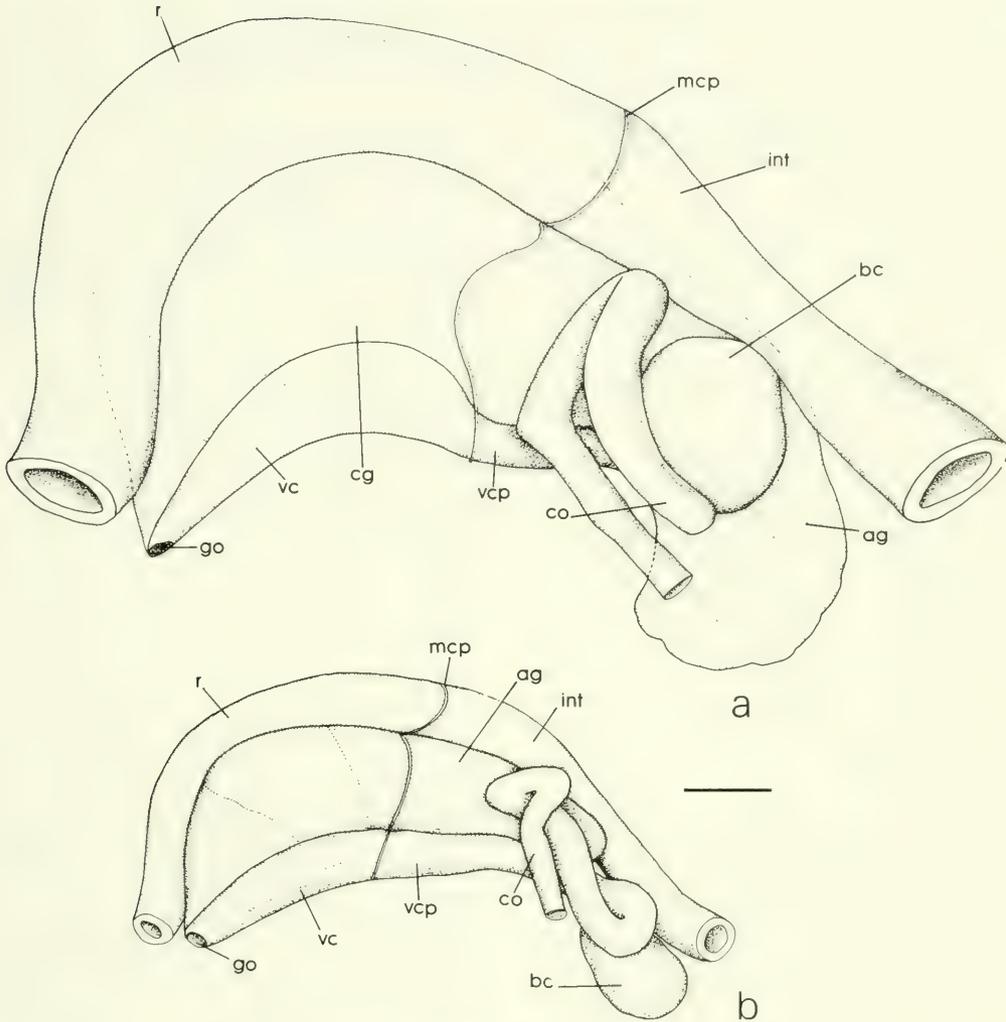


FIG. 38. Female genitalia of species of *Trochidrobia*.

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: 0.1 mm

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*.

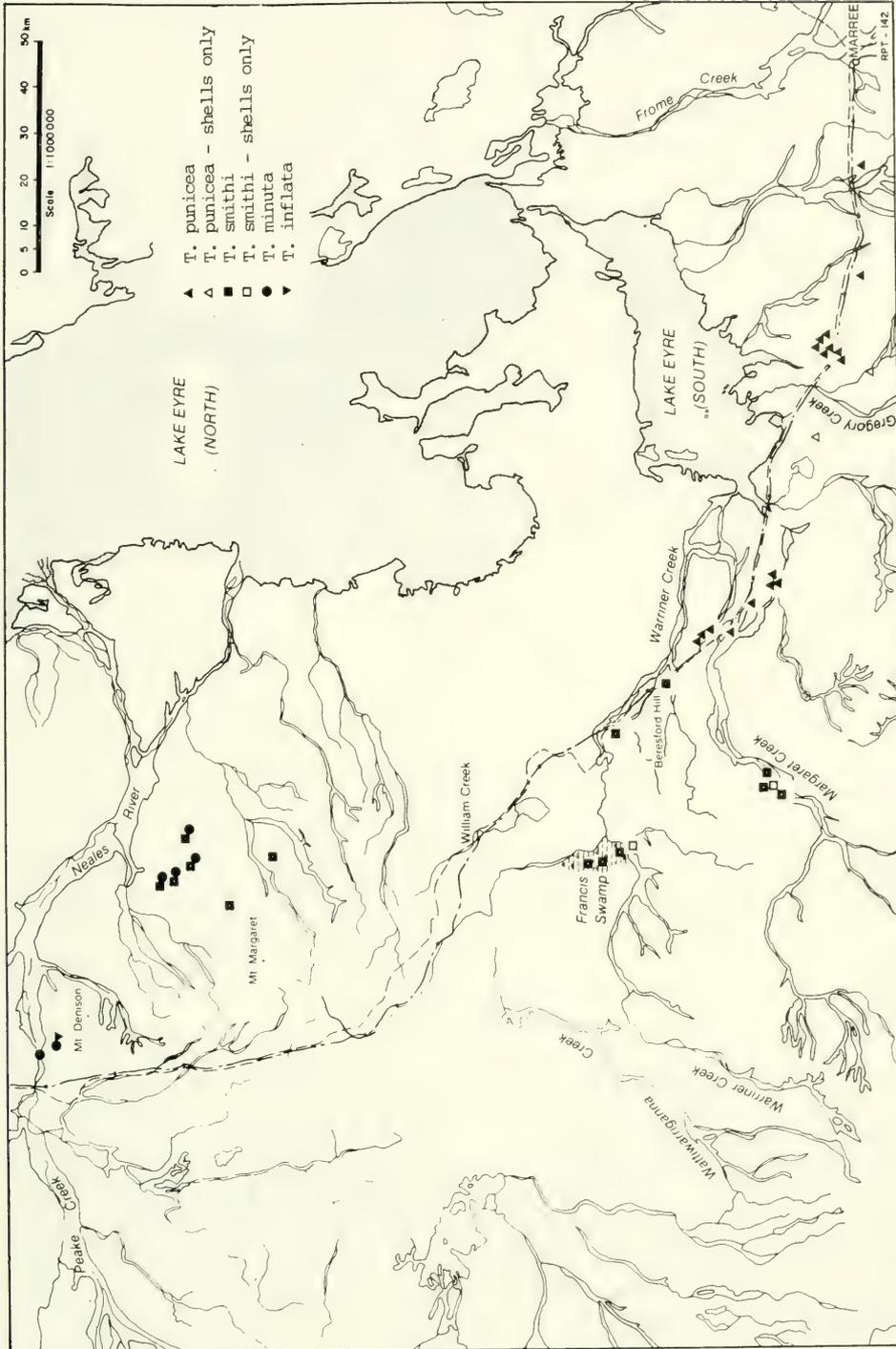


FIG. 39. Distribution of the species of *Trochidrobia*.

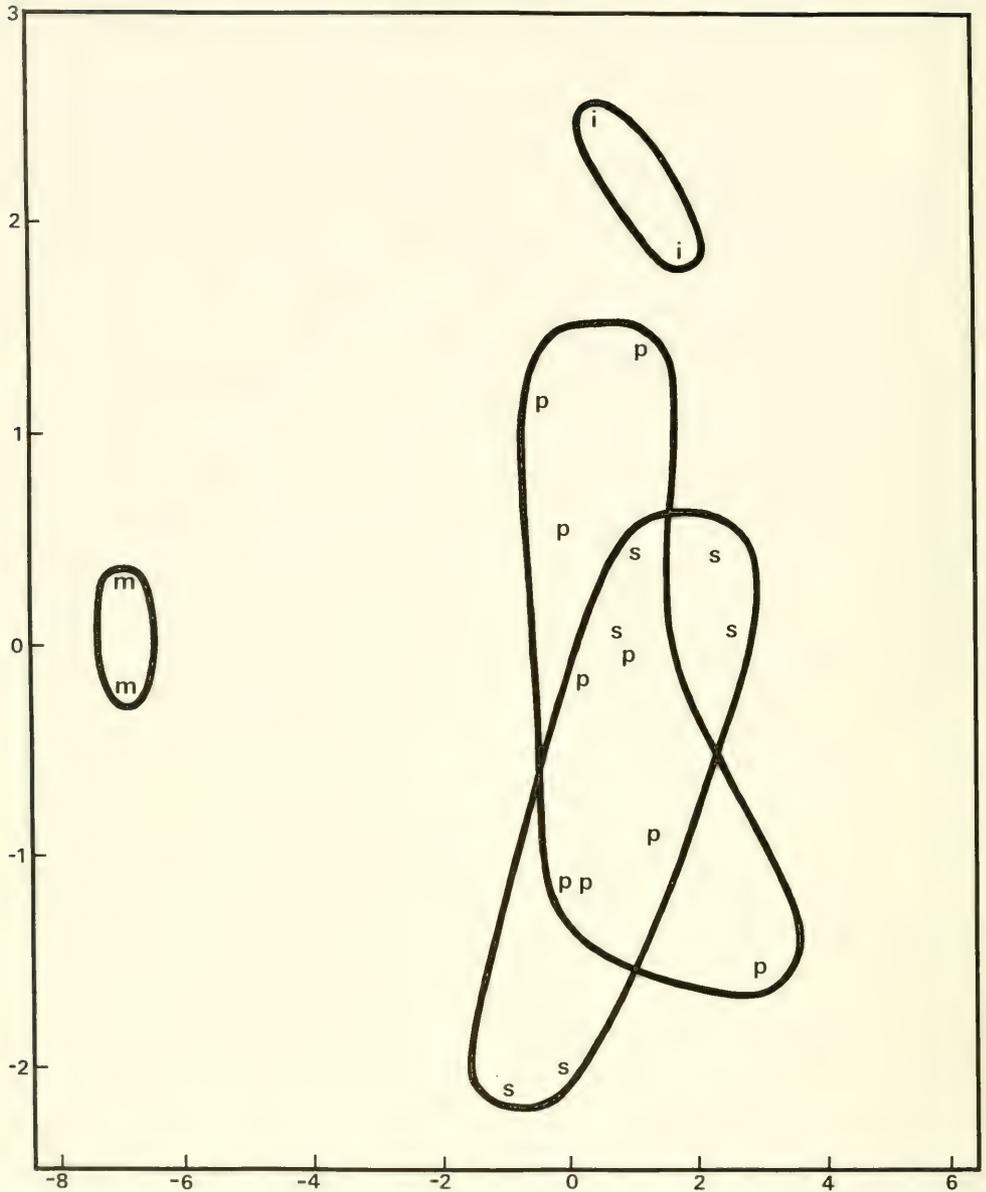


FIG. 40. Plot of group centroids, using first two canonical axes, obtained from discriminate analysis of populations of species of *Trochidrobia* using shell measurements. Males and females of each population are, for the purpose of this analysis, treated as distinct populations. The axes contain the 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 vari-

able used in the discriminate analyses gave the following results:

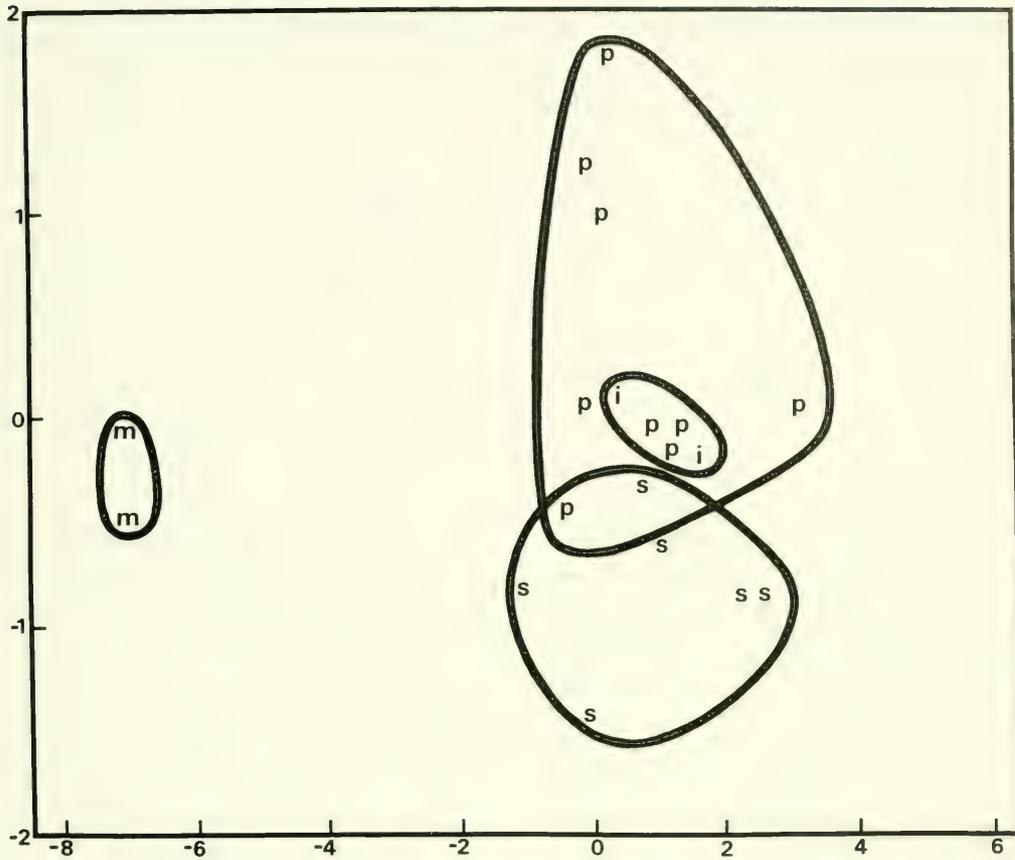


FIG. 41. Plot of group centroids, using first and third canonical axes, obtained from discriminate analysis of populations of species of *Trochidrobia* using shell measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct populations. The axes contain 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*

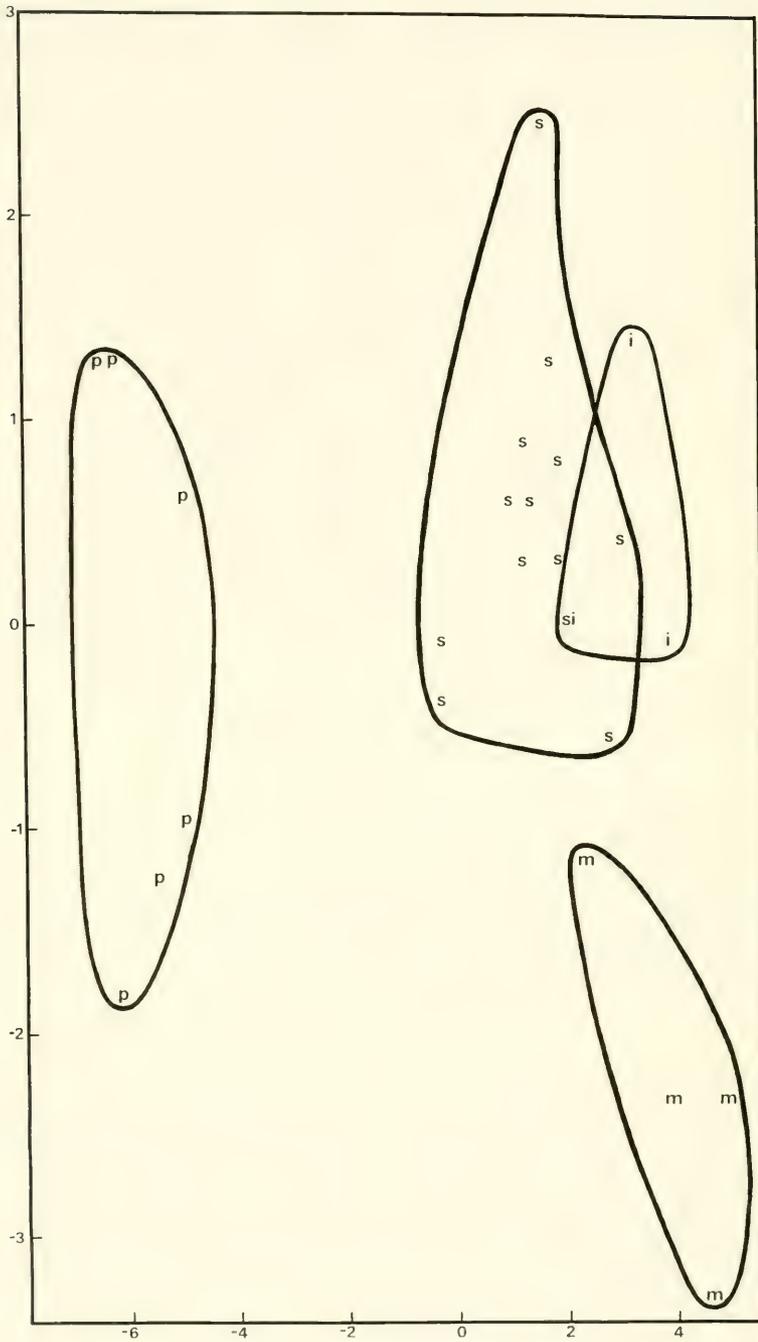


FIG. 42. Plot of discriminate scores for individuals, using first two canonical axes, obtained from discriminate analysis of specimens of *Trochidrobia* using female genital measurements. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: GO, 51.32%; 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.

	<i>T. punicea</i>	<i>T. smithi</i>	<i>T. minuta</i>	<i>T. inflata</i>	
<i>T. punicea</i>	X	0.128 0.271	1.383 1.149	0.239 0.219	Right side: Female, shell Male, shell
<i>T. smithi</i>	0.155 2.646	X	1.462 1.414	0.274 0.385	
<i>T. minuta</i>	1.306 4.301	1.437 1.675	X	1.356 1.142	
<i>T. inflata</i>	0.243 3.377	0.324 0.744	1.248 0.999	X	

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 unpig-

mented 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

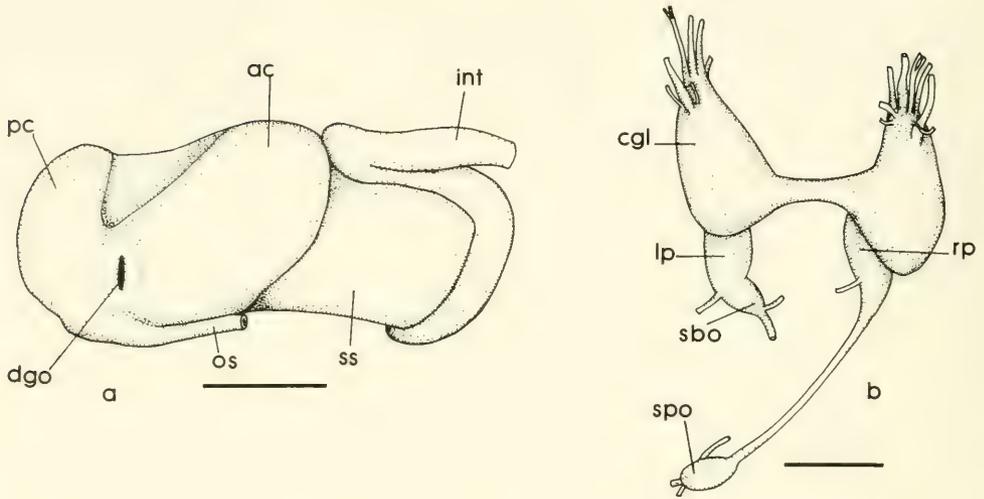


FIG. 43. a. Stomach of *Fonsochlea accepta* form A, Welcome Springs, viewed from its inner (left) side. b. Circum-oesophageal ganglia of *F. accepta* form A, Welcome Springs viewed dorsally (pedal ganglia omitted). ac, anterior chamber of stomach; cgl, left cerebral ganglion; dgo, digestive gland opening; 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. zeidlereri*) 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-

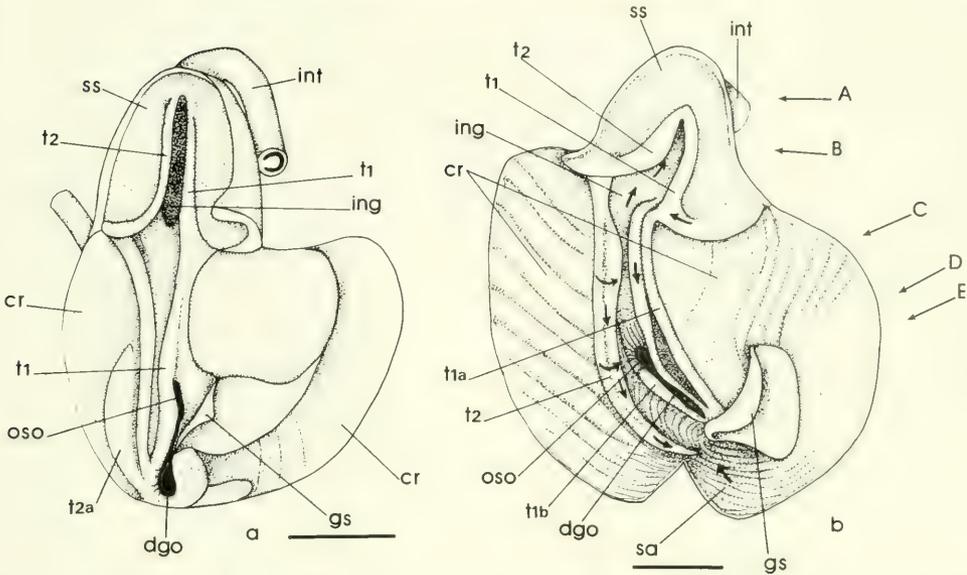


FIG. 44. Stomachs of *Trochidrobia punicea* (a) and *F. accepta* form A (b) opened from outer (right) sides. Arrows in b indicate directions of main ciliary currents; letters A–E correspond approximately to sections with same letters in Fig. 45. cr, chitin-lined ridges; dgo, digestive gland opening; 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 ventricle and auricle. No renopericardial 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-

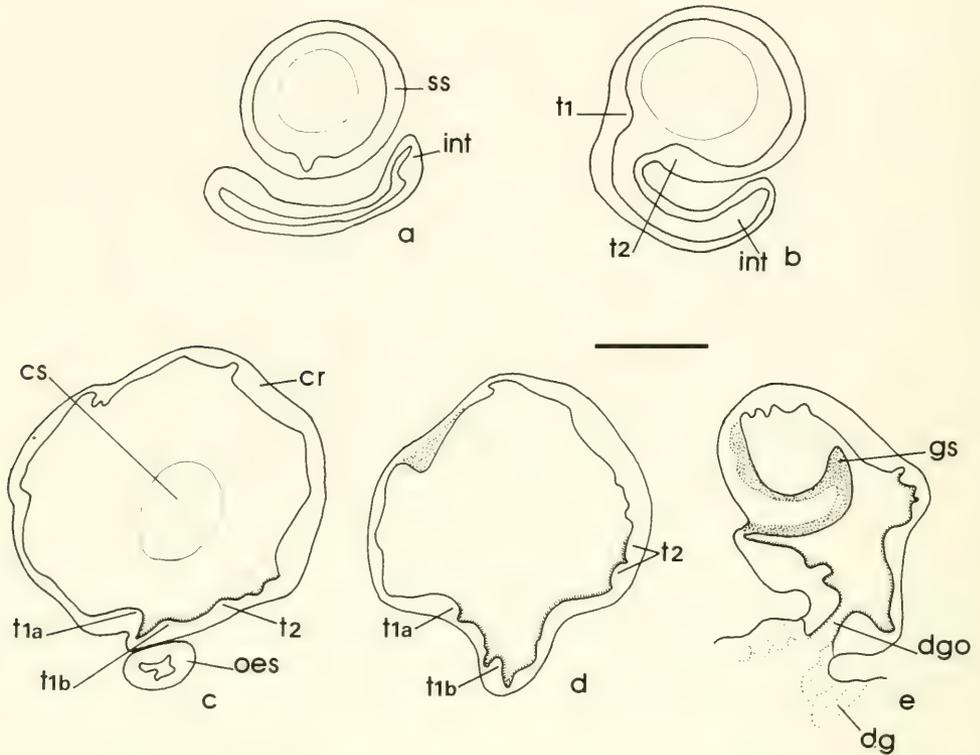


FIG. 45. Sections through stomach of *Fonscochlea zeidlerii* form A. Approximate positions indicated in Fig. 44b. cr, chitin-lined ridges; cs, crystalline style; dg, digestive gland; dgo, digestive gland opening; gs, gastric shield; int, intestine; oes, oesophagus; ss, style sac; t1, major typhlosole;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

tive (rp-spo) and the left pleural (lp) and sub-oesophageal 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 immedi-

ately 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

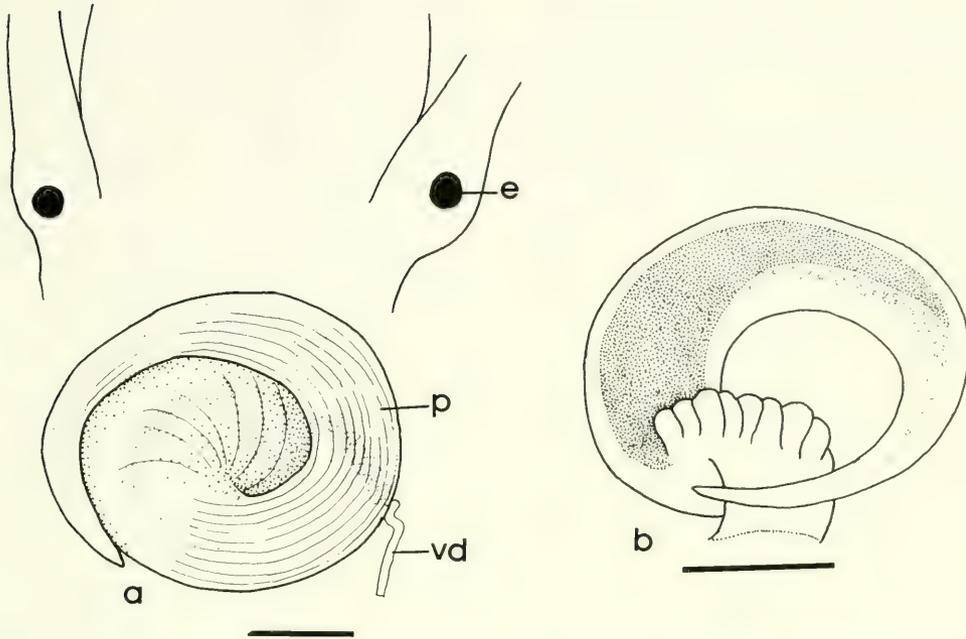


FIG. 46. a. Dorsal view of penis of *Fonscochlea accepta* form A, Welcome Springs, preserved material. b. Ventral view of living penis of *Fonscochlea zeidleri* form A, Blanche Cup. e, eye; p, penis; vd, pallial vas deferens. Scale: 0.25mm.

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-gonadal 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

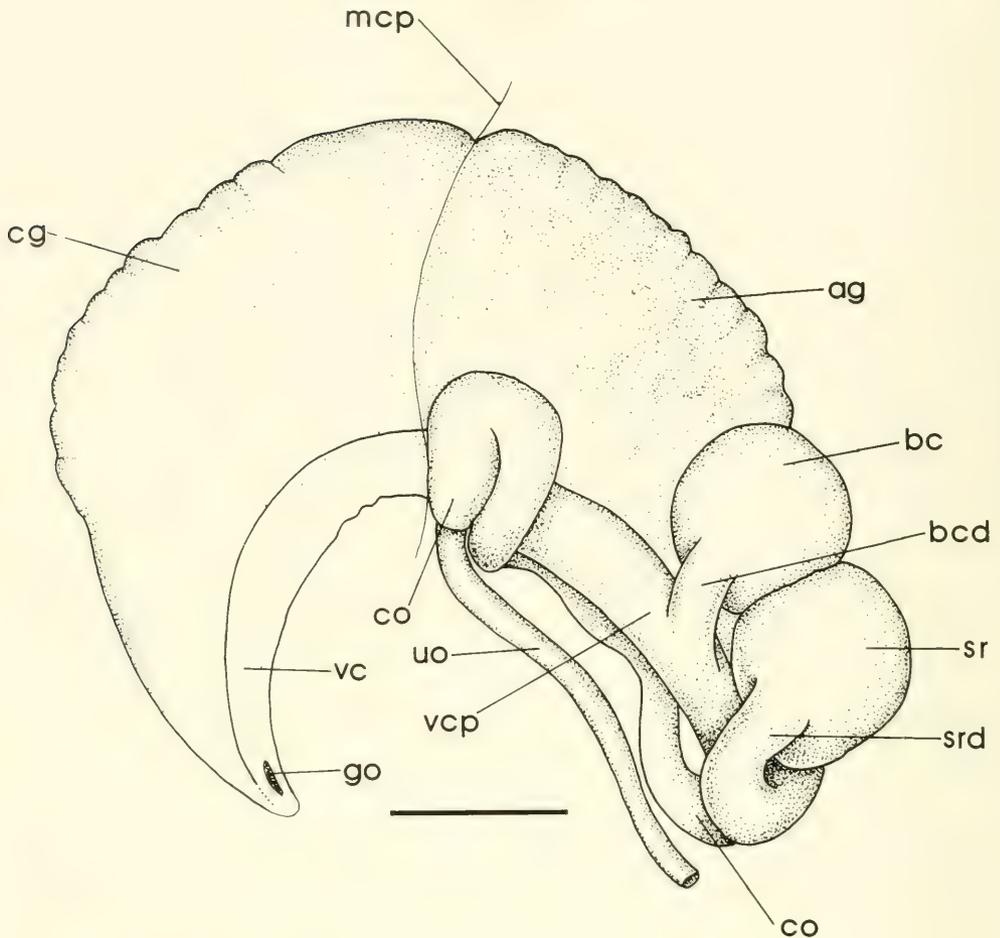


FIG. 47. Female genitalia of *Fonscochlea zeidlerii* form A, from the left side.

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. zeidlerii* (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-

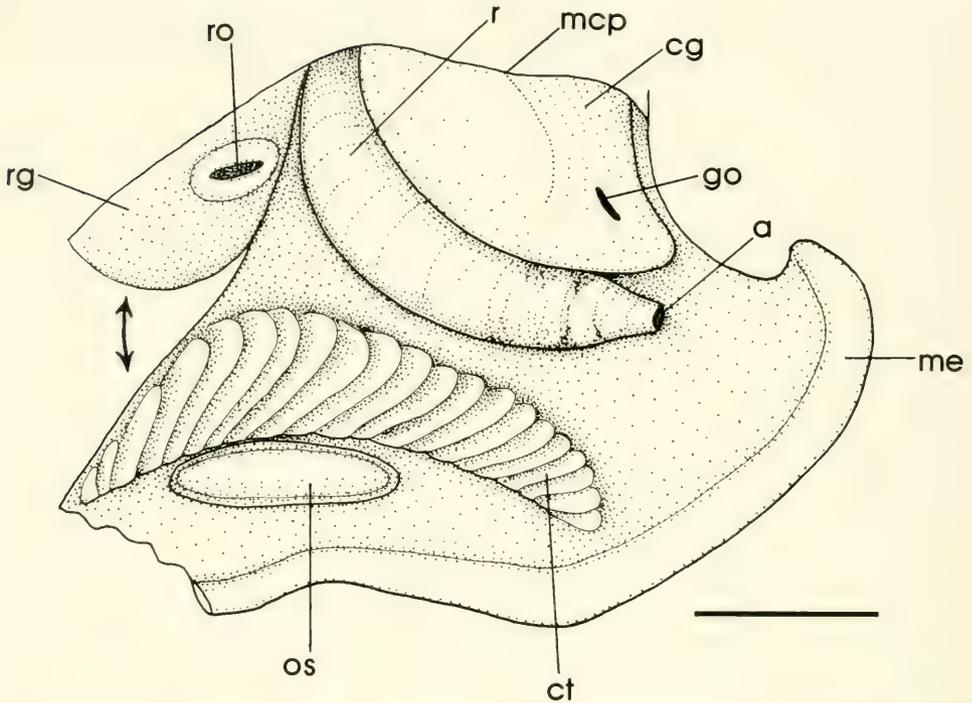


FIG. 48. Dissection of pallial cavity of *Trochidrobia punicea*. Double-headed arrow indicates separation of kidney from dorsal pallial wall. a, anus; cg, capsule gland; ct, ctenidium; go, female genital opening; mcp, posterior limit of mantle cavity; me, mantle edge; os, osphradium; r, rectum; rg, renal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

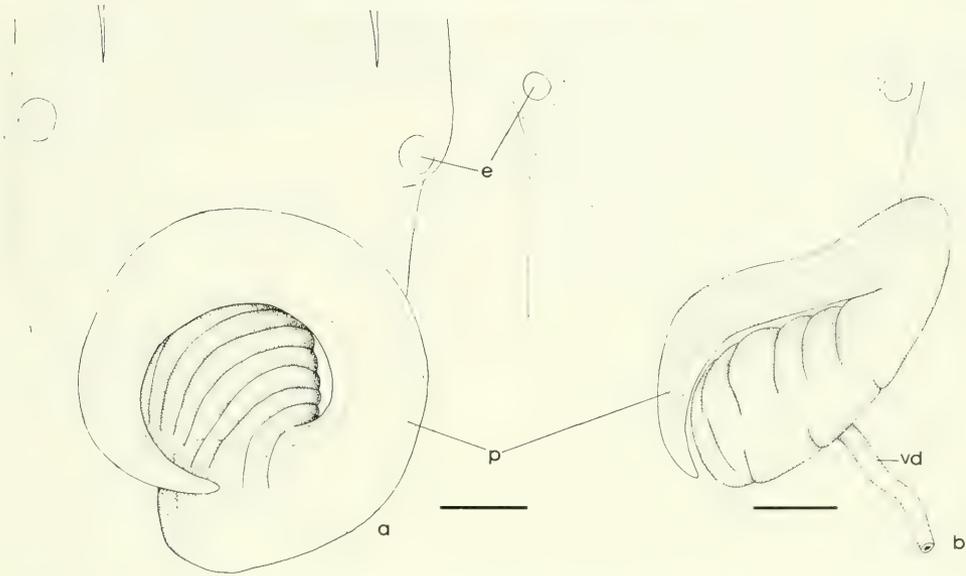


FIG. 49. Penes of *Trochidrobia punicea*, Blanche Cup (a.) and *Trochidrobia smithi*, Outside Springs (b.). a, eye; p, penis; vd, pallial vas deferens. Scale: 0.1mm

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 al-

most 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

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

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

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.

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.

Number of hours	Species (population)										
	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

¹commenced at 6:30PM ²commenced at 3:34PM ³commenced at 8:40AM ⁴dish 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 compari-

sons, $P < 0.05$). 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-

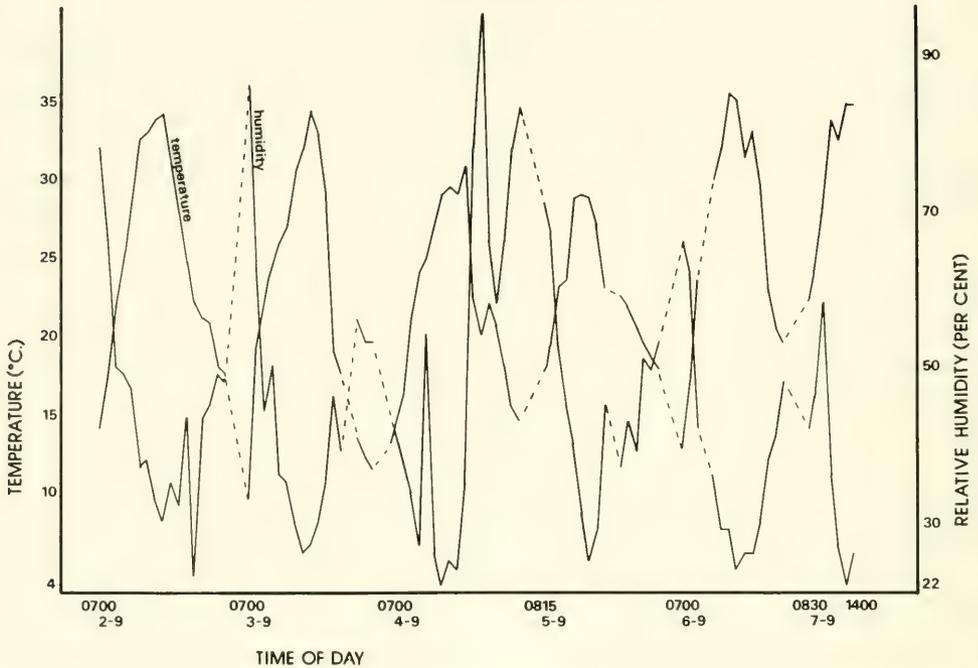


FIG. 50. Running record of air temperature and humidity in tent for duration of experiments. Readings taken hourly, generally from 0600 to 2200; dashed lines indicate intervals at night during which readings were not taken.

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 acclimatization 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, $P < 0.025$).

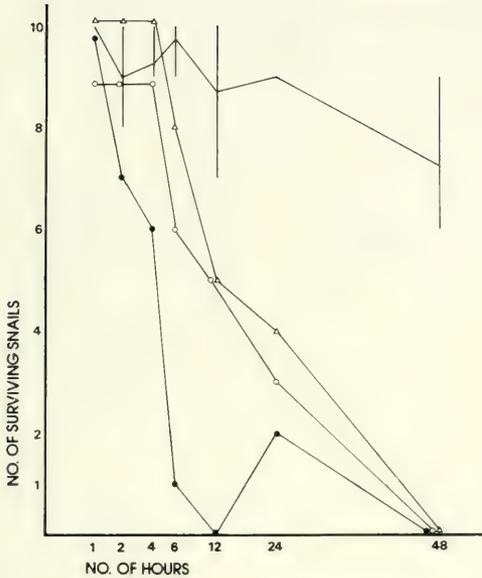


FIG. 51. Survivorship of large-sized species of *Fonscochlea* in dry dishes. *Fonscochlea accepta* form A, solid circles; *F. accepta* form B, open triangles; *Fonscochlea aquatica* form A, open circles; *F. zeidleri* form A represented by line with error bars, representing range of results among populations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

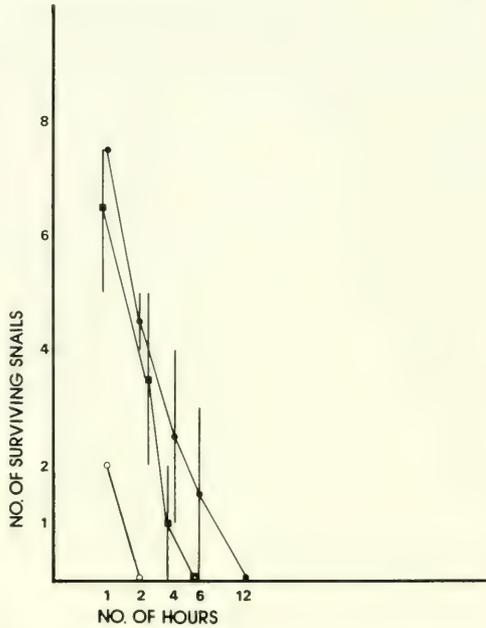


FIG. 52. Survivorship of small-sized species of *Fonscochlea* and *Trochidrobia punicea* in dry dishes. *Trochidrobia punicea*, solid squares (two runs pooled); *Fonscochlea conica*, open circles; *Fonscochlea variabilis* form A, solid circles (runs for different populations of this species pooled).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

vival 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 = Finnis Springs, CSRB = Coward Springs Railway Bore, BC = Blanche Cup.

Species (population)	Salinity	6‰						9‰						12‰						Date, time commenced		
		Number of hours						Number of hours						Number of hours								
		1	2	3	6	12	24	1	2	3	6	12	24	1	2	3	6	12	24			
<i>F. zeidleri</i> (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	
<i>F. zeidleri</i> (CSRB)	2	10	10	10	10	10	9	10	10	10	10	10	10	2	3	7	8	9	8	1.9	9:30AM	
<i>F. zeidleri</i> (BC)	3.6	10	10	10	10	9	10	10	10	10	10	7	8	9	10	9	8	7	6	9	30.8	10:20AM
<i>F. aquatica</i>	3.6	10	10	8	10	9	10	8	8	7	7	8	9	9	6	6	5	3	7	30.8	12:52PM	
<i>F. accepta</i> 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	
<i>F. variabilis</i> (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	
<i>F. variabilis</i> (CRSB)	2	10	9	9	7	10	7	10	2	0	0	1	2	0	0	0	0	0	0	2.9	9:30AM	
<i>T. punicea</i>	1.8	10	10	9	9	10	10	8	10	8	9	6	2	0	0	0	0	0	0	28.8	8:20AM	

¹11 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 = Finnis Springs, BC = Blanche Cup, and CS = Coward Springs Railway Bore.

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

¹⁶16 specimens used ¹⁸18 specimens used ¹⁹19 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 Finnis 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 = Finnis 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	
<i>F. zeidler</i> (FS)	—	0	2	3	5	7	20	20	20	20	20	20	20	7	6	0	—	—	—	2.9
<i>F. zeidler</i> (BC)	0	—	3	2	3	20	20	20	20	20	20	20	18	11	15	8	0	—	—	30.8
<i>F. zeidler</i> (CS)	—	—	—	—	0	9	15	20	20 ¹	20	20	20	20	19	20	20	1	0	—	1.9
<i>F. aquatica</i>	0	—	—	2	4	4	17	19	20	20	20	20	18	16	18	0	—	—	—	30.8
<i>F. accepta</i> form B	—	—	—	0	9	16	20	20	20	20	20	20	20	15	11	2	4	0 ²	—	1.9
<i>F. accepta</i> form A	—	—	0	2	3	5	19	20	20	20	20	20	20	20	20	10	4	0	—	3.9
<i>F. variabilis</i> (BC)	—	—	—	—	0 ³	1	4	20	20	20	20	19	20	20	19	3	0	—	—	30.8
<i>F. variabilis</i> (CS)	—	—	—	—	—	0	2	19	19 ¹	20	20	20	20	20	20	16	5	0	—	1.9
<i>F. conica</i>	—	—	—	—	—	0	10	19	29	29	29	29	29	19	19	19	18	0	—	3.9
<i>T. punicea</i>	—	—	—	0	1	8	20	20	20	20	20	20	20	18	5	0	—	—	—	1.9

¹14.5° ².44° ³1.5°

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. zeidler* 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 punicea* had significantly less activity at 37° than had all other taxa except *F. zeidler* from Finnis 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. zeidler* from Finnis 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 zeidler* from Finnis 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. zeidler* populations tested, those from Finnis 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. zeidler* 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
<i>F. aquatica</i>	2	19	9
<i>F. accepta</i> form B (N = 103)	9	51	43
<i>F. accepta</i> form A	3	9	38
<i>F. variabilis</i> (BC)	27	17	6
<i>F. variabilis</i> (CS)	41	9	0
<i>F. zeidleri</i> (FS)	4	19	29
<i>F. zeidleri</i> (BC)	16	9	25
<i>F. zeidleri</i> (CS)	25	17	8
<i>F. conica</i>	18	32	0
<i>T. punicea</i> (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 = Finnis Springs, CS = Coward Springs Railway Bore, BC = Blanche Cup.

Species (population)	NUMBER OF SNAILS IN GIVEN ZONES							S.L.	Date, Time Commenced	
	Light	Light- Middle	Dark- Middle	Dark	Light & Light-Middle	Dark & Dark-Middle				
<i>F. accepta</i> form A	41	6	11	42	47	53	P < 0.02	28.8	6:20PM	
	50	14	17	18	64	35		28.8		
<i>F. accepta</i> form B	23	16	14	47	39	61	P < 0.05	3.9	8:45AM	
	42	11	8	35	53	43		3.9	5:35PM	
<i>F. aquatica</i>	1	0	0	99	1	99	NS (Fisher's Exact Test)	30.8	4:15PM	
	2	4	6	88	6	94		28.8		
<i>F. variabilis</i> (BC)	11	0	3	86	11	89	—	31.8		
<i>F. variabilis</i> (CS)	2	2	2	94	4	96	NS	2.9	2:50PM	
	1	6	26	67	7	93		1.9		
<i>F. conica</i>	14	7	24	55	21	79	NS	3.9	2:50PM	
	10	9	17	64	19	81		3.9		
<i>F. zeidleri</i> (FS)	58	12	8	22	70	30	P < 0.001	2.9	10:25AM	
	7	3	15	75	10	90		28.8	10:55AM	
<i>F. zeidleri</i> (CS)	4	27	28	41	31	69	P < 0.001	1.9	8:45AM	
	27	30	30	13	57	43		2.9	1:00PM	
<i>F. zeidleri</i> (BC)	16	25	32	27	41	59	—	30.8		
<i>T. punicea</i>	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* DeDecker, 1979 (family Cyprididae) both belong in endemic subfamilies. Two additional endemic ostracodes have been found amongst the material collected on this survey (DeDecker, 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 occurring 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 "super-population" 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 inter-population 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 mound-spring 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 Finnis 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. zeidlereri* 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. zeidlereri* 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

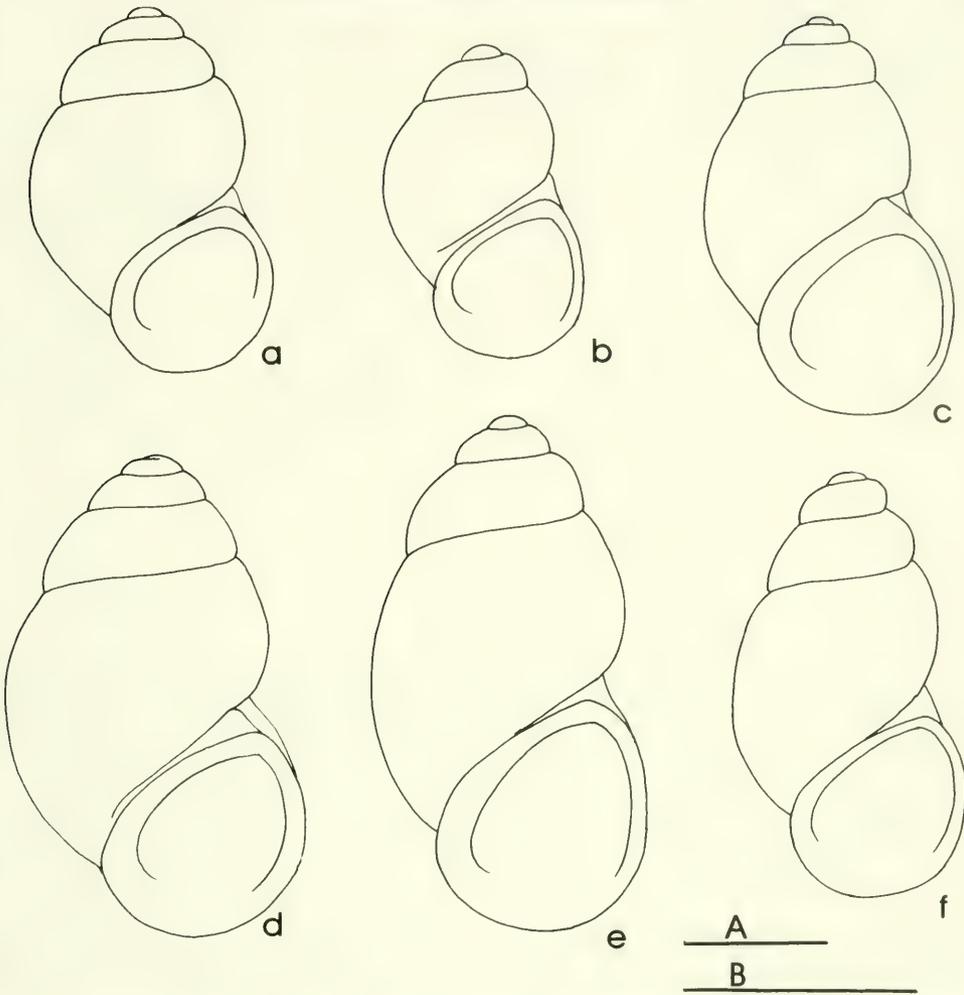


FIG. 53. Comparison of shell shape between specimens from Kewson Hill Springs (Stn 742, a-c) and Elizabeth Springs (Stn 024, d-f; 767, e).
 a,d. *Fonscochlea zeidleri* form A (a, AMS, C.152976; d, AMS, C.152975).
 b,f. *Fonscochlea conica* (b, AMS, C.152971; f, AMS, C.152972).
 c,e. *Fonscochlea aquatica*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

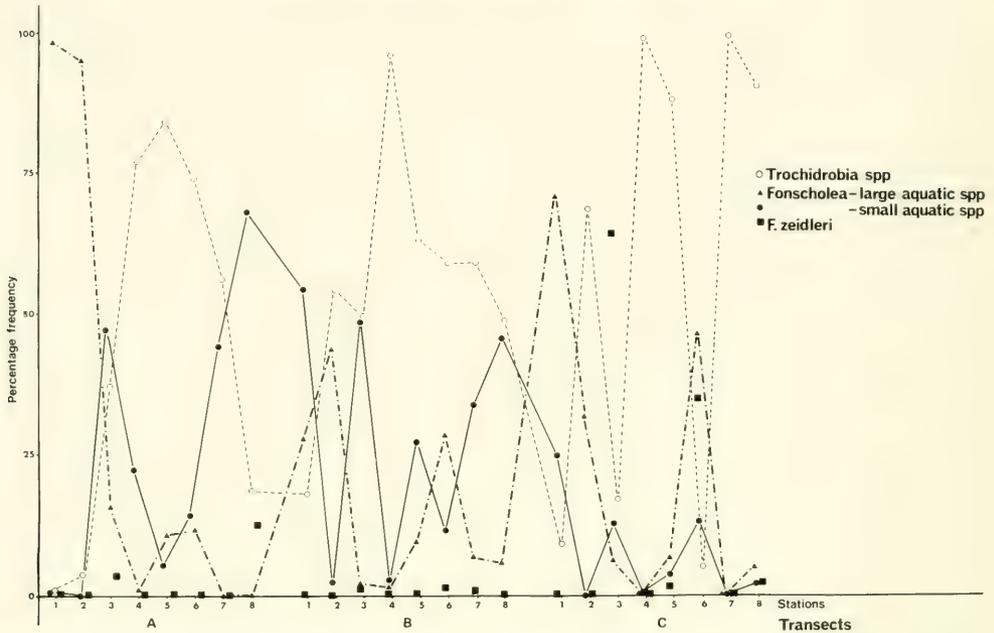


FIG. 54. Percentage frequencies of hydrobiids in three zones, demonstrating lack of any preference for a particular zone by any of the main aquatic groups, large aquatic *Fonscochlea*, small aquatic *Fonscochlea* and *Trochidrobia*. Data summarized from eight springs. Zone A, head of spring; Zone B, 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

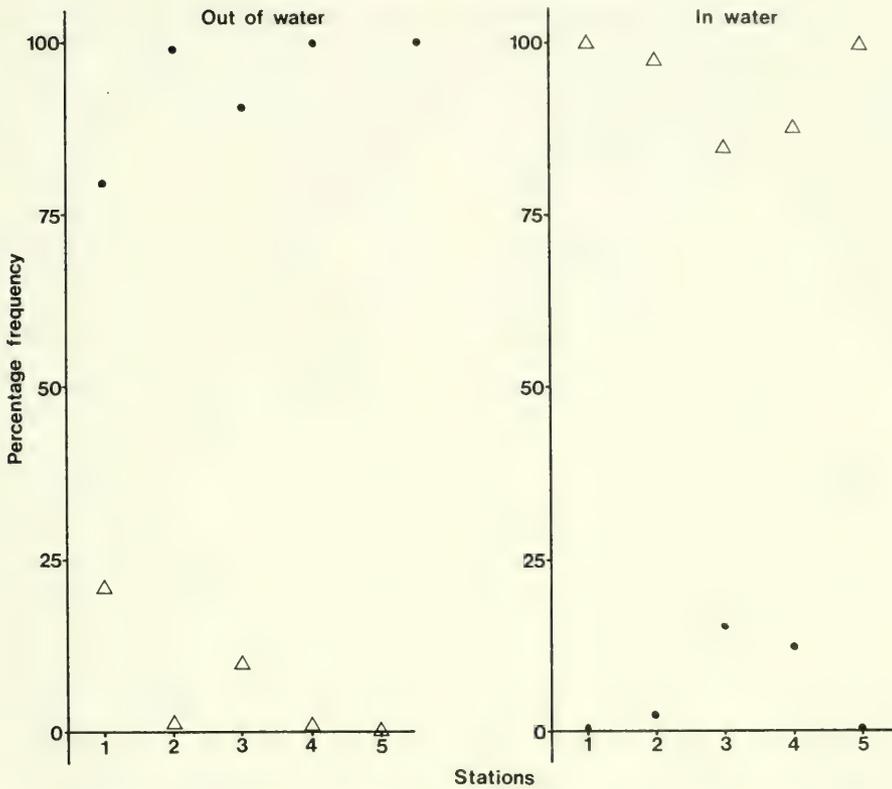


FIG. 55. Percentage frequencies of *Fonsochlea zeidlerii* form A, closed circles; large aquatic species *Fonsochlea accepta* and *F. aquatica*, open triangles, out of, and in, water in five springs. Data from quantitative samples. 1, Welcome Springs (755); 2, Julie Springs (772); 3, Elizabeth Springs (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 Free-living 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	$\bar{x}(\text{large})/\bar{x}(\text{smaller})$
<i>F. accepta</i> form A	755	3.43	0.17	1.92
<i>F. conica</i>		1.79	0.16	
	003	3.16	0.15	1.48
		2.14	0.13	
<i>F. aquatica</i> form A	739	4.31	0.17	1.92
<i>F. variabilis</i> form A		2.25	0.21	
<i>F. aquatica</i> form A	032-033	4.24	0.18	1.47
<i>F. variabilis</i> form B		2.88	0.28	
<i>F. aquatica</i> form A	679	3.96	0.27	1.45
<i>F. billakalina</i>		2.73	0.15	
<i>F. aquatica</i> form A	764,020	3.93	0.18	1.80
<i>F. conica</i>		2.18	0.24	
<i>F. aquatica</i> form B	045,046	3.88	0.15	1.41
<i>F. variabilis</i> form C		2.75	0.34	
	665	4.23	0.22	1.57
		2.69	0.21	
<i>T. inflata</i>	043	1.49	0.16	1.35
<i>T. minuta</i>	045	1.10	0.06	

ious *F. zeidler* 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

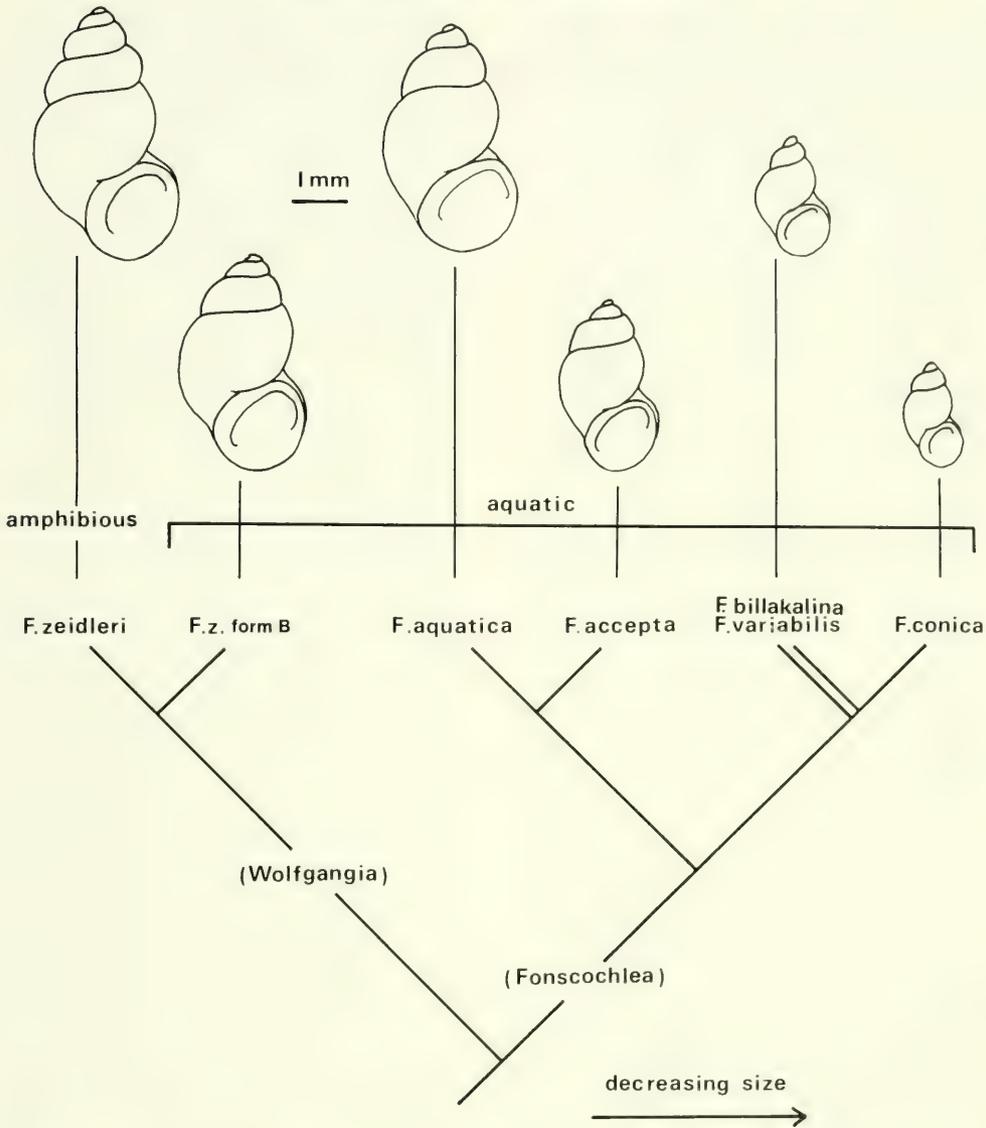


FIG. 56. Diagrammatic representation of probable relationships of species of *Fonscochlea*, as well as sizes and habitats. This figure is not a cladogram and the distances between branches are not intended to indicate degree of taxonomic separation.

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 zeidlereri* 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. zeidlereri* 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 zeidlereri* occupies both the amphibious and aquatic microhabitats at this locality, possibly because *F. aquatica*, which is similar in size to *F. zeidlereri*, 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. zeidlereri* 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. zeidlereri* 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. zeidlereri* 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 solely to simple physiological limitations, at least in the ability of *F. zeidlereri* 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. zeidlereri* 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. zeidlereri* 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. zeidlereri*, 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.

Trochidobia 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 occurrence 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 Finnis 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; DeDecker & 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. zeidlerii*, again implying more specialization for near-terrestrial life. After 48 hours in dry dishes, there was mortality in *F. zeidlerii* whereas there was 100% survival in all species of *Pomatiopsis* and *Oncomelania*. While it is unlikely that *F. zeidlerii* 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 zeidlerii*, 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. zeidlerii* 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 *Trochidrobina* 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. zeidlerii* from which the aquatic form, *F. zeidlerii* 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. zeidlerii* 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. zeidlerii* form B not included in

distribution maps but occurring at Big Cad-naowie 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 of-

ferred 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 Irrapantana). 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 Tidiampurkuna 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 Finnis 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 Finnis 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 Finnis 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 Finnis 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 Finnis 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 Finnis 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 Finnis 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 Cardajalburra 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 Cadibarawirra. 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 433388 (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 Finnis 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 Finnis 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

Kerlatroaboortallina 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:

Tidiampurkuna (667), Nilpinna (050, 1007-8), Cardajalburana (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 Finnis 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.

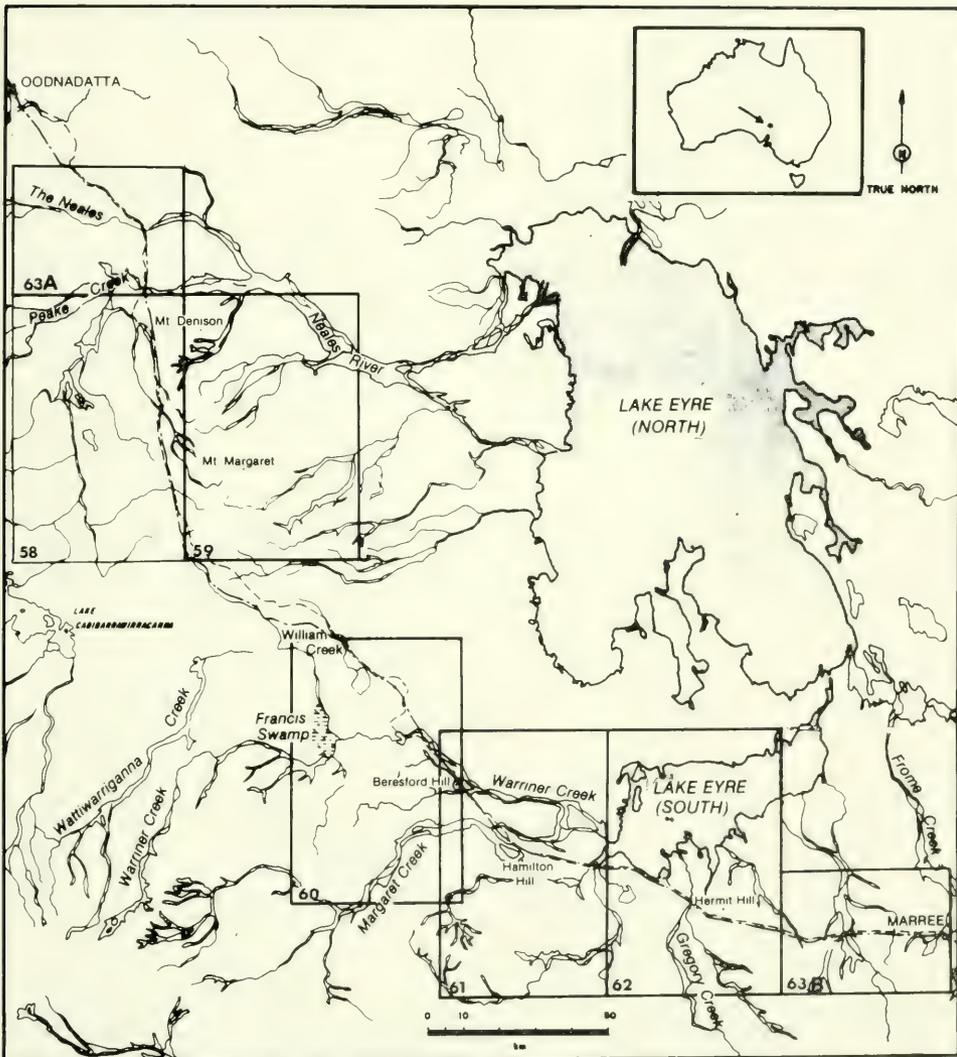


FIG. 57. General location map. Numbered rectangles refer to Figs. 58–63. On each of the following maps only sampled springs are indicated.

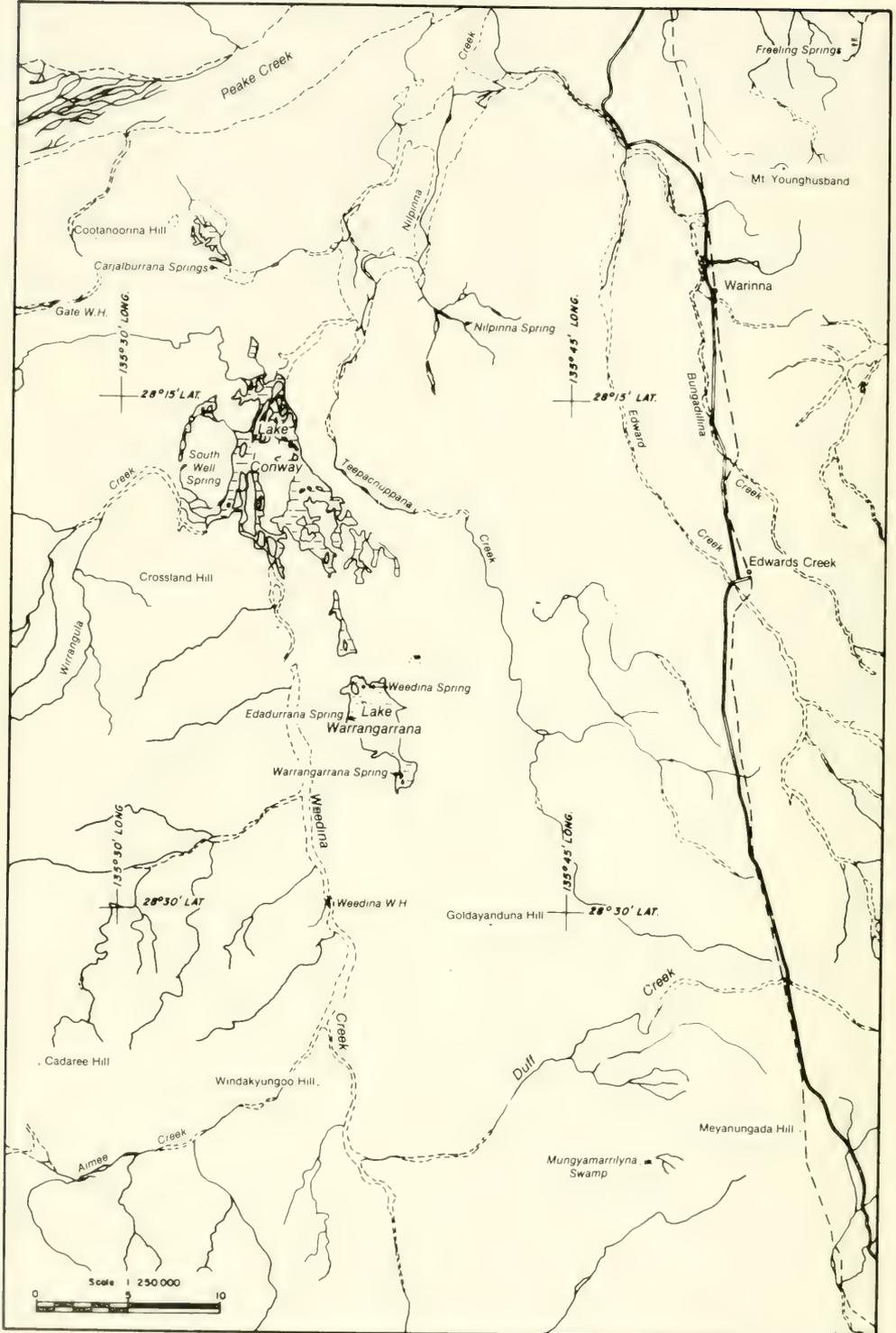


FIG. 58. The North Western Springs and Freeling Springs.

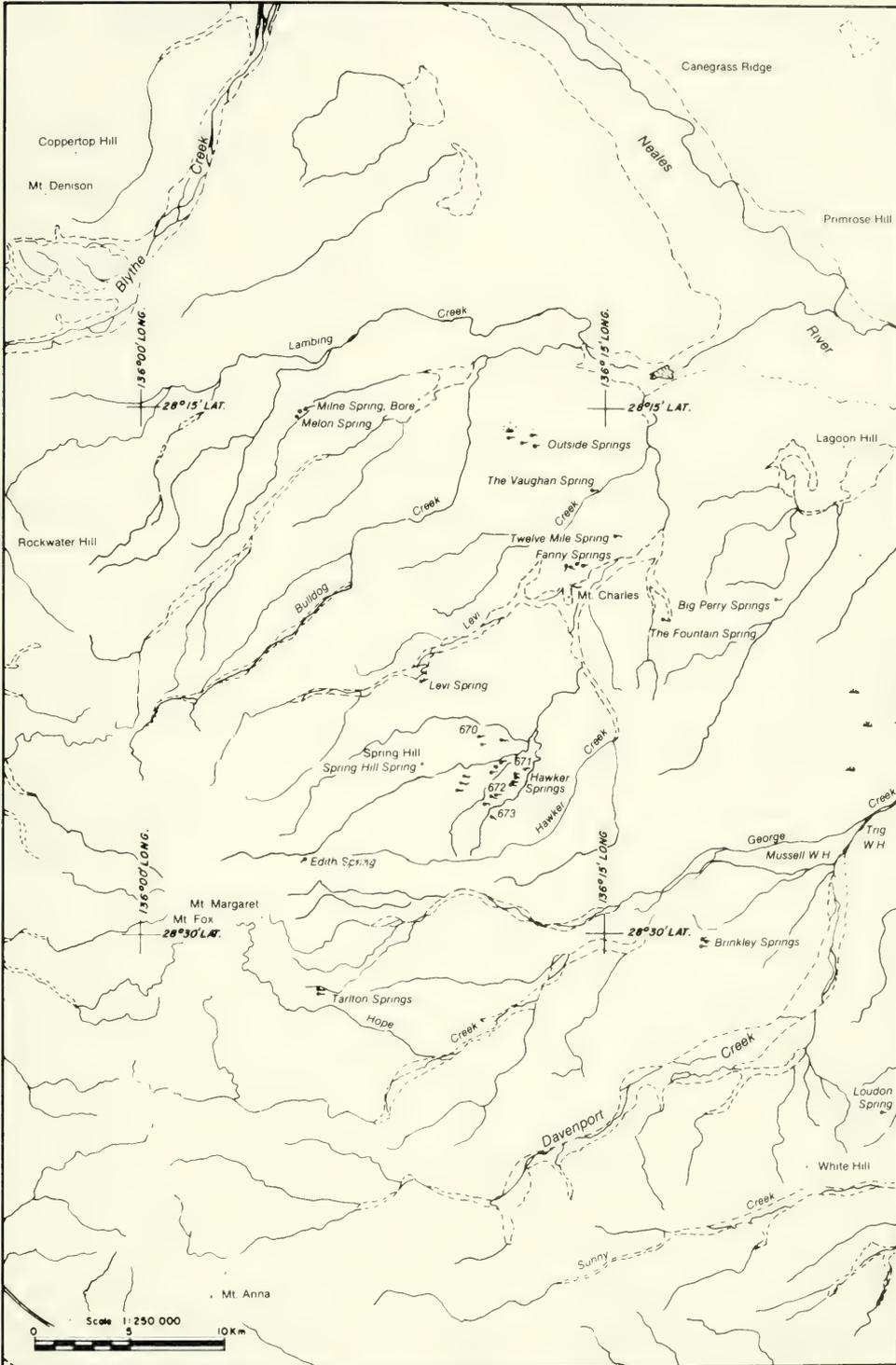


FIG. 59. The Northern Springs.

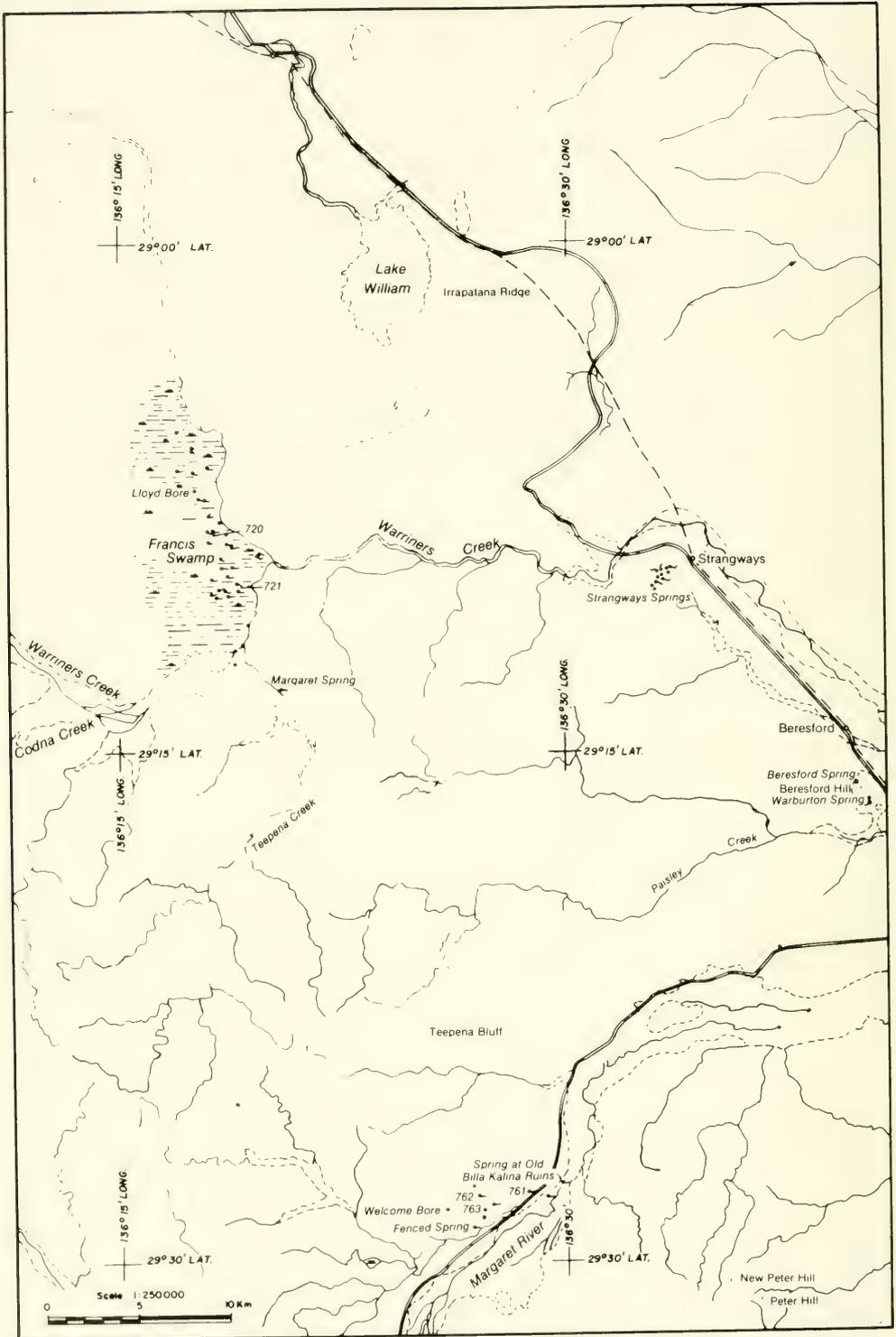


FIG. 60. The South Western Springs and the Beresford Spring Complex.

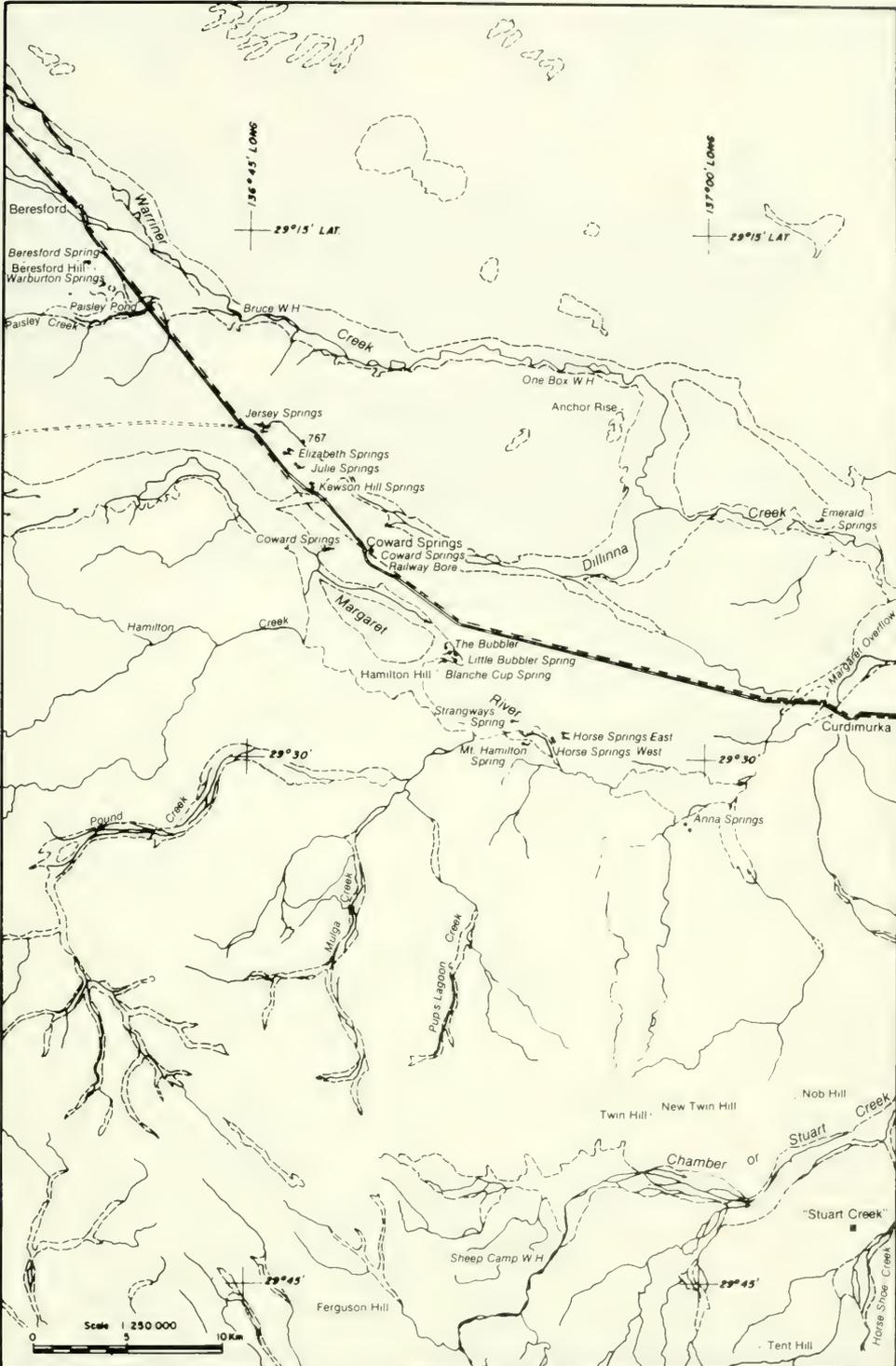


FIG. 61. The Middle Springs and Emerald Springs.

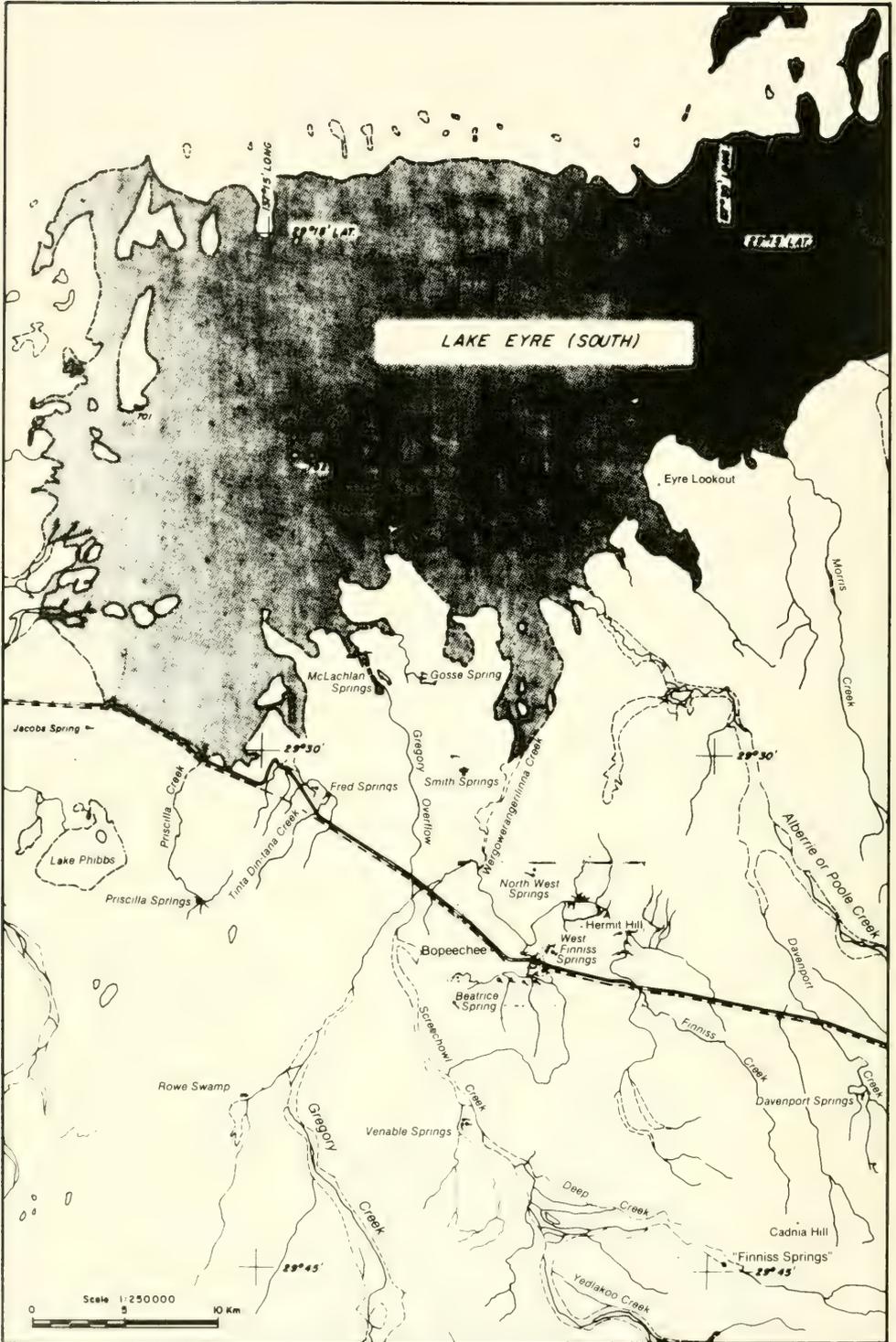


FIG. 62. The western Southern Springs.

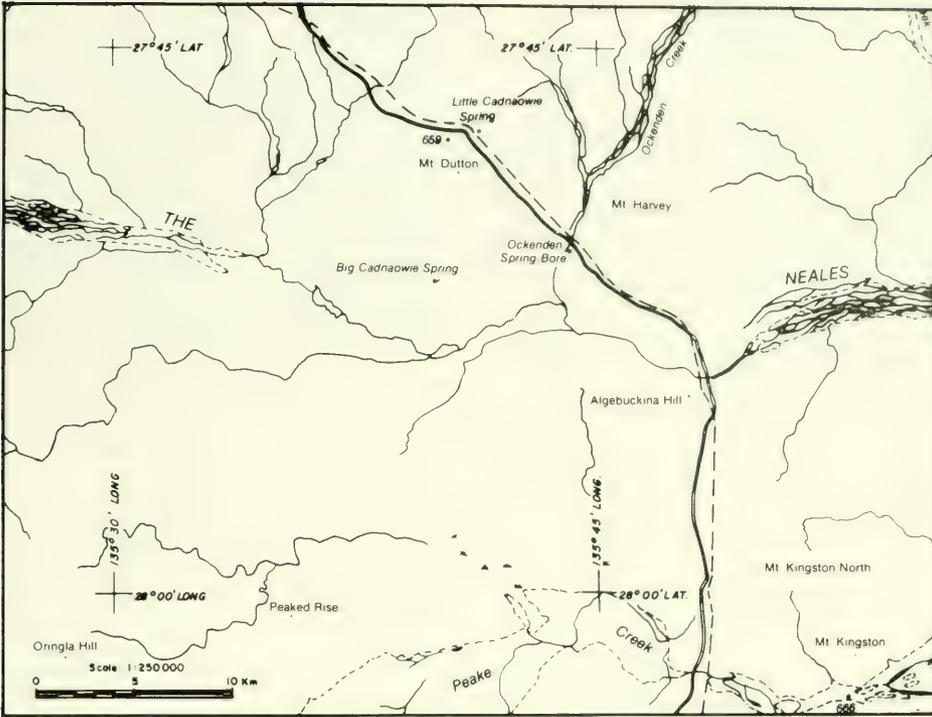


FIG. 63A. The Odnadatta Springs and one of the Freeling Springs Group (station 666).

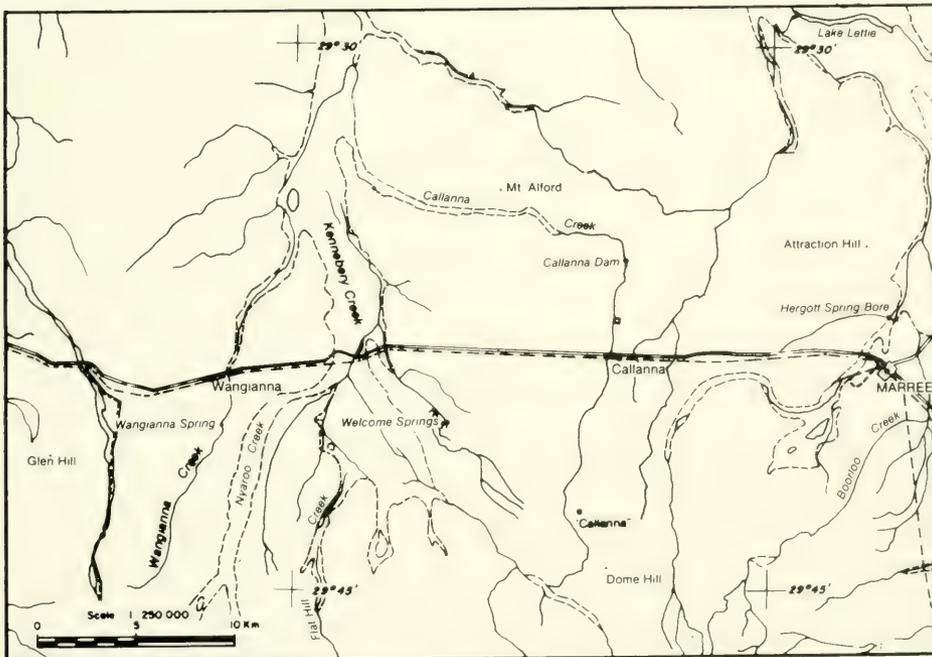


FIG. 63B. The easternmost Southern Springs.

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
<i>F. accepta</i> form A (Stations 002, 003, 753, 755)														
F	3.40	2.02	1.46	1.44	2.57	1.80	0.18	1.50	3.18	0.48	1.30	0.17	0.26	3.71
(39)	s	0.230	0.175	0.104	0.156	0.096	0.035	0.017	0.213	(33)	(31)	(31)	(31)	(31)
M	3.30	1.96	1.43	1.43	2.51	1.77	0.17	1.50	3.12	0.48	1.30	0.17	0.25	3.74
(56)	s	0.225	0.166	0.097	0.074	0.083	0.033	0.034	(50)	(50)	(50)	(50)	(50)	(50)
<i>F. accepta</i> form B (Stations 689, 690, 691, 692, 693, 694A, 694B, 694C, 711, 712, 733, 735)														
F	3.04	1.82	1.32	1.30	2.29	1.66	0.19	1.50	3.04	0.46	1.21	0.15	0.26	3.51
(158)	s	0.254	0.132	0.115	0.100	(138)	(138)	(133)	(157)	(131)	(135)	(135)	(135)	(135)
M	2.97	1.79	1.31	1.29	2.25	1.65	0.18	1.48	3.01	0.46	1.20	0.15	0.26	3.49
(316)	s	0.259	0.133	0.112	0.109	(266)	(266)	(252)	(308)	(250)	(126)	(126)	(126)	(126)
<i>F. accepta</i> form C (Station 703)														
F	3.26	1.97	1.51	1.45	2.45	1.77	0.19	1.44	3.09	0.44	1.26	0.17	0.25	3.13
(20)	s	0.150	0.097	0.095	0.049	(7)	(7)	0.064	0.143	(16)	(16)	(16)	(16)	(16)
M	3.28	1.97	1.52	1.43	2.46	1.69	0.18	1.48	3.09	0.45	1.26	0.19	0.29	3.73
(15)	s	0.169	0.115	0.084	0.075	(3)	(3)	0.021	0.143	0.027	(11)	(11)	(11)	(11)
<i>F. aquatica</i> form A (Stations 006, 033, 039, 679, 683, 739, 741, 747, 764, 767)														
F	4.19	2.37	1.86	1.70	3.06	2.09	0.18	1.50	3.23	0.55	1.49	0.10	0.20	2.55
(124)	s	0.386	0.201	0.145	0.131	(67)	(67)	0.050	0.238	(107)	(111)	(111)	(111)	(111)
					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	0.17	1.49	3.20	0.53	1.52	0.10	2.44
(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
<i>F. aquatica</i> 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	0.19	1.51	3.30	0.55	1.58	0.13	2.85
(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
M	\bar{x}	4.14	2.38	1.86	1.71	3.02	2.06	0.18	1.49	3.26	0.54	1.54	0.12	3.02
(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
<i>F. aquatica</i> cf. form A (Stations 683, 741, 767)														
F	\bar{x}	3.84	2.17	1.74	1.57	2.91	1.91	0.17	1.49	3.02	0.55	1.36	0.04	1.24
(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
M	\bar{x}	3.48	2.01	1.59	1.47	2.65	1.79	0.17	1.50	2.99	0.51	1.32	0.04	1.07
(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
<i>F. aquatica</i> form B (Stations 046, 665)														
F	\bar{x}	4.14	2.32	1.82	1.61	2.85	2.13	0.23	1.54	3.33	0.54	1.52	0.14	3.15
(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
M	\bar{x}	3.98	2.32	1.79	1.61	2.74	2.06	0.21	1.49	3.30	0.52	1.49	0.15	3.00
(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

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	
<i>F. accepta</i> 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
<i>F. accepta</i> 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
<i>F. accepta</i> 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	0.120	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
<i>F. aquatica</i> 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
<i>F. aquatica</i> 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
<i>F. aquatica</i> 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
<i>F. aquatica</i> 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
<i>F. accepta</i> 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
<i>F. accepta</i> 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)	(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
<i>F. accepta</i> 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)								
(4)	s	0.078	0.078	0.304	0.047	0.209	0.063	0.279	0.138	0.142
<i>F. aquatica</i> 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
<i>F. aquatica</i> 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
<i>F. aquatica</i> 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)								
(9)	s	0.092	0.106	0.546	0.096	0.412	0.104	0.189	0.153	0.125
<i>F. aquatica</i> 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)								
(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
<i>F. accepta</i> 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	0.10
(10)	s	0.383	0.102	0.081	0.046	0.593	0.108	(7) 0.046	0.086
<i>F. accepta</i> 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
<i>F. accepta</i> 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	0.66	0.64	2.32	0.55	0.25	0.10
(4)	s	0.102	(3) 0.012	0.048	0.078	0.184	0.089	(3) 0.035	0.042
<i>F. aquatica</i> 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	0.61	0.77	0.65	2.33	0.51	0.35	0.11
(18)	s	(16) 0.286	0.114	0.126	(18) 0.124	(13) 0.743	(14) 0.114	(12) 0.065	(12) 0.089
<i>F. aquatica</i> 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	0.73	2.52	0.55	0.38	0.11
(15)	s	0.262	0.093	(7) 0.150	0.063	(8) 0.874	(9) 0.115	(7) 0.055	(8) 0.108
<i>F. aquatica</i> 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	0.43	0.30	0.10
(9)	s	0.193	0.113	0.049	0.122	(5) 0.320	(5) 0.073	(5) 0.048	(4) 0.038
<i>F. aquatica</i> 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
<i>F. accepta</i> form A (Stations 002, 003, 752)															
\bar{x}	1.82	1.03	0.78	0.21	0.19	0.03	0.26	0.21	0.06	1.15	0.12	0.06	0.31	0.63	0.04
(10)	s	0.322	0.202	0.140	0.042	0.030	0.009	0.033	0.025	0.542	0.016	0.009	0.222	0.099	0.010
<i>F. accepta</i> form B (Stations 692, 711)															
\bar{x}	1.77	1.04	0.68	0.19	0.16	0.03	0.28	0.18	0.03	1.52	0.11	0.06	0.45	0.64	0.05
(4)	(4)	(4)	(3)	(9)	(9)	(9)	(9)	(9)	(9)	(4)	(4)	(4)	(4)	(4)	(2)
(5)	s	0.049	0.058	0.082	0.055	0.043	0.008	0.076	0.019	0.265	0.005	0.006	0.068	0.085	0
<i>F. accepta</i> 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	0.32	0.49	0.05
(4)	s	0.071	0.068	0.080	0.033	0.022	0.015	0.024	0.015	0.126	0.006	0.006	0.073	0.015	0.008
<i>F. aquatica</i> form A (Stations 028, 030, 039, 679, 683, 720, 723, 739, 741, 747, 767, 771)															
\bar{x}	1.75	0.95	0.81	0.21	0.21	0.04	0.25	0.23	0.05	1.85	0.11	0.06	0.88	0.40	0.06
(32)	(32)	(32)	(32)	(32)	(32)	(32)	(32)	(32)	(30)	(32)	(27)	(29)	(32)	(33)	(21)
(34)	s	0.292	0.166	0.158	0.053	0.046	0.028	0.053	0.029	0.305	0.019	0.011	0.243	0.133	0.017
<i>F. aquatica</i> form A (Typical form: Stations 028, 030, 039, 679, 720, 723, 739, 747, 767, 771)															
\bar{x}	1.86	0.99	0.87	0.24	0.23	0.047	0.26	0.23	0.07	2.00	0.11	0.07	0.97	0.42	0.07
(19)	(19)	(19)	(19)	(19)	(19)	(19)	(19)	(19)	(17)	(15)	(15)	(17)	(19)	(11)	(11)
(20)	s	0.279	0.177	0.138	0.048	0.044	0.023	0.058	0.037	0.264	0.023	0.008	0.173	0.158	0.014
<i>F. aquatica</i> cf. form A (Stations 683, 741, 767, 771)															
\bar{x}	1.60	0.90	0.71	0.17	0.17	0.04	0.25	0.22	0.04	1.59	0.11	0.05	0.75	0.36	0.06
(13)	(13)	(13)	(13)	(13)	(13)	(13)	(13)	(13)	(13)	(12)	(12)	(12)	(13)	(13)	(10)
(14)	s	0.240	0.140	0.135	0.021	0.023	0.045	0.040	0.015	0.167	0.012	0.010	0.280	0.072	0.016
<i>F. aquatica</i> form B (Station 046, 665)															
\bar{x}	1.78	0.94	0.84	0.25	0.21	0.02	0.22	0.24	0.05	1.61	0.11	0.06	1.03	0.33	0.05
(6)	(6)	(6)	(6)	(8)	(8)	(7)	(8)	(8)	(8)	(8)	(8)	(8)	(8)	(8)	(6)
(10)	s	0.068	0.092	0.023	0.028	0.024	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
<i>F. variabilis</i> form A (Stations 014, 018, 739)														
F	\bar{x}	2.42	1.42	1.03	1.77	1.23	0.18	1.51	2.80	0.41	0.86	0.15	0.24	3.14
	s	0.199	0.131	0.083	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	1.70	1.13	0.18	1.50	2.73	0.41	0.81	0.14	0.24	2.96
	s	2.221	0.138	0.095	0.127	0.066	0.051	0.076	0.048	0.037	0.069	0.027	0.048	0.759
<i>F. variabilis</i> (small Blanche Cup form: Station 739)														
F	\bar{x}	1.44	0.93	0.68	1.176	0.89	0.17	0.30	1.98	0.41	0.57	0.08	0.10	1.42
	s	0.145	0.071	0.053	0.082	0.118	0.049	0	0.065	0.053	0.052	0.029	0.048	0.607
M	\bar{x}	1.40	0.90	0.65	1.13	0.85	0.19	1.35	2.15	0.38	0.54	0.09	0.1	1.75
	s	0.148	0.073	0.062	0.104	0.077	0.049	0.071	0.071	0.014	0.045	0.021	0.038	0.508
<i>F. variabilis</i> form B (Stations 032, 034, 037, 673)														
F	\bar{x}	2.79	1.64	1.19	2.01	1.39	0.19	1.50	2.98	0.41	0.95	0.11	0.31	4.85
	s	0.357	0.186	0.141	0.130	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	1.87	1.26	0.16	1.50	2.89	0.41	0.88	0.10	0.28	3.88
	s	0.184	0.138	0.091	0.113	0.106	0.047	0	0.193	0.021	0.059	0.022	0.054	0.907

(continued)

<i>F. variabilis</i> form C (Stations 045, 665)														
F	2.84	1.72	1.24	1.26	2.10	1.49	0.20	1.50	2.96	0.42	1.03	0.16	0.43	4.44
(18)	s	0.013	0.157	0.112	0.098	0.030	0.032	0	0.234	0.026	0.013	0.017	0.062	1.097
M	2.60	1.61	1.16	1.15	1.95	1.35	0.23	1.50	2.84	0.40	0.91	0.13	0.37	4.36
(14)	s	0.248	0.120	0.092	0.076	0.047	0.006	0	0.220	0.022	0.021	0.030	0.048	0.477
<i>F. billakalina</i> (Stations 026, 029, 679, 721, 723, 763)														
F	2.64	1.55	1.17	1.14	1.94	1.29	0.14	1.51	2.77	0.44	0.94	0.07	0.13	1.59
(83)	s	0.273	0.149	0.111	0.115	0.095	0.047	0.077	0.246	0.029	0.093	0.030	0.089	1.056
M	2.60	1.51	1.15	1.13	1.92	1.27	0.15	1.51	2.75	0.43	0.93	0.07	0.13	1.39
(67)	s	0.289	0.161	0.125	0.118	0.102	0.048	0.028	0.273	0.028	0.102	0.028	0.080	1.021
<i>F. conica</i> (Stations 003, 007, 019, 020, 021, 023, 024, 681, 755, 766, 769)														
F	2.07	1.20	0.86	0.85	1.52	1.02	0.16	1.50	2.67	0.40	0.71	0.10	0.18	2.64
(127)	s	0.237	0.130	0.090	0.088	0.150	0.044	0.038	0.231	0.040	0.068	0.024	0.045	0.906
M	1.95	1.14	0.82	0.80	1.44	1.00	0.13	1.49	2.57	0.39	0.67	0.10	0.17	2.48
(114)	s	0.224	0.119	0.091	0.088	0.156	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	
<i>F. variabilis</i> form A (Stations 008, 014)																				
F	\bar{x}	1.72	0.80	0.16	—	0.74	0.19	17.00	0.21	0.20	0.15	0.16	—	—	—	1.04	0.90	0.44	0.51	0.40
		(1)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(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	—
<i>F. variabilis</i> form B (Station 031)																				
F	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	(1)
M	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	(1)
<i>F. variabilis</i> form C (Station 042)																				
F	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	(1)
M	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	(1)
<i>F. billakalina</i> (Stations 026, 029)																				
F	\bar{x}	2.28	0.94	0.33	0.90	1.07	0.33	27.00	0.27	0.33	0.11	0.23	1.53	0.49	1.28	0.91	0.36	0.52	0.32	(5)
		(4)	(2)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)
(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	2.18	0.05	1.09	1.48	0.29	25.67	0.24	0.29	0.11	0.22	1.45	0.33	1.35	0.75	0.30	0.49	0.33	(3)
		(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
(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
<i>F. conica</i> (Stations 005, 007, 020, 024, 748)																				
F	\bar{x}	1.29	0.39	0.29	0.80	0.72	0.18	20.40	0.17	0.19	0.08	0.12	0.83	0.38	0.84	0.54	0.24	0.37	0.23	(10)
		(7)	(8)	(7)	(7)	(7)	(7)	(7)	(9)	(9)	(9)	(9)	(9)	(8)	(8)	(6)	(6)	(6)	(6)	(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	0.65	0.21	0.56	0.63	0.16	17.55	0.13	0.14	0.07	0.13	0.11	0.78	0.33	0.68	0.40	0.21	0.30	0.21
		(9)	(8)	(7)	(9)	(10)	(10)	(10)	(10)	(10)	(10)	(9)	(9)	(10)	(9)	(10)	(9)	(10)	(9)	(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 alburmen 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
<i>F. variabilis</i> form A (Stations 008, 014)																		
F	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	(Station 014) M	1.10	0.53	0.31
(5)	(2)	(2)	(2)	(2)	(2)	(3)	(3)	(3)	(3)	(2)	(3)	(2)	(2)	(2)	(2)	(2)	(2)	(2)
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
<i>F. variabilis</i> 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)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
<i>F. variabilis</i> 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)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
<i>F. billakalina</i> (Stations 026, 029)																		
F	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	(station 26) M	1.11	0.44	0.14
(5)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(2)	(4)	(4)	(2)	(4)	(4)	(3)	(3)	(3)	(3)
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
<i>F. conica</i> (Stations 005, 007, 020, 024, 748)																		
F	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	(Stations 005,748) M	0.87	0.29	0.09
(9)	(8)	(8)	(8)	(8)	(8)	(8)	(8)	(8)	(4)	(8)	(7)	(7)	(8)	(8)	(9)	(7)	(7)	(7)
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 zaidleri*, 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
<i>F. zaidleri</i> 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	1.52	3.55	0.53	1.35	0.31	0.39	4.02
(132)	s	0.538	0.287	0.156	0.189	0.256	0.161	0.069	(119)	(119)	(100)	(100)	(100)	(100)
M	\bar{x}	3.66	2.26	1.53	1.46	2.55	2.05	1.51	3.52	0.52	1.33	0.32	0.39	4.02
(121)	s	0.447	0.295	0.148	0.160	0.228	(46)	(112)	(116)	(112)	(102)	(102)	(102)	(102)
<i>F. zaidleri</i> form B (Station 661)														
F	\bar{x}	3.46	2.23	1.62	1.37	2.62	1.96	1.51	3.09	—	1.31	0.30	0.34	3.40
(21)	s	0.177	0.016	0.095	0.107	0.109	(5)	(10)	(10)	(10)	(20)	(20)	(20)	(20)
M	\bar{x}	3.37	2.21	1.58	1.37	2.58	1.93	1.50	3.00	0.55	1.31	0.29	0.35	3.85
(15)	s	0.189	0.130	0.089	0.112	0.122	(5)	(7)	(7)	(1)	(13)	(13)	(13)	(13)
							0.049	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
<i>F. zeidleri</i> 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
<i>F. zeidleri</i> 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
<i>F. zeidleri zeidleri</i> (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
<i>F. zeidleri</i> 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
<i>F. zeidleri</i> 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
<i>F. zeidleri</i> 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
<i>F. zeidleri</i> 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
<i>F. zeidleri</i> 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
<i>T. punicea</i> (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
<i>T. smithi</i> (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
<i>T. minuta</i> (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
<i>T. inflata</i> (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
<i>T. punicea</i> (Stations 002, 007, 009, 020, 024, 693, 748)																				
F	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)	(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	0.104	0.144	0.149	0.115	0.060	0.060	0.058
M	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)	(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	0.090	0.093	0.013
<i>T. smithi</i> (Stations 027, 029, 033, 037, 038, 039, 679, 681, 721)																				
F	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)	(7)	(13)	(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	0.048
M	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)	(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
<i>T. minuta</i> (Stations 043, 045)																				
F	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)	(2)	(1)	(2)	(2)	(2)	(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
M	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)	(2)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(3)	(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	0.050
<i>T. inflata</i> (Stations 043, 044)																				
F	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)	(1)	(3)	(2)	(2)	(3)	(3)	(3)	(3)	(3)	(3)	(2)	(3)	(2)	(3)	(3)	(3)	(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	0.085
M	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)	(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

TABLE 21C. *Trochidrobotia* species, female and male genital measurements. AG, length of alburmen 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
<i>T. punicea</i> (Stations 002, 007, 009, 020, 693)															
F	\bar{x}	1.13	0.53	0.61	0.28	0.27	1.43	0.13	0.05	0.34	(Stations 007, 009, 024, 693, 748)	1.06	0.51	0.26	0.19
	(9)	(9)	(9)	(9)	(9)	(9)	(8)	(8)	(7)	(6)	M	(7)	(7)	(4)	(7)
(10)	s	0.240	0.180	0.230	0.106	0.194	0.253	0.034	0.014	0.160	(10)	0.126	0.095	0.060	0.031
<i>T. smithi</i> (Stations 027, 033, 036, 037, 038, 039, 681, 721)															
F	\bar{x}	0.99	0.48	0.52	0.16	0.03	0.79	0.06	0.04	0.06	(Stations 033, 037, 038, 039, 679)	0.68	0.29	0.11	0.16
	(15)	(15)	(15)	(14)	(14)	(14)	(11)	(11)	(10)	(9)	M	(4)	(4)	(2)	(6)
(15)	s	0.196	0.153	0.108	0.027	0.014	0.085	0.011	0.003	0.039	(8)	0.099	0.075	0	0.059
<i>T. minuta</i> (Stations 043, 045)															
F	\bar{x}	0.63	0.32	0.30	0.17	0.09	0.51	0.04	0.03	0.24	M	0.56	0.27	—	0.11
	(3)	(3)	(3)	(3)	(3)	(2)	(2)	(2)	(2)	(2)	(4)	(2)	(2)	—	(2)
(3)	s	0.092	0.066	0.055	0.012	0.006	0.104	0.006	0	0.070	(4)	0.106	0.063	—	0.007
<i>T. inflata</i> (Stations 043, 044)															
F	\bar{x}	1.03	0.55	0.42	0.18	0.14	0.50	0.06	0.04	0.10	M	0.87	0.25	—	0.10
	(3)	(3)	(3)	(3)	(2)	(2)	(3)	(3)	(2)	(2)	(3)	(2)	(2)	—	(2)
(4)	s	0.078	0.118	0.165	0.025	0.023	0.190	0.015	0	0.014	(3)	0	0.051	—	0.021

ULTRASTRUCTURAL CHANGES IN THE DIGESTIVE TRACT OF
DEROCERAS RETICULATUM (MÜLLER) INDUCED BY A CARBAMATE
MOLLUSCICIDE AND BY METALDEHYDE

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ABSTRACT

Electron microscope investigations reveal different reactions of cells in the digestive tract of *Deroceras reticulatum* to intoxication with carbamate or metaldehyde molluscicides. All enterocytes are more strongly attacked by the carbamate compound Mesurol than by metaldehyde. The better efficiency of Mesurol is primarily attributed to its severe impact on nuclei, leading to other cell damage and finally to an increased macrophage reaction.

Metaldehyde leaves the enterocyte functions more or less intact except for that of mucus cells. It activates mucus extrusion immediately after the onset of intoxication. This mucus serves to dilute the toxin, which passes through the digestive tract and is voided. The severe attack of metaldehyde on the immature mucus cells results in cessation of mucus production, leading to a fatal mucus deficiency in the digestive tract.

Key words: Gastropoda; molluscicides; carbamate; metaldehyde; digestive tract; ultrastructure

INTRODUCTION

To date, the most efficient pesticides against slugs are carbamate compounds, such as Mesurol, which act as nerve toxins by inhibition of the cholinesterase activity (Getzin & Cole, 1964; Pessah & Sokolove, 1983). During the last decade, Mesurol has replaced metaldehyde as the primary commercial molluscicide, because metaldehyde loses most of its efficiency in humid climates (Martin & Forrest, 1969). In the literature (Pappas et al., 1973), however, it is not only Mesurol but also such other carbamate compounds as Carzol, Furadan and Zectran that are mentioned as having an increased efficiency compared to metaldehyde (Getzin, 1965; Prystupa et al., 1987). Whereas in most investigations LD₅₀ tests are used (Bakhtawar & Mahendru, 1987), there are only a few publications concerning cellular mechanisms induced by molluscicides (Ishak et al., 1970; Banna, 1977, 1980a, b; Pessah & Sokolove, 1983). Up to the present, little attention has been paid to the fact that both carbamate compounds and metaldehyde are in use as oral toxins (cf. Henderson, 1969), and, as a consequence, the first possible targets for molluscicidal action might be the cells of the intestinal epithelia.

In fact, only one study covers the influence of molluscicidal agents on the cells and tissues of the alimentary tract of slugs after intoxication (Manna & Ghose, 1972). To the best of my knowledge, ultrastructural investigations are completely lacking. Thus, the present electron microscope study was designed to investigate the different cellular responses to molluscicidal intoxication in the digestive tract of the grey garden slug, *Deroceras reticulatum*. A further purpose of the paper is to elucidate the reasons for the superior efficiency of carbamate molluscicides by comparing the ultrastructural damage after oral application of carbamate and metaldehyde.

MATERIALS AND METHODS

Laboratory-reared specimens of *Deroceras reticulatum* were fed pellets containing 4% of the carbamate compound Mercaptodimethur (4-(methylthio)-3,5-xylyl-methyl-carbamate; Mesurol; Bayer) or 4% metaldehyde (Spiess Urania 2000). The pellets were weighed before and after the slugs had fed, and the amount of toxicant effectively ingested was calculated. On an average, the animals took

up 200 µg Mesurol or 9 mg metaldehyde/g wet weight. Animals fed carbamate were dissected after one, five and 16 hours. The metaldehyde group was fixed after five hours. For primary fixation a 2% glutaraldehyde solution in cacodylate buffer (0.01 M, pH 7.4) was injected into the body cavity. Then oesophagus, crop, stomach, intestine and digestive gland were isolated in fixative and fixed for two hours in 2% glutaraldehyde at 4°C. The tissues were rinsed in cacodylate buffer and postfixed in 1% osmium-ferrocyanide (Karnovsky, 1971) for two hours. After rinsing in cacodylate and 0.05 M maleate buffer (pH 5.2), the specimens were stained en bloc in 1% uranylacetate in 0.05 M maleate buffer overnight at 4°C. The samples were dehydrated and embedded either in Araldite or in Spurr's medium (Spurr, 1969).

Ultrathin sections cut on a Reichert ultramicrotome were counter-stained with lead citrate for 30 minutes and finally examined in a Zeiss EM 9.

RESULTS

Macroscopic observations

The macroscopic reactions of the animals after molluscicide application correspond to the reactions described as typical for carbamate or metaldehyde intoxication by Godan (1979). By 30 minutes after ingestion of Mesurol pellets, the animals show violent muscle convulsions. The anterior body begins to swell while the posterior flattens. The tentacles are relaxed, the animals release a lucid mucus and take up liquid from the environment. After three hours they lie almost motionless on one side. Usually they die 20 to 30 hours later, but recovery is also possible.

After the application of metaldehyde, the animals lose much more slime than after carbamate ingestion. In this case, muscle convulsions and relaxation of the tentacles could not be observed.

Electron microscopical investigations

Histology of the epithelia in control animals

Oesophagus: The oesophageal epithelium consists of four cell types, three of which reach the lumen (Fig. 1a):

Type I: Columnar storage cells (Figs. 2a, 5) characterized by high amounts of lipid and storage carbohydrate (glycogen or galacto-

gen) (Fig. 34). In the central cytoplasm, the nucleus, small Golgi complexes, mitochondria and a few peroxisome-like vesicles are located, while smooth and granular endoplasmic reticulum occasionally appear in basal regions of the cells. Under the microvillous border a band of mitochondria can be found (Fig. 10).

Type II: Columnar secretory cells of an eccrine type (Fig. 1a), with basally situated granular endoplasmic reticulum and an elaborate Golgi apparatus (Fig. 29) producing electron-lucent secretory vesicles. Mitochondria and small amounts of lipid and glycogen are dispersed over the cytoplasm. The nucleus is located in the center of the cell.

Type III: Secretory cells of a holocrine type (mucus producing goblet cells, in the following called "mucus cells") (Figs. 1a, 3a, 5, 25), with conspicuous granular endoplasmic reticulum characterized by a spacious lumen, large Golgi apparatus and mucus vacuoles that merge in the apical part of the cells. The nuclei of these cells are situated in the basal, dilated regions. Young mucus cells (Fig. 3a) do not contain high amounts of mucus vacuoles and are characterized by a conical cell shape.

Type IV: Small electron-lucent cells (Fig. 5), conical in shape, that are dispersed amongst the other cells. Their apices do not reach the lumen. Containing characteristic lysosomes, dictyosomes and a prominent nucleus, they resemble the haemolymph macrophages.

The basal surfaces of all cell types have no infoldings (Fig. 5). In addition to numerous microvilli, the luminal surface of cell types I and II may bear cilia (Fig. 2a). The microvilli of the mucus cells are smaller than those of the other cell types (Fig. 3a).

A strong muscle layer, connective tissue cells and nerves with different neurosecretory vesicles can be found subtending the epithelium (Fig. 2a, 40, 42). In longitudinal section, the muscle filaments are all roughly parallel, while in transverse section there is a quasi-lattice of thick and thin filaments (Fig. 40). In the haemolymph space some macrophages can be observed. They are characterized by a large nucleus, small Golgi apparatus and a few small vesicles of various electron-density (Fig. 2a).

Crop: Apart from a few mucus (Type III) and small electron-lucent cells (Type IV), the cylindrical epithelium of the crop is dominated by a single cell type, resembling the storage

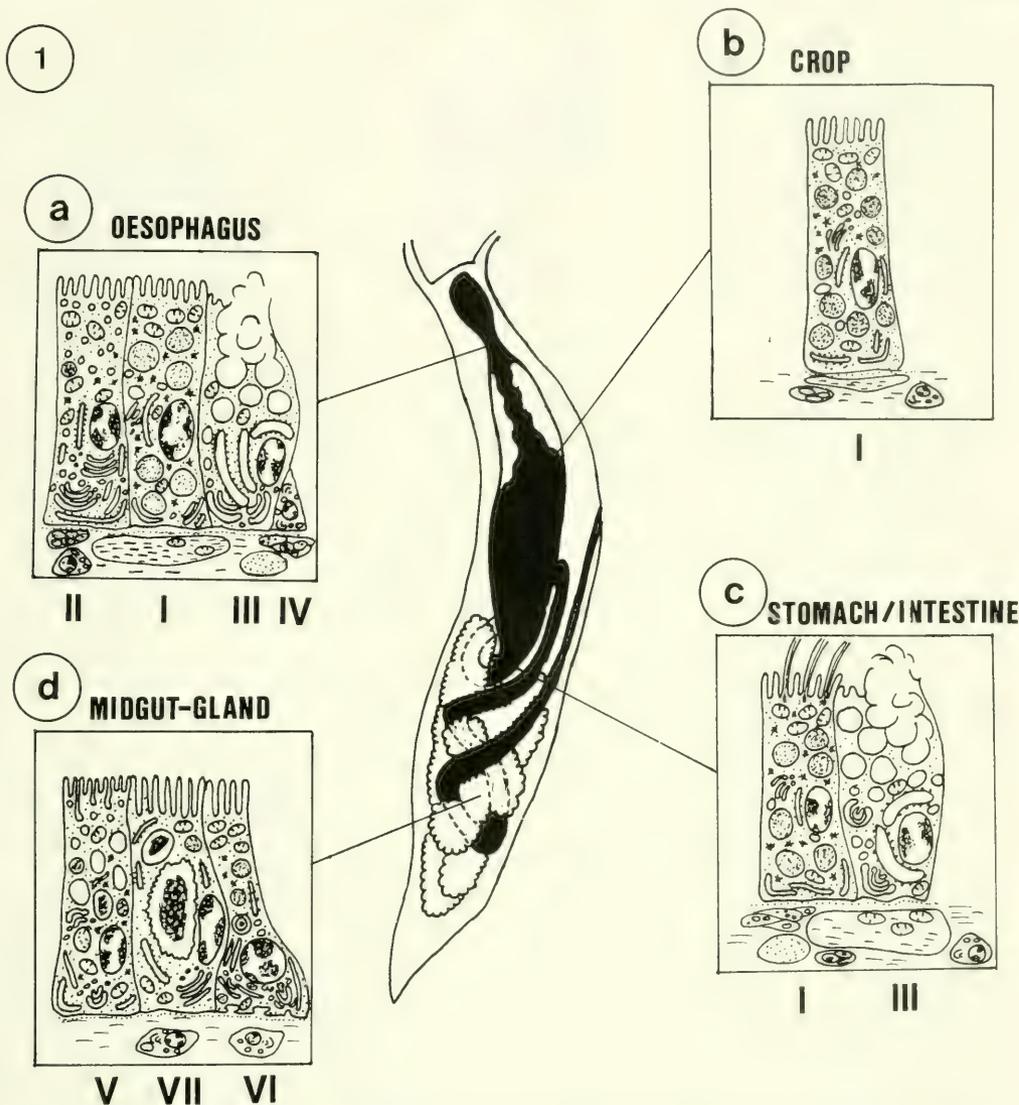


FIG. 1. Diagram of the digestive tract of *Derocheras reticulatum* illustrating the cells investigated in the present study.

1a. Oesophagus: Storage cell (I), secretory cell of an eccrine type (II), secretory cell of a holocrine type, called mucus cell (III), and small electron-lucent cell (IV)

1b. Crop: Storage cell

1c. Stomach and adjacent intestine: Storage (I) and mucus cell (III)

1d. Mid-gut gland: Digestive cell (V), crypt cell (VI), and excretory cell (VII)

cell (Type I) of the oesophagus (Fig. 1b). Only in regions of the crop adjacent to the stomach do these cells bear cilia.

A small muscle layer with associated connective tissue and nerves underlies the epithelium.

Stomach and adjacent intestine: Half of the stomach epithelium is made up by cells resembling the storage cells of the oesophagus with respect to their ultrastructural organisation and storage products (Fig. 1c). The cells always bear microvilli and cilia (cf.

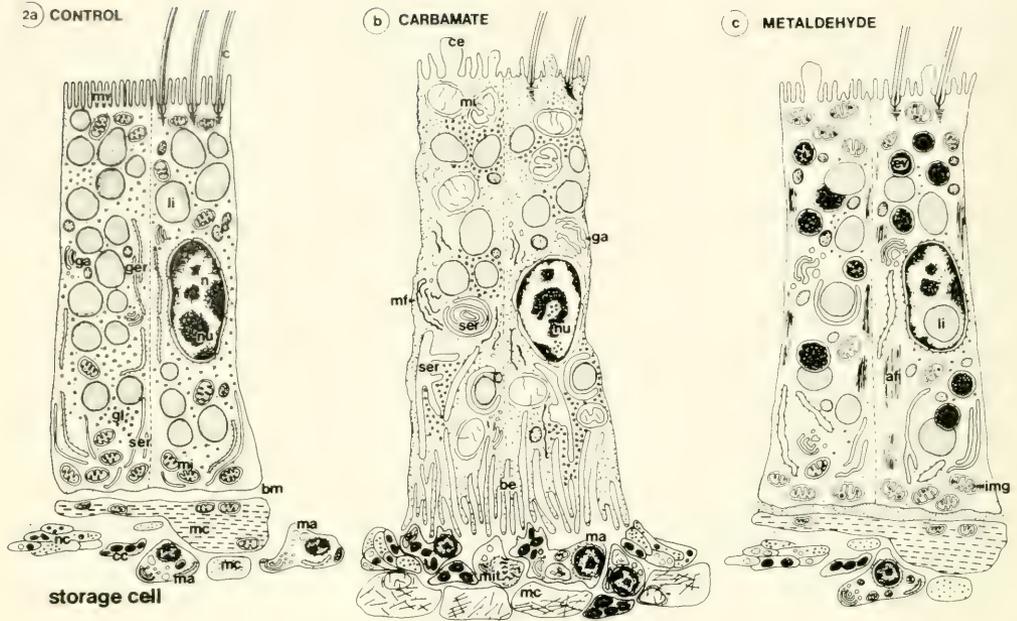


FIG. 2. Reconstruction of an unciliated or ciliated storage cell (2a) and its habit after carbamate (2b) and metaldehyde (2c) intoxication

Walker, 1972). In the stomach crypts, the cilia are longer and more numerous (cf. Häffner, 1924). The rest of the epithelium is made up by mucus cells (Type III). In the adjacent intestine, half of the cells are mucus cells (Type III), and only a quarter are storage cells (Type I). The other quarter of the cells are secretory (Type II). An underlying muscle layer is well developed. It can be compared with that of the oesophagus (Fig. 40). Many nerve fibres can be detected.

Mid-gut gland: The epithelium of the mid-gut gland is arranged in tubules that are bound together by a meshwork of connective tissue. An underlying muscle layer is lacking. Three cell types can be distinguished (Fig. 1d, 4a):

Type V: The columnar digestive cells, highly vacuolized absorptive cells, that dominate the epithelium. The vacuoles vary in size and are generally largest towards the basal regions of the cells. Pinocytotic vesicles develop along the apical plasma membrane, where endocytotic channels can also be found. The absorptive area is increased by numerous microvilli. The digestive cell cytoplasm contains a little granular endoplasmic

reticulum, a few mitochondria and an occasional small Golgi apparatus. Lipid and glycogen storage can be found. The nuclei of these cells are basally located.

Type VI: The crypt cells are conical in shape with broad bases abutting on to the haemolymph space. Serving secretory functions, they are characterized by a large amount of granular endoplasmic reticulum (Fig. 22), a great number of Golgi stacks and secretory vesicles in the perinuclear cytoplasm. The nuclei are basally situated, possess a large nucleolus and have scattered patches of heterochromatin. Mitochondria are located near the apical and the basal surfaces of the cells. Lipid and carbohydrate storage, as well as membrane-bound spherites are present (Fig. 4a). The microvilli are longer than those of the digestive cells, and the basal labyrinth is well developed.

Type VII: The goblet-like excretory cells are characterized by large and small vacuoles containing electron-dense material (Fig. 27). The membrane of the large vacuole shows numerous infoldings. In the cytoplasm a small Golgi apparatus, a small amount of smooth and granular endoplasmic reticulum and lipid, and a few mitochondria can be found. The

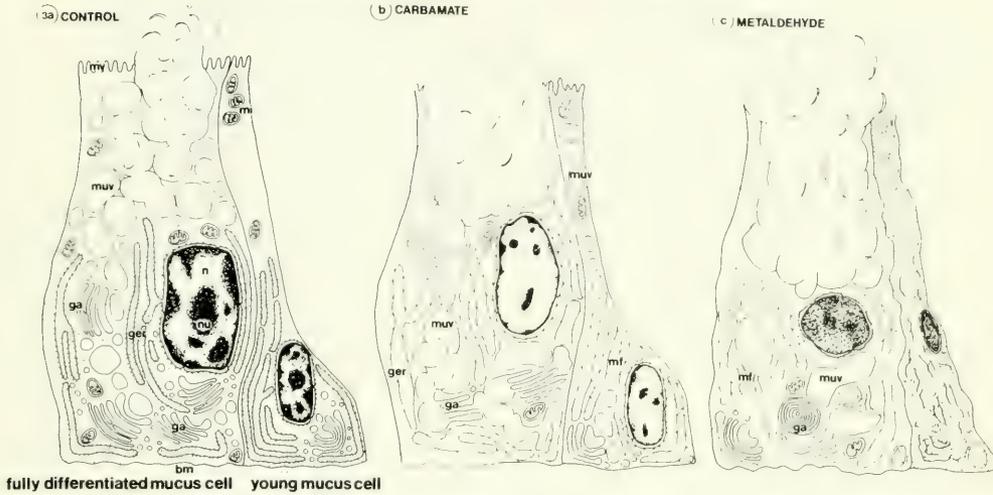


FIG. 3. Reconstruction of a young and a fully differentiated mucus cell in control animals (3a), after carbamate (3b), and after metaldehyde intoxication.

microvilli of these cells are as long as those of the crypt cells.

To compare the different theories concerning the genealogy of these cells and the different nomenclatures, see David & Götze (1963) and Walker (1970).

Histopathological alterations (Figs. 2, 3, 4)

Generally speaking, the cytological reactions in the digestive tract originate in isolated cells and spread over the epithelium during the following hours. Sixteen hours after ingestion of the molluscicides, a high percentage of the cells are significantly damaged.

The reactions observed after five and 16 hours generally resemble those after one hour, but they are more intense.

Reactions that appear in the anterior part of the digestive tract immediately after the molluscicide treatment became apparent in cells of the posterior part with a time lapse corresponding to the transport rate of toxic food-stuff.

Sixteen hours after carbamate ingestion, a lot of cells have been extruded from the epithelium.

Reactions of the basal and apical cell surfaces

MESUROL: Immediately after the application of Mesurol, the basal surfaces of storage and secretory cells (Type I and II) are slightly

stretched (Comp. Figs. 5 and 6). After five and 16 hours, the cells exhibit considerably extended basal cell extensions (Fig. 7) that sometimes contact nerve or muscle cells (Fig. 8). In the mid-gut gland the basal cell extensions are less distinct than in the alimentary tract. However, the basal labyrinth of crypt cells is distended, and the intercellular spaces are enlarged (Fig. 35).

Comparable to the reactions of the cell bases, the apical surfaces of the cells react very quickly with a reduction of microvilli and cytoplasmic protrusions in the anterior, and after five or 16 hours in the posterior parts of the digestive tract (Figs. 10, 11, 12).

An intensified vacuolization in the digestive cells often leads to a breakdown of the apical membrane.

METALDEHYDE: After intoxication with metaldehyde, basal cell extensions are lacking; the basement membrane is thickened and becomes more electron-dense (Fig. 9).

Protrusions of the apical cytoplasm and reduction of microvilli can occasionally be found.

After intoxication with carbamate and metaldehyde, the shape of all cell types becomes more irregular (Figs. 2, 3, 4).

Reactions of the cytoplasm

MESUROL: After carbamate intoxication, the cytoplasm of storage and secretory cells appears slightly condensed (Fig. 7) or elec-

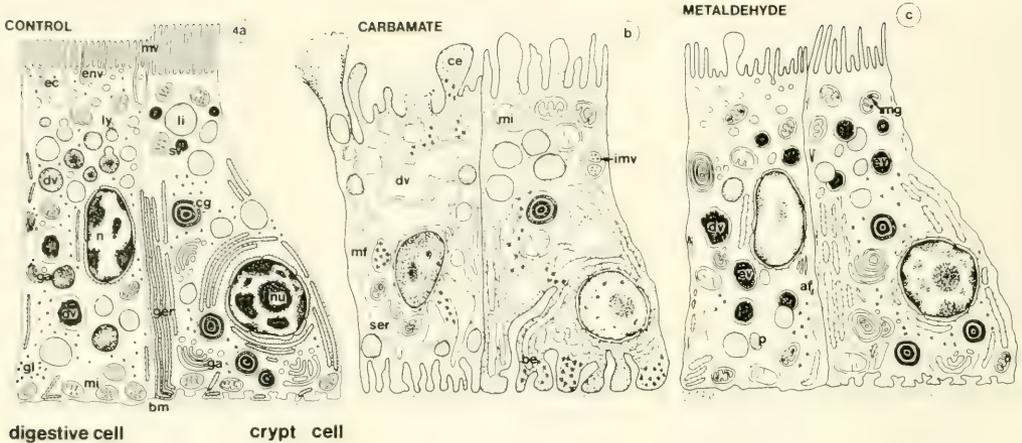


FIG. 4. Reconstruction of a digestive and a crypt cell of the mid-gut gland (4a) and its variable habit after carbamate (4b) and metaldehyde (4c) ingestion.

tron-lucent (Fig. 13). In the digestive cells of the mid-gut gland, it is either extremely electron-lucent, or totally electron-dense, depending on the degree of vacuolization. Electron-dense cytoplasmic areas often surround the nuclei.

METALDEHYDE: In mucus cells the cytoplasm is displaced by the enlarged mucus vacuoles (Fig. 33). In all cell types it appears less electron-dense.

Reactions of the nuclei

MESUROL: One hour after intoxication the nuclei are severely damaged.

The karyoplasm becomes less electron-dense (Fig. 13, 14, 15), lipid droplets can be detected in it (Fig. 15), the nucleoli are irregularly deformed (Fig. 16), and the amount of heterochromatin is reduced. In some cases, the karyoplasm appears totally condensed (Fig. 17), or, especially in crop cells, small vesicles can be found in it (Fig. 16). Mitotic processes are evident. However, even after 16 hours, there are still some unaffected nuclei next to totally damaged ones (Fig. 17), emphasizing the heterogeneity in cellular reaction.

METALDEHYDE: After metaldehyde ingestion, damage to the nuclei is less intense than after carbamate application. The karyoplasm becomes less electron-dense, and in a few cases it bears lipid droplets (comp. Fig. 14). Especially in the crypt cells of the mid-gut

gland, the amount of heterochromatin is reduced.

Reactions of the mitochondria

MESUROL: After carbamate intoxication, mitochondrial effects originate in the oesophagus and crop cells from the cell apex, while in the posterior parts of the digestive tract mitochondria located in the basal cytoplasm are afflicted earlier.

Especially in the stomach and the digestive gland, electron-dense granules different from the common intramitochondrial granules can be found in mitochondria, located in membrane-bound compartments (Fig. 18). Furthermore, the organelles are heavily inflated and their cristae are reduced (Fig. 19).

METALDEHYDE: After metaldehyde intoxication, the mitochondria are less afflicted than after carbamate ingestion. The common intra-mitochondrial granules are often enlarged (Fig. 20), and only in a few cases the organelles are swollen.

Reactions of the endoplasmic reticulum

MESUROL: After Mesurol application, the smooth and granular endoplasmic reticulum proliferates in basal regions of storage, digestive and crypt cells. In most cases, the smooth endoplasmic reticulum is heavily distended (Fig. 21). Degranulation of granular endoplasmic reticulum can be observed in basal re-

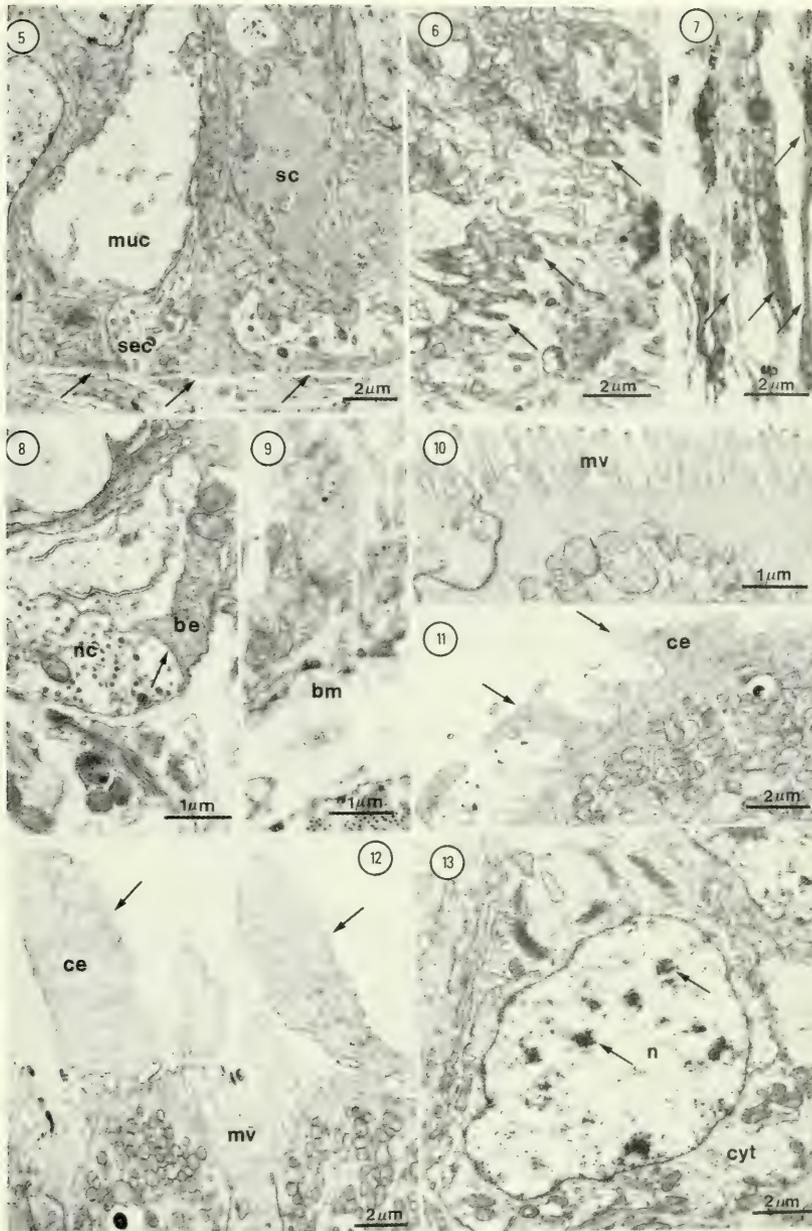
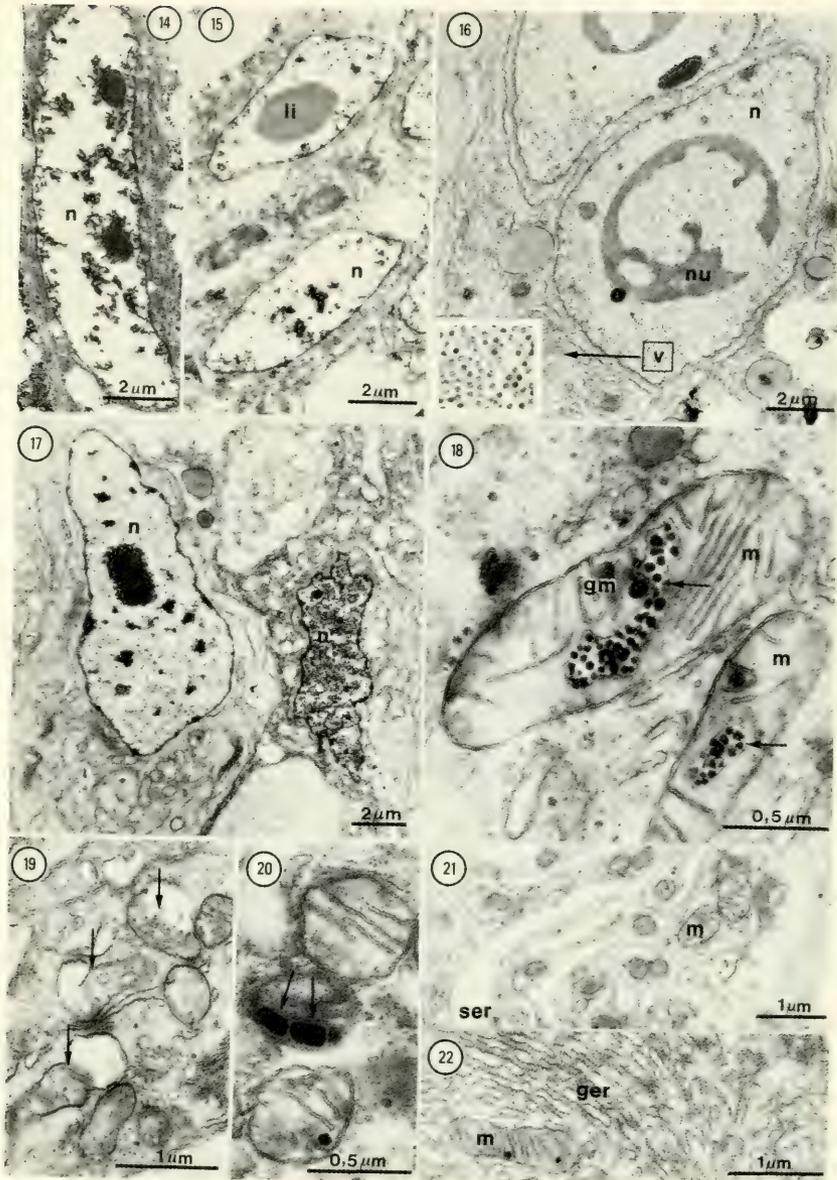


FIG. 5. Oesophagus, control: Section through the basal part of the oesophagus epithelium showing a mucus (muc), storage (sc) and small light cell (slc). There are no infoldings of the cell basis (arrows).
 FIG. 6. Oesophagus, Mesurol, 1 h: Slight basal extensions (arrows).
 FIG. 7. Oesophagus, Mesurol, 5 hs: Strong basal extensions (arrows).
 FIG. 8. Oesophagus, Mesurol, 1 h: Contact of a basal cell extension (be) to a nerve cell (nc, arrow).
 FIG. 9. Oesophagus, Mesurol, 5 hs: Thickening of the basal membrane (bm).
 FIG. 10. Crop, control: Apex of a storage cell, showing regularly orientated microvilli (mv).
 FIG. 11. Oesophagus, Mesurol, 1 h, storage cell: Slight cytoplasm extrusions (ce, arrows).
 FIG. 12. Oesophagus, Mesurol, 1 h, storage cell: Intensified cytoplasm extrusions (ce, arrows).
 FIG. 13. Oesophagus, Mesurol, 16 hs, secretory cell: Electron-lucent cytoplasm (cyt) and nucleus (n) with the heterochromatin reduced (arrows).



- FIG. 14. Oesophagus, Mesuroloca, 5 hs, storage cell: Nucleus (n) with a totally dissolved karyoplasm.
- FIG. 15. Stomach, Mesuroloca, 5 hs: Nuclei with lipid inclusions (li) in an electron-light karyoplasm.
- FIG. 16. Crop, Mesuroloca, 1 h: Nucleus with an irregularly formed nucleolus (nu) and small vesicles (v) in the karyoplasm (inset, $\times 6$).
- FIG. 17. Crop, Mesuroloca, 16 hs: Totally damaged nucleus next to an unaffected one in the adjacent crop cell.
- FIG. 18. Mid-gut gland, Mesuroloca, 16 hs, crypt cell: Mitochondrion (m) with inclusions in membrane-bound areas (arrows); common intramitochondrial granules (gm) are visible.
- FIG. 19. Oesophagus, Mesuroloca, 1 h, secretory cell: Destruction of cristae in mitochondria (arrows).
- FIG. 20. Stomach, metaldehyde, 5 hs, storage cell: Mitochondrion with enlarged intramitochondrial granules (arrows).
- FIG. 21. Intestine, Mesuroloca, 5 hs, storage cell: Dilatation of smooth endoplasmic reticulum (ser) in the basal parts of the cell.
- FIG. 22. Mid-gut gland, control, crypt cell: Cisternae of the granular endoplasmic reticulum (ger).

gions of the crypt cells (comp. Figs. 22 and 23).

In mucus cells the granular endoplasmic reticulum is dilated and disorientated. After several hours, the membranes become fragmented.

METALDEHYDE: The damage to the granular endoplasmic reticulum in mucus cells is more intense after metaldehyde than after carbamate intoxication. The cisterna are heavily dilated, and the membranes are disarranged, ruptured and sometimes coiled to form myeline figures (comp. Figs. 25 and 26).

In the crypt and excretory cells of the mid-gut gland, the granular endoplasmic reticulum disintegrates into short cisternae with fragmented membranes, frequently devoid of ribosomes (Fig. 28). The cisternae of the endoplasmic reticulum often form fingerprint-like structures (Fig. 24). In many instances, the membranes are ruptured.

Reactions of the Golgi apparatus

MESUROL: In the oesophagus, the Golgi complexes of the secretory cells (Type II) are heavily damaged. Especially the trans-face cisternae are either compressed or highly inflated (comp. Figs. 29 and 30). Associated with this is a reduction in the number of secretory vesicles.

In the mucus cells, the cisternae of the Golgi apparatus are strongly dilated (Fig. 31), and the regular arrangement of the Golgi stacks is often lost.

METALDEHYDE: Except for the mucus cells, the reaction of the Golgi apparatus is less intense after metaldehyde than after carbamate ingestion. The trans-faces of the cisternae are slightly dilated. In the mucus cells, the Golgi cisternae are swollen, often the membranes are arranged as concentric whorls (Fig. 32), and the mucus containing vacuoles are enlarged (Fig. 33).

Alteration of storage products

MESUROL: After carbamate ingestion, compact areas containing glycogen or galactogen can be found between lipid droplets, especially in central and basal parts of digestive cells and in crypt cells of the mid-gut gland (Fig. 35).

METALDEHYDE: In storage, secretory, digestive, crypt and excretory cells, the amounts of lipid and glycogen are reduced after metaldehyde poisoning (comp. Figs. 34 and 36). This reduction is related to the presence of vesicles containing electron-dense material with a typical lamellar fine-structure (Fig. 37). Furthermore, an increased number of peroxisome-like structures appears.

Reaction of the cytoskeleton

MESUROL: After Mesurol intoxication, no reaction of the cytoskeleton is visible.

METALDEHYDE: In the center of storage and secretory cells (Type I and II), condensed actin-like microfilaments appear (Figs. 38, 39).

Reactions of the underlying muscle, connective and nerve tissues

MESUROL: After the application of the carbamate molluscicide, the muscle tissue is fragmented, and the regular arrangement of the muscle filaments is disturbed (comp. Figs. 40 and 41). Granules similar to peroxisomes (with regard to their size and their electron-density) appear in connective tissue cells showing intensive contact to smooth muscle and nerve cells, as well as in nerve cells themselves (Figs. 42, 43).

METALDEHYDE: After application of metaldehyde, no reactions of muscle, nerve and connective tissue could be found.

Reactions of the macrophages

MESUROL: After ingestion of Mesurol, the number of macrophages in the haemolymph space increases. In many cases, mitotic processes can be observed (Fig. 44). Particularly 16 hours after intoxication, many of these cells penetrate the epithelium (Fig. 45). Other macrophages contain membrane fragments incorporated into vacuoles (Fig. 46).

METALDEHYDE: Reactions of the macrophages are lacking.

DISCUSSION

The present study reveals the impact of the carbamate compound Mesurol and of metal-

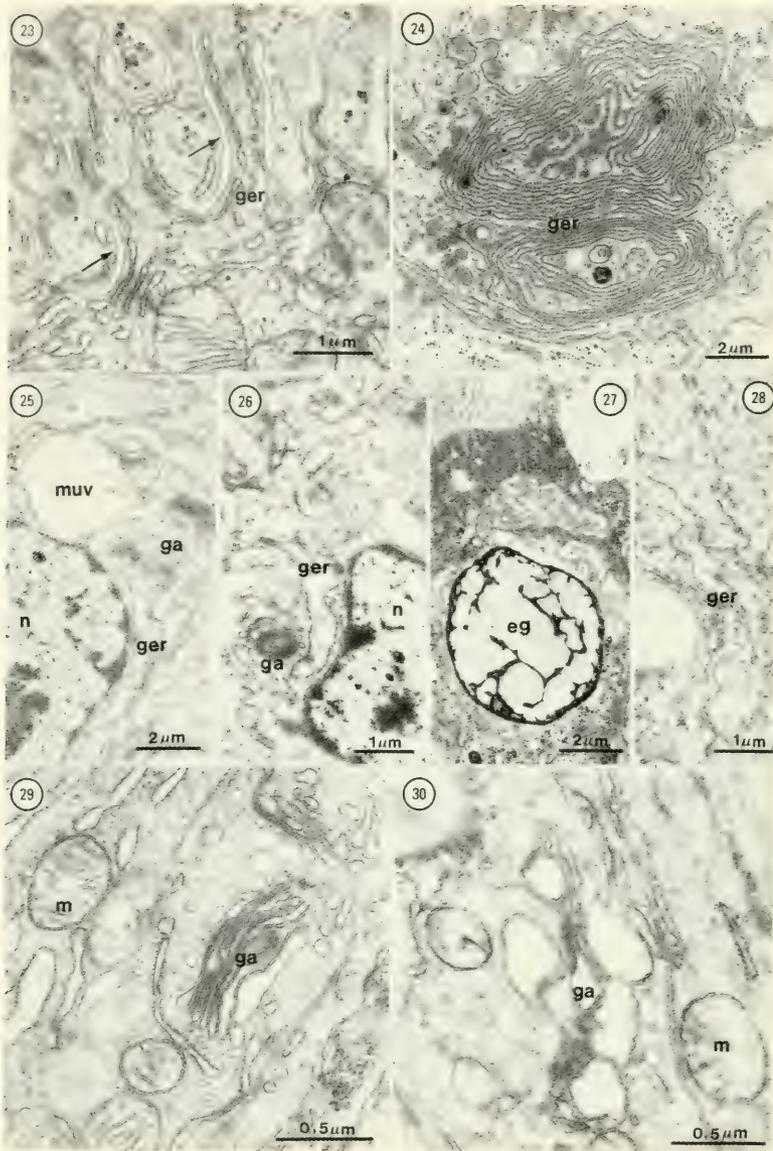


FIG. 23. Mid-gut gland, Mesurol, 1 h, crypt cell: Degranulation of granular ER in the basal part of the cell (arrows).

FIG. 24. Mid-gut gland, metaldehyde, 5 hs, crypt cell: Granular ER (ger) forming fingerprint-like structures.

FIG. 25. Oesophagus, control, mucus cell: Elaborate Golgi system (ga), granular ER (ger) and mucus vacuoles (muv) in a regular arrangement.

FIG. 26. Oesophagus, metaldehyde, 5 hs, mucus cell: Dilated, electron-lucent cisternae of the granular ER and Golgi membranes (ga) forming concentric circles in a cellular disarrangement; nucleus (n) with an electron-lucent caryoplasm.

FIG. 27. Mid-gut gland, control, Excretory cell: excretory cell with excretory granule (eg).

FIG. 28. Mid-gut gland, Mesurol, 5 hs, crypt cell: Short, fragmentary cisternae of the granular ER (ger) frequently devoid of ribosomes.

FIG. 29. Oesophagus, control, secretory cell: Trans- and cis-face of the Golgi apparatus (ga) can clearly be distinguished.

FIG. 30. Oesophagus, Mesurol, 1 h, secretory cell: Heavily inflated cisternae of a Golgi apparatus (ga).

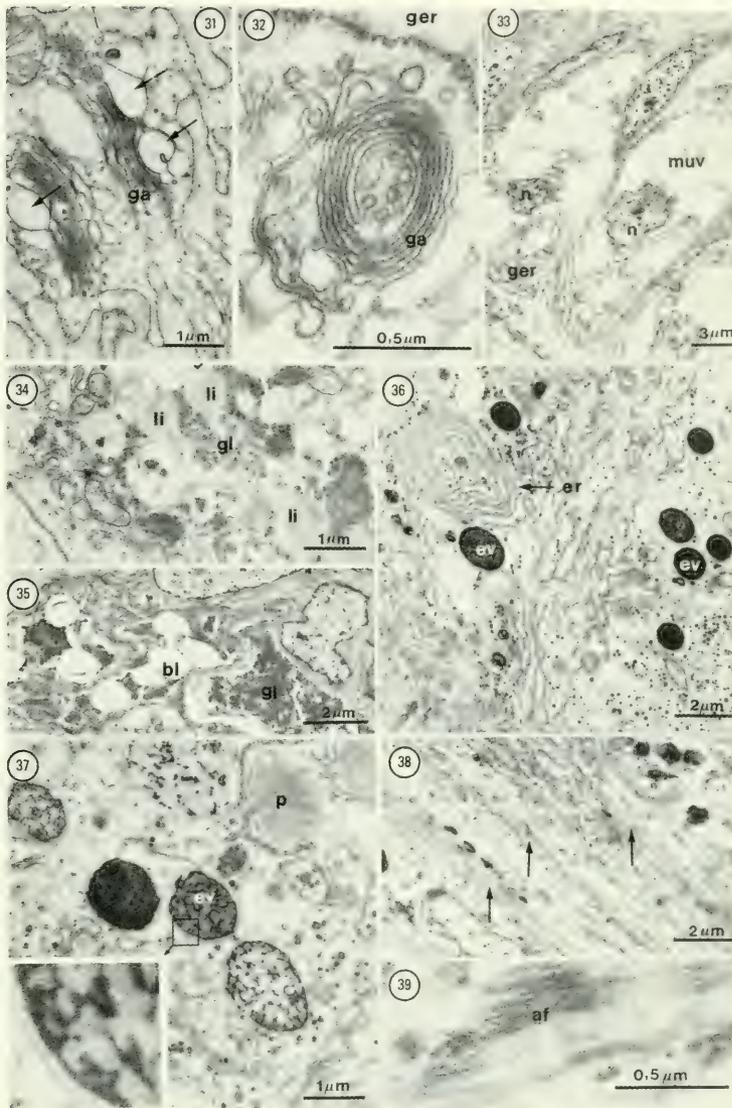


FIG. 31. Stomach, Mesuroli, 5 hs, mucus cell: Golgi apparatus (ga) with dilated cisternae (arrows).

FIG. 32. Oesophagus, metaldehyde, 5 hs, mucus cell: Membranes of the Golgi apparatus (ga) are arranged as concentric whorls surrounding Golgi vesicles.

FIG. 33. Stomach, metaldehyde, 5 hs: General view of the mucus cells after metaldehyde application; dilated cisternae of the Golgi apparatus and the granular ER, large mucus vacuoles (muv) and nuclei (n) with an electron-lucent karyoplasm.

FIG. 34. Oesophagus, control, storage cell: High amount of stored lipid (li) and glycogen or galactogen (gl).

FIG. 35. Mid-gut gland, Mesuroli, 5 hs, digestive cell: Condensation of glycogen (gl) and dilation of the sER and the basal labyrinth (bl).

FIG. 36. Oesophagus, metaldehyde, 5 hs, storage cell: Lipid and carbohydrate reduction; electron-dense vesicles (ev) and ER membranes forming a fingerprint-like structure (arrow).

FIG. 37. Oesophagus, metaldehyde, 5 hs, storage cell: Electron-dense vesicles (ev) characterized by a typical lamellar fine-structure (inset, $\times 4$) and by peroxisome-like organelles (p) in the center of the cell.

FIG. 38. Crop, metaldehyde, 5 hs: Reduction of storage products and aggregation of actin-like filaments (arrows).

FIG. 39. Crop, metaldehyde, 5 hs: Actin-like filaments (af) in the center of the enterocytes.

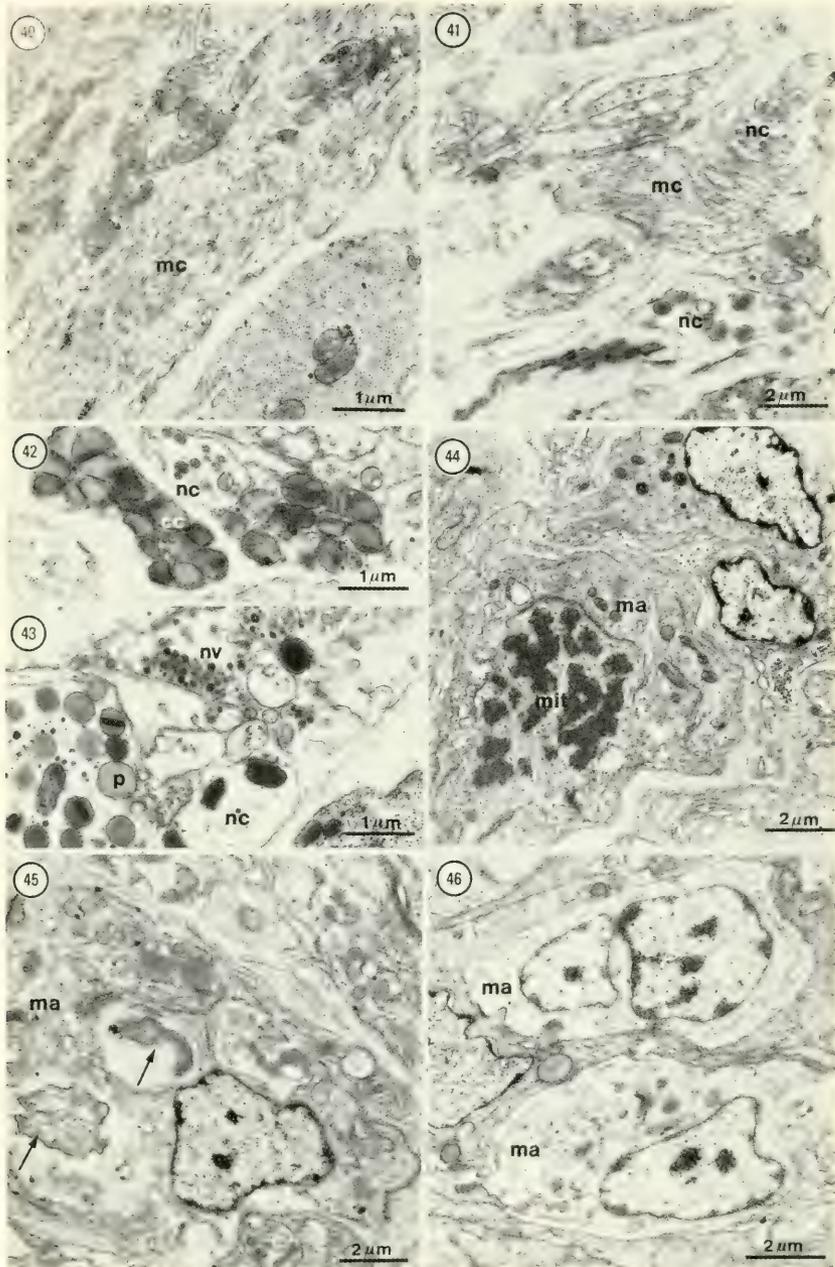


FIG. 40. Oesophagus, control: Muscle cell (mc) with regularly orientated muscle fibres.
 FIG. 41. Oesophagus, MesuroI, 5 hs: Fragmentation of muscle tissue in isolated portions and irregular orientation of muscle fibres. Intense contact of nerve (nc) and muscle cell (mc).
 FIG. 42. Oesophagus, MesuroI, 1 h: Nerve (nc) and connective tissue cells (cc) containing electron-dense, peroxisome-like structures.
 FIG. 43. Oesophagus, MesuroI, 5 hs: Nerve with peroxisome-like structures (p).
 FIG. 44. Oesophagus, MesuroI, 5 hs: Mitosis taking place in a macrophage (ma).
 FIG. 45. Oesophagus, MesuroI, 16 hs: Macrophage bearing membrane fragments in vacuoles (arrows).
 FIG. 46. Oesophagus, MesuroI, 1 h: Two macrophages that penetrate the epithelium.

dehyde on the ultrastructure of the digestive tract of *Deroceras reticulatum*. In addition to the results of Tegelsstrom & Wahren (1972), Godan (1979) and Pessah & Sokolove (1983), who attributed the molluscicidal effects to influences on cholinesterase activity and water regulation, it can clearly be demonstrated that both chemicals interact with several different types of enterocytes.

As evident by the present cytological findings, the carbamate compound Mesurol is absorbed immediately after ingestion in the anterior parts of the digestive tract, i.e. in the oesophagus and the crop. The rapid reactions in these two regions and the quick and intense reaction of the whole animal one hour after feeding support the findings of Fretter (1952), Walker (1972) and Horst et al. (1986), who describe the high absorptive activity of the crop using radioactive labelling and biochemical methods. With regard to the time lapse resulting from the passage of food through the intestinal tract, the cellular responses after one hour in the anterior parts can be compared with those in the posterior parts of the digestive system after five hours. Analysis of cellular responses to metaldehyde and carbamate poisoning after five hours allows three types of reaction to be distinguished: carbamate-specific reactions, metaldehyde-specific reactions, and cell responses that appear in both experiments but with different intensity.

Reactions such as cytoplasm condensation, cytoplasmic protrusions also called "surface blebs" (Whyllie, 1981; Réz, 1986), reduction of microvilli, mitochondrial swelling (Goyer & Rhyne, 1975; Triebkorn, 1988) and dilation of Golgi cisterna (Triebkorn, 1988), endoplasmic reticulum and intercellular spaces (Smuckler & Arcasoy, 1969), as well as ER-membrane proliferation or destruction (Moore, 1979, 1985; Nott & Moore, 1987) resemble those described in bivalves and vertebrates as cellular stress symptoms after intoxication with different xenobiotics. Likewise, the degranulation of the granular ER and the formation of membrane whorls or myelin-like membranes by ER are discussed as general changes of the cell in response to toxicants (Réz, 1986). Most of these reactions are attributed to membrane destabilization and increased membrane permeability to ions under the influence of toxicants, followed by osmotic effects and finally cell death (Sparks, 1972).

Swelling of mitochondria is suggested to be

the result of an increased Ca^{2+} influx (Packer et al., 1967; Smuckler & Arcasoy, 1969). Bayne et al. (1985), Moore (1985) and Nott & Moore (1987) relate the sER proliferation to an increase of sER-bound detoxification enzymes, such as the NADPH-neotetrazolium-reductase and many others.

In the digestive tract of *Deroceras reticulatum*, such unspecific reactions are more intense after carbamate than after metaldehyde treatment except for the mucus cells of oesophagus, stomach and intestine. This might arise from the fact that the amount of metaldehyde taken up by the animals is supposed to be closer to the sublethal dose than that of carbamate. Therefore, after Mesurol intoxication, many more cellular reactions associated with cell death are involved. However, the comparison of reactions to different molluscicides in several regions of the digestive tract, as well as in several cell types at three times allows reactions of general nature to be distinguished from specific ones. Thus, for example, in mucus cells the destruction of Golgi cisternae, rER and mitochondria is more prominent after metaldehyde than after carbamate ingestion. This severe impact of metaldehyde on the mucus producing cells correlates well with the known influence of this molluscicide on water regulation. Metaldehyde enhances the extrusion of available mucus immediately after intoxication. This mucus might serve to dilute the toxin but may also have the capacity to detoxify it (Triebkorn, 1988). It passes the digestive tract and is voided quickly due to the intensified mucus extrusion of the whole animal. Furthermore, the replacement of the necessary mucus is blocked by destruction of the cellular secretory apparatus, especially in immature cells. If the resulting loss of liquid cannot be compensated, the animal will desiccate. Therefore, the effects of metaldehyde are reversible in a humid climate.

These considerations are in line with other investigations studying the advantages of carbamates compared with metaldehyde using LD_{50} tests (Riemschneider & Heckel, 1979; Prystupa et al., 1987). They support the findings of Getzin & Cole (1964), who postulate the effect of metaldehyde to be the result of water loss by stimulation of mucus secretion.

Furthermore, metaldehyde poisoning reduces cellular lipids, increases the number of electron-dense vesicles and peroxisome-like particles, and leads to a thickening of the basement membrane and the condensation

of actin-like filaments in the cytoplasm. Until now, there are no targets known for the attack of toxins in the cytoskeletal system. Nor is there any intelligible explanation for the thickening of the basement membrane.

With regard to lipid reduction, my own enzyme-histochemical studies have shown that catalase activity can be found in the periphery of lipid droplets after molluscicide intoxication (Triebskorn, in prep.). One might speculate that the observed lipid reduction is correlated with lipid peroxidation (cf. Tappel, 1975). To reinforce this idea, the presence of detoxification products resulting from such reactions as well as the nature of the electron-dense vesicles and the peroxisome-like structures should be investigated. Beyond this, the reaction of macrophages and connective tissue cells after intoxication with Mesurol could be of interest. While the present study demonstrates an increased number of peroxisome-like structures in connective tissue cells after Mesurol intoxication, Sminia (1972) was able to demonstrate peroxidase activity in haemolymph cells, localized in similar peroxisome-like vesicles. In addition, my own light-microscope investigations reveal an intensified catalase activity in the connective tissue underlining the epithelium of the digestive tract and in the haemolymph, where macrophages can be found (Triebskorn, in prep.). Because peroxidative reactions are known to be involved in detoxification (Belding et al., 1970; Recknagel, 1967), I assume that similar processes are of importance in the digestive tract of slugs after molluscicide intoxication. Whereas they might be found after metaldehyde treatment in the enterocytes themselves, carbamate poisoning leads to a disturbance of essential functions of these cells so quickly that detoxification processes cannot be established in them in time. This deficiency might be compensated by macrophage activity. The function of these cells in detoxification is also verified by the results of Moore (1979). He could demonstrate the activation of MFO-enzymes in the haemolymph cells of *Mytilus edulis* after polycyclic hydrocarbon poisoning. Furthermore, the haemocytes are known to be able to penetrate the gut epithelium and to phagocytise decaying cells (Sminia, 1972).

The macrophage reaction, nucleic damage and a changed glycogen metabolism appear one hour after the ingestion of the carbamate. The Mesurol attack on the nucleus seems to be the most important effect of this chemical

and accounts for its better molluscicidal activity compared with metaldehyde. While karyolysis is often described as a late reaction to intoxication in vertebrates and invertebrates (Bayne et al., 1985), the reaction of nuclei in the present study does not seem to be an ultimate one revealing cell death, but a primary cell response that leads to cell death. Since, in most cells with damaged nuclei, other cell death symptoms are lacking, the heterochromatin disorganization and increase in mitotic activity seem to reflect a central process in intoxication. The damage to the nuclei could explain the reinforcement of other cellular responses, such as the disturbances in glycogen metabolism or the destruction of Golgi apparatus, already described by Flickinger (1971).

In contrast to these reactions, the formation of basal cell extensions requires several hours. This is probably due to the inhibition of cholinesterase activity by carbamates. The blockade of the esterase center of the enzyme (Wegler, 1970) interrupts nerve stimuli conduction, leading to uncontrolled muscle contraction and finally to muscle atony. Uncontrolled contractions in the muscle layer that underlies the gut epithelium are responsible for the basal cell deformation.

In conclusion, the present results suggest that the cells might respond to environmental stress in different ways. Lipid mobilization in storage cells, for example, only takes place after intoxication with less effective molluscicides, such as metaldehyde. Carbamate ingestion stimulates the activity of the macrophages. Furthermore, peroxidative reactions have been suggested to be the biochemical pathway of detoxification of carbamate and metaldehyde. According to this opinion, the detoxification processes in molluscs resemble those described for insects by Wegler (1970).

The present electron microscope study was able to extend former observations on whole animal behavior following intoxication. Suggestions about cellular mechanisms induced by different molluscicides are developed. However, other techniques, such as enzyme histochemistry, biochemistry and autoradiography, are necessary to further specify these results and to give more detailed information about the function of the structures described.

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ABBREVIATIONS

af	:	actin-like filament
be	:	basal extension
bl	:	basal labyrinth
bm	:	basal membrane
c	:	cilia
cc	:	connective tissue cell
ce	:	cytoplasmic extrusion
cg	:	calcium granule
cyt	:	cytoplasm
dv	:	digestive vacuole
ec	:	endocytotic channel
eg	:	excretory granule
env	:	endocytotic vesicle
ev	:	electron-dense vesicle
ga	:	golgi apparatus
ger	:	granular endoplasmic reticulum
gl	:	glycogen
gm	:	intramitochondrial granule
imv	:	intramitochondrial vesicle
li	:	lipid
ly	:	lysosome
ma	:	macrophage
mc	:	muscle cell
mf	:	membrane fragments
mi	:	mitochondria
mit	:	mitosis
muc	:	mucus cell
muv	:	mucus vacuole
mv	:	microvilli
n	:	nucleus
nc	:	nerve cell
nu	:	nucleolus
nv	:	neurosecretory vesicle
p	:	peroxisome-like vesicle
sc	:	storage cell
sec	:	small electron-lucent cell
ser	:	smooth endoplasmic reticulum
sv	:	secretory vesicle

RETRACTION/EXTENSION AND MEASUREMENT ERROR IN A LAND SNAIL: EFFECTS ON SYSTEMATIC CHARACTERS

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ABSTRACT

Multivariate analyses were performed on replicated measurements from a collection of 56 preserved *Ningbingia dentiens* Solem, 1985 (Gastropoda: Stylommatophora: Camaenidae), that ranged from full extension to full retraction. The positions of body landmarks during retraction/extension vary complexly such that the only reliable indicator is the position of the foot tip relative to the remaining body wall. Shell size is no predictor of retraction/extension state. The nerve ring dilates, then compresses, as the buccal mass passes through it. From fully extended, to partially retracted, to fully retracted specimens, vagina length decreases 25%, then increases 10%; spermatheca length remains constant, then decreases 20%; and penis length decreases 15%, then increases 5%.

Counting shell whorls (mean = 5.0) to the nearest 0.1 whorl was exactly as precise as measuring shell height (mean = 8.4 mm) to the nearest 0.1 mm; both were 1/7 as precise as measuring shell diameter (mean = 17.1 mm) to the nearest 0.1 mm. Distances among body landmarks within the shell had measurement errors $30\times$ to $340\times$ greater than for shell diameter. Measurement error was about 10% of total variance for vagina length, 20% for spermatheca length, and 30% for penis length. The effects of measurement error and retraction/extension equaled or surpassed individual variation for all three of these measurements.

Key words: Gastropoda, Pulmonata, Camaenidae, *Ningbingia dentiens*, retraction, measurement error, anatomy, systematics.

INTRODUCTION

When a pulmonate land snail retracts into its shell, it invaginates the anterior part of the body, during which air is vented from the mantle cavity and blood redistributes among sinuses of the hemocoel (Jones, 1975). This process alters the relative positions, lengths, and shapes of the snail's organs. Since no fully reliable method has yet been found for always killing and fixing pulmonate land snails in an extended state (the success rate of the standard procedure of drowning in water or in a weak solution of chloryl hydrate or nicotine varies widely, depending on the taxonomic group and on field conditions), land-snail systematists must often compare specimens differing widely in their degree of body retraction/extension.

The effect of retraction/extension on body organs is poorly understood. Studies on body retraction in pulmonates (reviewed by Jones, 1975) have so far been physiological in approach, with little information on anatomical variation relevant to systematists. The most relevant study to date (Dale, 1974) noted only

that "the genital and digestive organs in the retracted snail are located [between] the mantle cavity floor [and the retracted head-foot]," resulting in an unspecified degree of distortion of these organs.

The role of measurement error in quantitatively assessing both shell and soft-parts has never been examined in great detail. For example, various gastropod systematists measure whorl-count to the nearest 1/4-whorl, 1/8-whorl, 1/10-whorl, and 1/16-whorl, rarely with a published demonstration that that is the limit of achievable accuracy. Soft-part measurements, primarily of the lower reproductive tracts, are frequently presented in the taxonomic literature, sometimes with caveats about measurement error, but seldom with explicit assessments of its effect.

Furthermore, when an investigator must choose which specimens to dissect from a preserved lot in which all are retracted within the shell, it would help to know whether the depth of retraction can be predicted from either shell size or the positions of body landmarks visible through the shell.

The purposes of this paper are, for a single

collection from a panmictic population of a pulmonate land snail, to (1) investigate the relative positions of body landmarks throughout a range of retraction/extension states; (2) test whether shell size is any predictor of retraction/extension state; (3) qualitatively and quantitatively assess the effects of retraction/extension on organ systems of systematic value; (4) compare the precisions of shell and soft-parts measurements; and (5) determine the relative contributions of retraction/extension, individual variation, and measurement error to the total variance in the lengths of the vagina, spermatheca, and penis.

MATERIALS AND METHODS

This study made use of a single collection of *Ninbingia dentiens* Solem, 1985, a camaenid snail endemic to the northern Ningbing Ranges, north of Kununurra, the Kimberley, Western Australia. Sixty live, paratopotypic adults (Western Australian Museum 14.84 and Field Museum of Natural History 205270) had been collected from a small pocket of talus on a limestone dome that was shaded by a 2.5-meter boulder by A. Solem, L. Price, and B. Duckworth on 15 June 1980. The total area of the colony was much less than one cubic meter, and other colonies were separated by at least 50 meters of barren rock. Because of these conditions, the specimens almost surely belonged to a single panmictic population.

The collection was made about two months into the dry season. All specimens therefore were in a state of estivation when collected. All were at least third-year adults, as evidenced by their full-sized albumen glands (see Solem & Christensen, 1984).

After drowning overnight in two or three water-filled, small jars, to each of which a few crystals of chloryl hydrate had been added, the specimens were fixed the next morning in 95% ethanol. On reaching Chicago two months later, they were transferred to 70% ethanol. The preserved specimens exhibited a complete range of retraction states, from fully extended to tightly retracted. They afforded the best opportunity I have yet encountered to investigate variation in body retraction/extension as it occurs in typical alcohol-preserved museum specimens.

From the 56 intact specimens—three had previously been dissected (Solem, 1985), and the shell of one was accidentally broken—I

measured shell height and diameter to the nearest tenth of a millimeter, and whorl count to the nearest twentieth of a whorl. Also to the nearest twentieth of a whorl, I measured the location, as seen from the ventral side, of the shell's basal lip, the mantle color, the tip of the foot, the auricular-ventricular junction (a-v junction) of the heart, and the base of the ommatophore (upper, eye-bearing antenna). The heart's position was occasionally difficult to locate through the shell; changing the angle of illumination helped to pinpoint it. The mantle collar and the tip of the foot of retracted snails were clearly visible through the shell. The base of the ommatophore of retracted snails, however, was impossible to accurately locate, so instead I measured the most apical point of the invaginated left ommatophore, which was visible as a black tube through the ventral shell. From the dorsal surface of the shell I also measured the position of the apex of the liver (posterior digestive gland), to the nearest tenth of a whorl. This was sometimes obscured by opacity of the shell apex or by the presence of denatured fluid in the empty apical whorls, but could be detected by moving the narrow-beam illuminator, particularly by reflecting the light off the table surface into the umbilicus of the shell. All whorl-increment measurements were taken under magnification over a subdivided circle; shell height and diameter were taken manually with dial calipers.

From these nine soft-part measurements, I calculated the following distances, all expressed to the nearest twentieth of a whorl: (1) MANTLP, from the mantle collar to the shell's basal lip; (2) FOOTIP, from the mantle collar to the tip of the foot; (3) ANTENN, from the base of the everted left ommatophore or the anterior extent of the inverted left ommatophore to the heart a-v junction; (4) PALCAV, from the mantle collar to the heart a-v junction (this was used as an index of the length of the pallial cavity, the actual apex of which was not reliably discernable); (5) VICMAS, an index of the length of the visceral mass, from the heart a-v junction to the apex of the liver; and (6) EMPAPX, the empty apex of the shell, from the zero-whorl apical notch to the apex of the liver.

To determine their precision, I took all measurements and performed all calculations three separate times. For each of the three shell measurements and the six calculated soft-part variables, I calculated two different indices of precision. The first was a mean co-

TABLE 1. Loadings of principal components extracted from soft-part measurements associated with retraction/extension. See text and Fig. 1 for explanation of variables.

Variable	PC1	PC2	PC3	PC4
MANTLIP	-0.38	-0.09	0.47	0.78
FOOTIP	0.30	0.65	0.30	0.01
ANTENN	0.46	0.46	-0.05	0.33
PALCAV	0.31	-0.20	-0.67	0.51
VICMAS	-0.47	0.43	-0.32	-0.06
EMPAPX	0.49	-0.36	0.35	-0.09
% Variance	44%	24%	19%	9%

efficient of variation. For each specimen, I calculated the coefficient of variation (standard deviation divided by the mean) of its three replicate measurements, and averaged these coefficients over all specimens. The second index was the percentage of specimens with a coefficient of variation of zero, i.e. with identical replicate measurements. For the shell variables only, I performed a third analysis of precision: making pairwise comparisons among the three sets of measurements, I categorized all deviations as to size, then averaged the percentage of specimens falling within each category of deviation.

Principal components analysis was used to explore the interrelationships among the soft-part distances during retraction/extension. To determine the influence of shell size and shape on this process, I computed the canonical correlations between the set of shell measurements and the set of soft-part distances. For these analyses, I used only the third set of measurements rather than the average of all three sets because of my belief that the accuracy of soft-part measurements increased with practice.

After measuring the shells and body landmarks, I cracked and removed the shells, dissected off the mantle collar and diaphragm (= floor of the mantle cavity) from each specimen, sewed on an identification tag, then ranked the specimens from 1 to 57 according to how much of the head-foot was showing beneath the folded body wall—from all of the head and foot to just the tip of the foot. I called this variable the retraction/extension rank (RETRAN). I calculated non-parametric correlation coefficients between RETRAN (which was non-normally distributed) and each of the first four principal components of soft-part distances.

I took five snails from each of four stages of the head-foot retraction series: "stage a,"

complete extension, ranks 1–5; "stage b," head invagination, ranks 20–24; "stage c," half-way foot retraction, ranks 35–39; and "stage d," full foot retraction, ranks 53–57. From each of these 20 snails I took the following genital measurements: (1) vaginal length, from its beginning where the free oviduct and the spermatheca unite in a V-junction to where it joins with the penis in a V-junction (the penioviducal angle) to form the atrium; (2) spermathecal length, from the free oviduct-spermathecal junction to its tip; (3) penis-plus-sheath length, from the penioviducal angle to the insertion of the penial retractor muscle; and (4) penis-minus-sheath length, from the penioviducal angle to the basal attachment of the sheath as best judged without dissection. After taking these measurements from the 20 snails and returning them to their vials, I repeated this measurement process twice. For each of the four genital measurements, I used two-way nested analysis of variance (ANOVA) to test for significant differences among retraction/extension stages and among snails within a stage; and to partition the variance among retraction/extension stage, individual variation, and measurement error.

I next slit and pinned open the uneverged penial tube and sheath of each of the 20 snails, and took five measurements of penial sculpture. These were: (1) left pilaster mid-width, (2) right pilaster mid-width, (3) number of wall ridges at the apical penis, (4) number of wall ridges at the mid-penis, and (5) central wall ridge mid-width. Means and standard deviations for each extension/retraction stage were calculated.

From each extension/retraction stage (a–d), I chose one well-dissected representative specimen (those with RETRAN ranks 1, 24, 38, and 54) for detailed dissection and illustration.

RESULTS

Four principal components accounted for 96% of the variation in distances among body landmarks during retraction/extension. The structures of these components are listed in Table 1 and are presented diagrammatically in Fig. 1, in which the relative contribution of each distance to each principal component is expressed as the width of its line, and the direction of its contribution is indicated by one or more arrowheads. The first two principal components (PC 1 and PC 2), accounting for 44% and 24% of the total variance, involve simultaneous eversion of the head and foot, but differ in the other changes that take place during this process. In PC 1 the visceral mass shortens, thereby emptying the shell apex, whereas the pallial cavity lengthens as the mantle collar slides toward the shell lip. In PC 2, on the other hand, the visceral mass lengthens, thereby partially filling the empty shell apex and slightly shortening the pallial cavity, with no shift in the mantle collar. The third principal component (PC 3) accounts for 19% of the total variance and primarily concerns a shortening of the pallial cavity as the mantle collar slides inward from the shell lip, and is weakly associated with shortening of the visceral mass, emptying of the shell apex, and protrusion of the foot. PC 4, which accounts for 9% of the total variance, also involves retraction of the mantle collar, but this time associated with a lengthening of the pallial cavity and a slight evagination of the head.

PC 1 and PC 2 were each significantly correlated with the retraction/extension rank (= RETRAN) (Spearman coefficients $-.61$ and $-.69$, $p = 0.0001$ for both). PC 3 was very weakly correlated ($-.28$, $p = 0.03$), and PC 4 was uncorrelated ($-.07$, $p = 0.63$).

Canonical correlation analysis between the set of shell variables and the set of soft-part distances yielded a single, highly significant (Wilks' Lambda = 0, $p = 0$) canonical variate, with a canonical correlation of 1.000. It is clear from the structure of this canonical variate (Table 2) that it is an artifact due to the fact that $EMPAPX + VICMASS + PALCAV + MANTLP = WHORLS$.

The true relationship between shell size and degree of retraction/extension is best shown by the squared multiple correlations between each soft-part distance and the canonical variate (Table 2): they are negligible, ranging from 0.00 to 0.07, except for $EMPAPX$ (0.14). Thus, except for a very slight

correlation between whorl count and the amount of empty apex, there is no real effect of shell size on the degree of retraction/extension.

External aspects of the four chosen stages of retraction/extension rank are shown in Fig. 2. Stage a (Fig. 2a) is fully extended, b (Fig. 2b) has just the head invaginated, c (Fig. 2c) has about half of the foot retracted within the body wall, and d (Fig. 2d) has most of the foot retracted within the body wall.

Fig. 3 shows changes in the retractor muscle system, the head-foot, and the anterior digestive system during the four stages of retraction/extension shown for the same four snails of Fig 2, in the same positions but in semi-diagrammatic mid-sagittal section. Fig. 4 shows changes in the nerve ring (= circumesophageal ganglion = brain) during ommatophoral and head retraction. Figures 5–7 show changes in the reproductive system during the four stages of head-foot retraction, illustrated by the same specimens shown in Figs. 2 and 3.

The sequence of muscular contractions during retraction (Fig. 3) is the same as that observed in *Helix pomatia* (Trappman, 1916; Jones, 1975): rhinophoral, ommatophoral, buccal, and then pedal.

In stage a of retraction/extension (Fig. 3a), the rhinophores are invaginated. In stage b, the ommatophores are also invaginated within the body cavity, where they are pressed folded against the body wall by the head-foot.

The head is nearly filled by the buccal mass, which contains the radular ribbon (with its generative sac), the odontophore, the jaw, and the highly complex musculature for manipulating these structures through the mouth during a feeding stroke (Carriker, 1946; Runham, 1975). During retraction/extension, the positions of the buccal mass, the mouth, and the foot relative to each other remain fairly constant (Fig. 3). At full extension (Fig. 3a), the mouth (BO) is bounded by upper and lower lips (dark stippling) which lie above the anterior lobe of the foot (light stippling). The upper lip shields the sharp, chitonous jaw. As the head-foot is retracted (Fig. 3b–d), the upper lip is overlapped by the lower lip, which in turn is overlapped by the anterior lobe of the foot. At extreme contraction (Fig. 3d), the mouth region is distorted: the anterior foot lobe and the lower lip, enclosed within the body wall, compress and stretch the upper lip.

The buccal mass (B), because of its thick

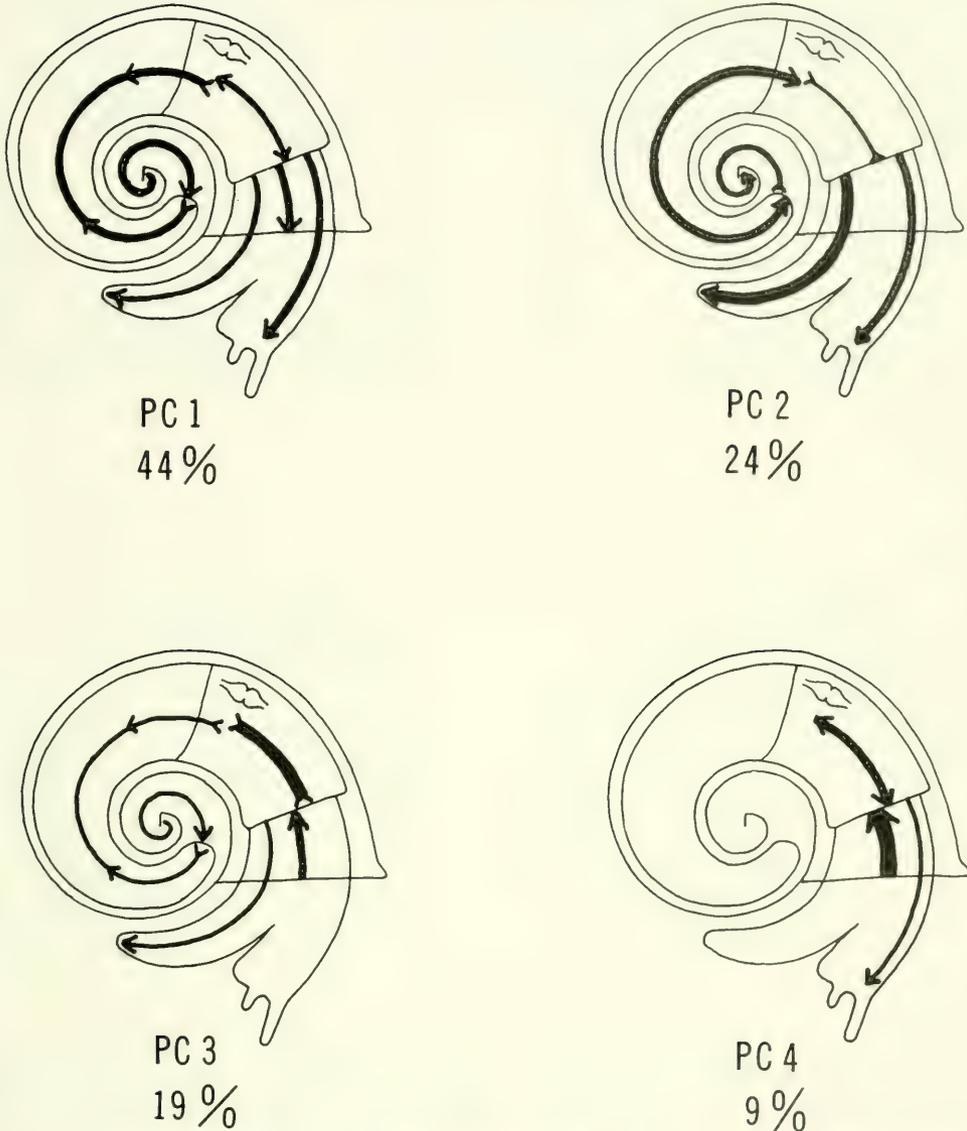


FIG. 1. Components of retraction/extension in preserved snails. The structures of four principal components (PC 1 to PC 4) are shown that explain 96% of the total variance in six soft-part measurements between homologous landmarks. The relative contribution of each measurement is indicated by the width of its line, and the direction of its contribution by the arrowhead(s).

musculature, remains relatively undistorted throughout retraction/extension (Fig. 3). The esophagus (O) is straight in stages a and b, but in stage c it has a kink and by stage d it is folded double, with the buccal mass in a posterior position. The stomach (IZ) is a simple sac in retraction/extension stages a and b, but

the compression of stages c and d makes it appear to have two lobes.

The cerebral nerve ring and its connectives are highly elastic. Fig. 4 shows in dorsal view how the nerve ring (N) is deformed during the earliest stages of retraction/extension of the buccal mass. During fullest extension (Fig.

TABLE 2. Canonical correlation between shell measurements and soft-part measurements associated with retraction/extension. Loadings of the variables are given on each of three canonical variates (CV), as well as the squared multiple correlation (R^2) of each variable with all variables in the other set.

Variable	CV1	CV2	CV3	R^2_1	R^2_2	R^2_3
Shell: Diameter	0.00	0.30	-1.25	0.09	0.14	0.17
Height	0.00	0.90	1.05	0.21	0.29	0.29
Whorls	1.00	-0.50	-0.11	1.00	1.00	1.00
Body: MANTLP	0.43	0.56	-0.39	0.00	0.03	0.04
FOOTIP	0.00	-1.35	-0.76	0.00	0.03	0.03
ANTENN	0.00	1.29	0.97	0.05	0.05	0.05
PALCAV	0.57	-0.54	-0.25	0.07	0.07	0.07
VICMAS	2.35	-0.37	0.69	0.00	0.01	0.04
EMPAPX	2.54	-0.14	-0.23	0.14	0.14	0.17

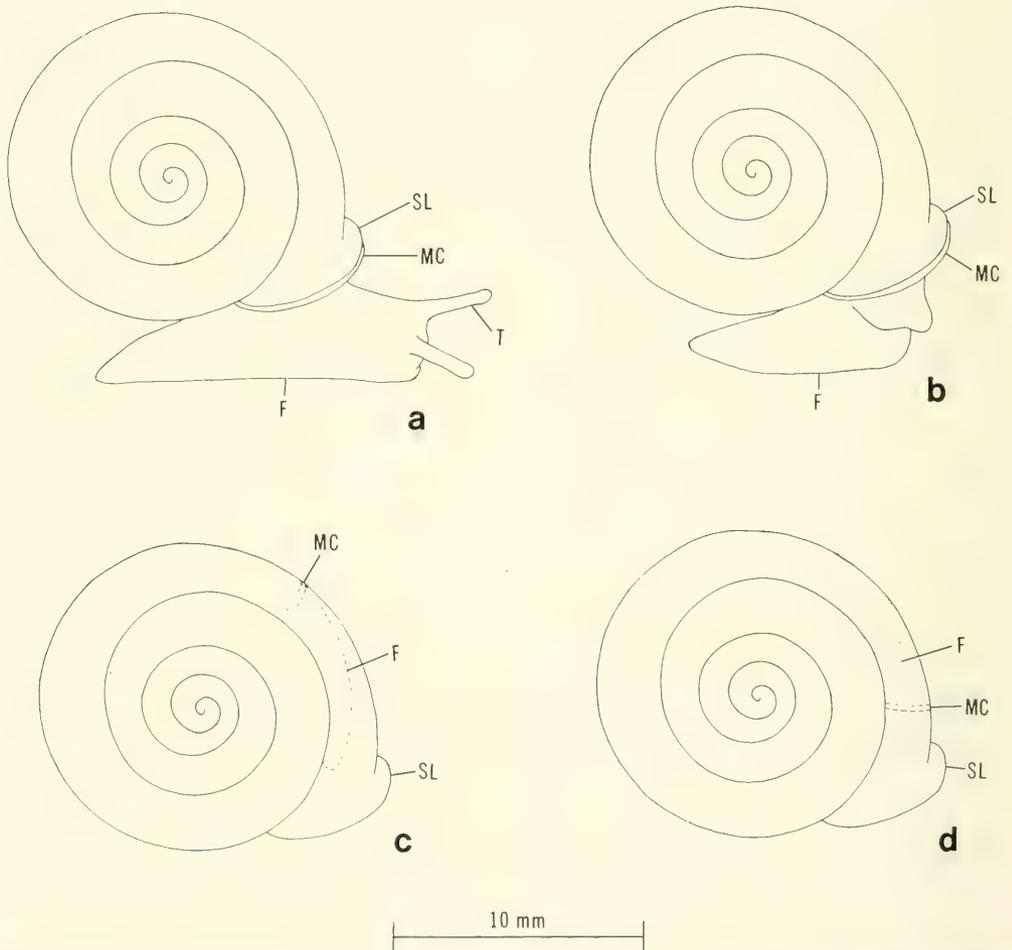


FIG. 2. Four stages (a-d) in the retraction/extension process: shell and head-foot. F = foot, MC = mantle collar, SL = shell lip.

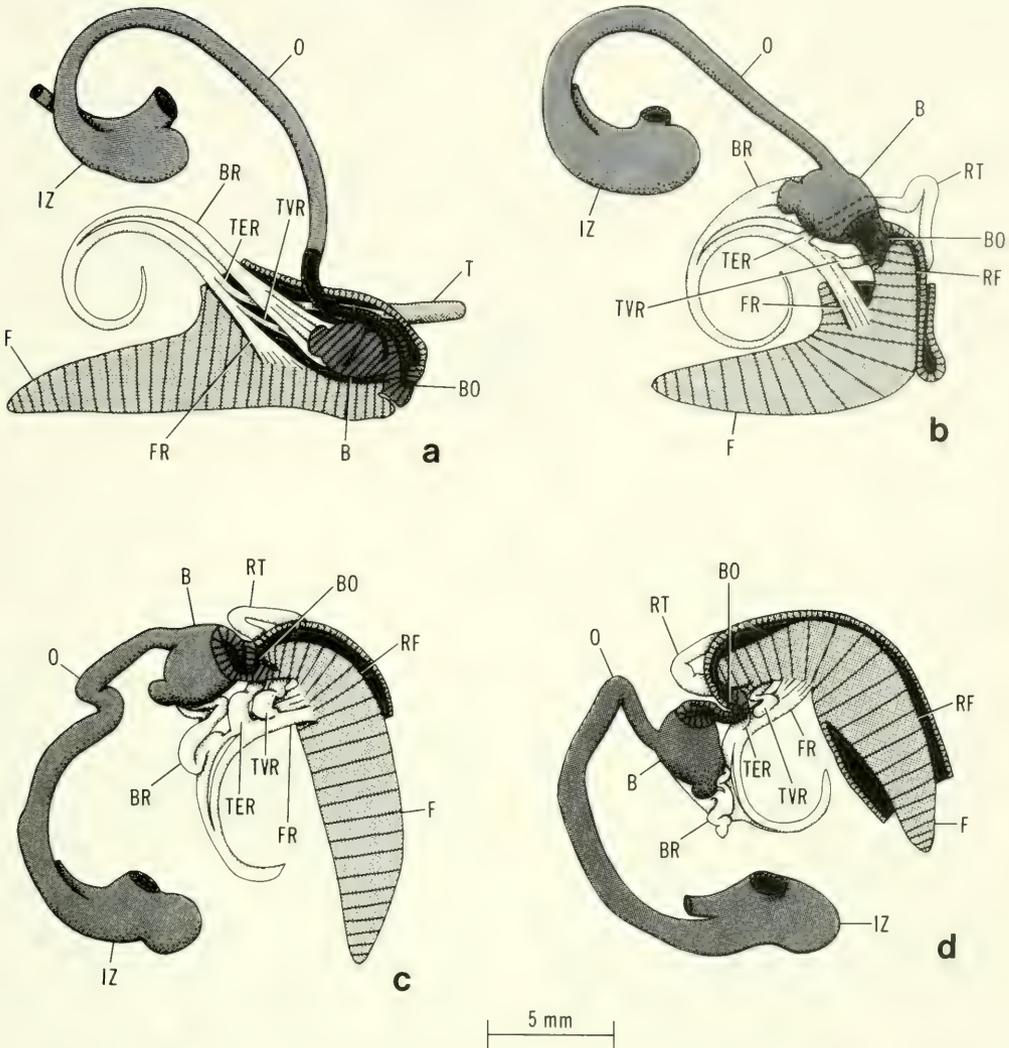


FIG. 3. Four stages (a-d) in the retraction/extension process: digestive and retractor-muscle systems and the head-foot. B = buccal mass, BO = mouth, BR = buccal retractor muscle, F = foot, FR = pedal retractor muscle, IZ = stomach, O = esophagus, RT = inverted (retracted) ommatophore, T = ommatophore, TER = ommatophoral retractor muscle, TVR = rhizophoral retractor muscle.

4a), the nerve ring encircles the esophagus (O) and the two anterior ducts of the salivary gland (OG), just posterior to the buccal mass. As the buccal mass begins to retract, however, it is pulled all the way back through the nerve ring (Figs. 4b and c). This process initially stretches the nerve ring in all dimensions (Fig. 4b), then compresses it longitudinally (Fig. 4c), producing substantial changes in both size and shape of the dorsal cerebral ganglion (N, dark stippling).

When retracted, the terminal portion of the reproductive system—from the genital pore to halfway up the prostate-uterus—is compressed between the retracted head-foot and the floor of the mantle cavity (Fig. 5). In the fully extended position (Fig. 5a), the genital pore (Y) opens on the right side of the head lateral to the anterior region of the buccal mass (B, stippled); the penis (P) is slightly bent and its retractor muscle (PR) is long and stretched; the vagina (V), spermatheca (S),

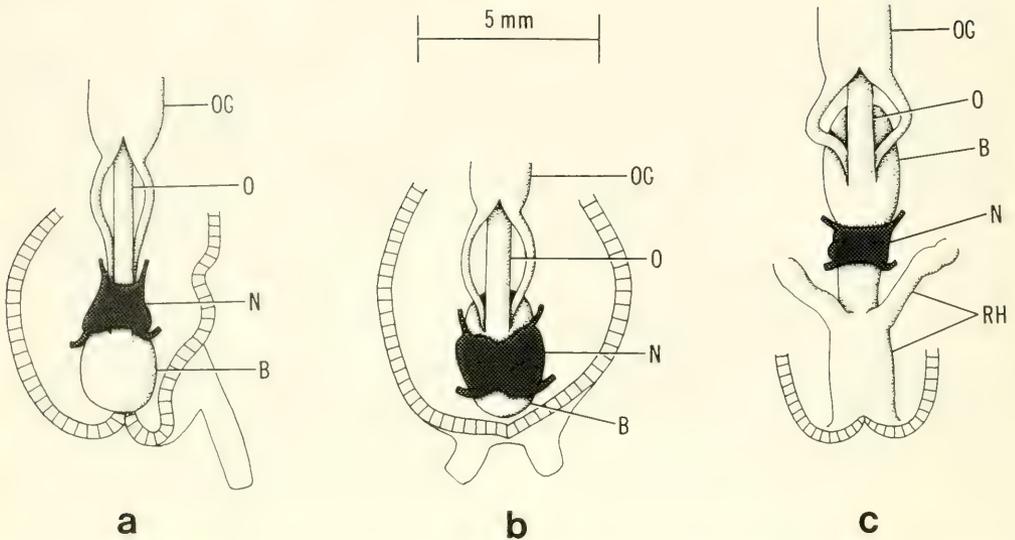


FIG. 4. Changes in the nerve ring (stippled) during early retraction/late extension. B = buccal mass, N = nerve ring, O = esophagus, OG = salivary glands, RH = retracted head.

and prostate-uterus (UT) are straight. (In Figs. 5–7, I have not differentiated between the tightly bound prostate and uterus, but have labeled them UT instead of the proper DG-UT.)

When the head and anterior foot are retracted (Fig. 5b), the genital pore is pulled back within the mantle collar (MC), adjacent to the retracted head-foot (RH-F, stippled); the buccal mass is pulled back to the level of the spermatheca; the penis is loosely contorted; the vagina is bowed and folded at its junction with the spermatheca (not visible); the prostate-uterus is doubled back on itself as it folds against the retracting buccal mass.

When the foot is half retracted (Fig. 5c), the genital pore retains its position near the apex of the retracted head-foot, the further retraction of which pushes the pore back toward the penis; the penis therefore is tightly contorted and its retractor muscle is contracted; the vagina is folded in half, with the apex of the fold held in place by connective tissue (not shown) to the anterior body wall; the prostate-uterus retains its tight folding adjacent to the buccal mass, which also apparently compresses the spermatheca (not labeled).

When the foot is nearly completely retracted (Fig. 5d), it has slid further past the genital pore, pushing the penis inward so that its retractor muscle is stretched; the penis re-

tains its tight contortion; the mid-way fold of the vagina remains attached by connective tissue to the anterior body wall, so that its length between this fold and the genital pore is stretched backward by the retracting head-foot; the prostate-uterus develops additional folds in the region of the further retracted buccal mass.

Figures 6 and 7 show the removed reproductive system and the terminal genitalia at stages a through d of retraction/extension. Table 3 summarizes the means and standard deviations of the lengths of the vagina, spermatheca, penis-plus-sheath, and penis-minus-sheath calculated from five measured snails, each snail the average of three repeated measurements. Vaginal length at full extension (stage a) averaged 4.5 mm, but when the head was invaginated (stage b), it only averaged 3.3 mm, a decrease of more than 25%. Later stages (c and d) of retraction actually increased the length of the vagina slightly to 3.6 mm (a 10% increase); as mentioned previously, this is due to stretching the vagina between its distal ligamental attachment to the body wall and its proximal attachment to the retracting genital pore. These interstadial differences in vaginal length were significant (two-way nested ANOVA, $F = 7.18$; degrees of freedom = 3, 16; $p < 0.005$), despite the high and significant variation among replicates at each retraction stage

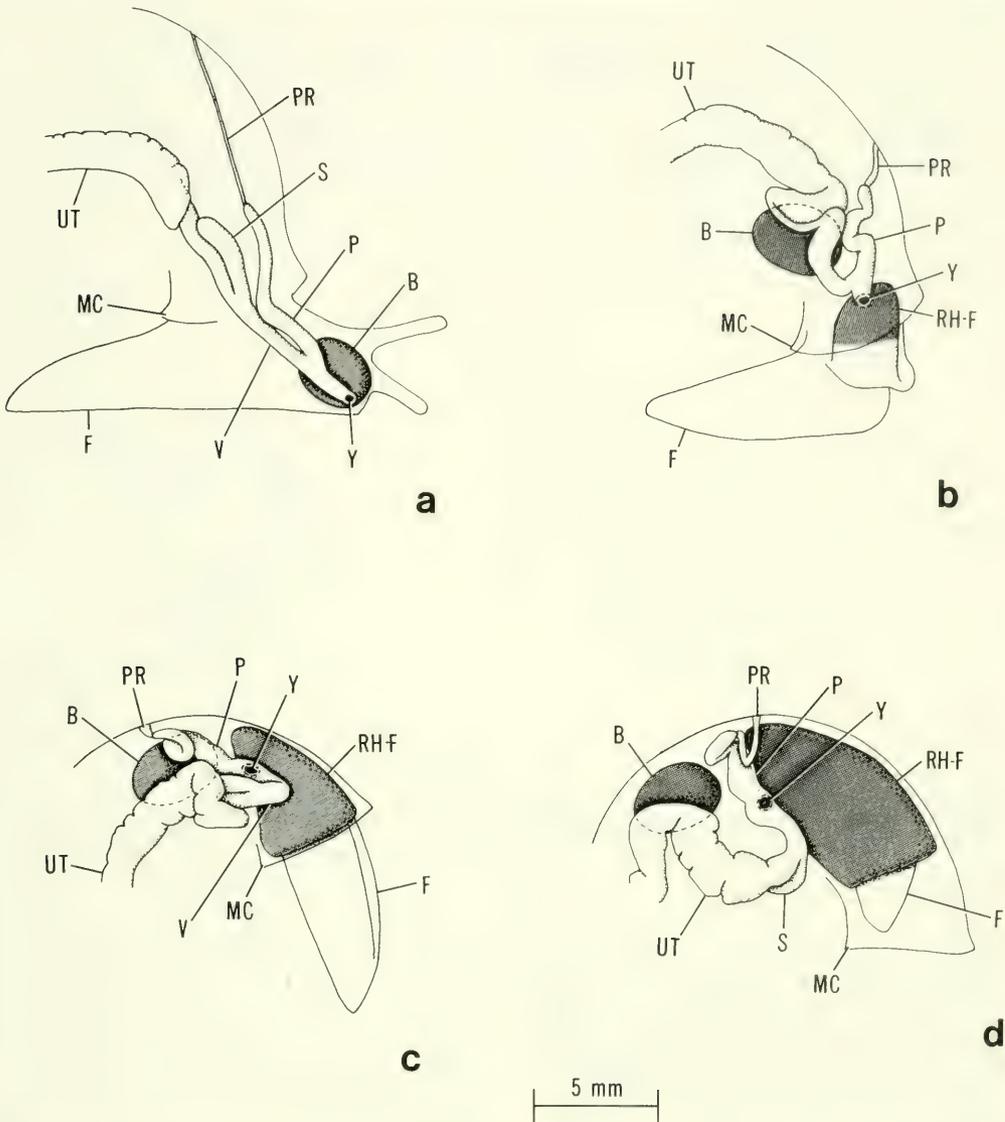


FIG. 5. Four stages in the retraction/extension process: reproductive system in relation to the buccal mass and retracted foot (both stippled). B = buccal mass, F = foot, MC = mantle collar, P = penis, PR = penial retractor muscle, RH-F = retracted head-foot, S = spermatheca, UT = prostate-uterus, V = vagina, Y = genital pore. In Fig. 5a, the genital pore opens toward the observer, whereas in 5b-d it opens away from the observer, into the space between the retracted foot and invaginated head skin, as indicated by the dashed circle around the pore.

($F = 16.36$; degrees of freedom = 16, 40; $p << 0.001$).

The spermatheca (= bursa copulatrix) was bound to the free oviduct (UV, Figs. 6 and 7) by connective tissue. Changes in the free oviduct were not quantified, but probably covaried with those of the spermatheca, the length

of which was significantly affected by head-foot retraction ($F = 9.55$, $p < 0.001$), but in a different way than vaginal length (Table 3). The spermatheca averaged 2.7 mm regardless of whether the snail was fully extended (stage a) or had invaginated its head (stage b). By the time it retracted half of its foot

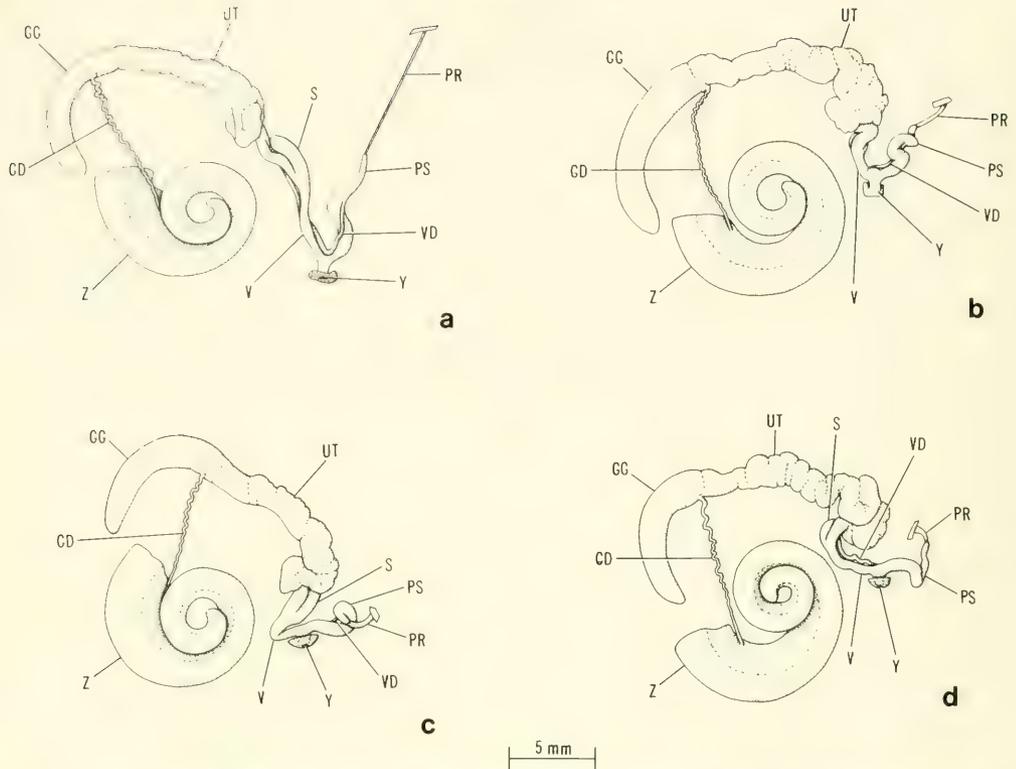


FIG. 6. Four stages in the retraction/extension process: reproductive system dissected out from the body cavity. GD = hermaphroditic duct, GG = albumen gland, PR = penial retractor muscle, PS = penial sheath, S = spermatheca, UT = prostate-uterus, V = vagina, Y = genital pore, Z = posterior digestive gland plus gonad.

(stage c), however, its spermatheca was shortened to 2.2 mm (an 18% reduction). Full foot retraction (stage d) shortened it even further to 2.0 mm. Within each of these retraction stages, however, there was highly significant variation among replicate snails ($F = 5.14$, $p < 0.001$), as evidenced by the high standard deviations in Table 3.

The length of the penis and its sheath showed a retraction-stage pattern similar to that of the vagina (Table 3). Head invagination (stage b) reduced its average length from 6.4 to 5.5 mm (a 14% reduction), which was maintained (stage c) until extreme foot retraction (stage d) stretched it slightly to 5.7 mm (a 5% increase). Extreme variation among replicates ($F = 6.77$, $p < 0.001$) kept this retraction effect just short of statistical significance ($F = 2.62$, $0.05 < p < 0.10$).

The length of the penis without the sheath varied insignificantly ($F = 1.92$, $0.10 < p < .25$), but in the same manner as penis-plus-

sheath length (Table 3). There was extreme variation among replicates ($F = 4.97$, $p < 0.001$).

The degree of retraction/extension had no effect on penial sculpture or on my ability to view it by dissection. Fig. 6 shows the complete reproductive systems, dissected free from the body cavity, of stages a–d. Despite increasing contortion of the penis and its sheath (PS) from stages a through d, the penis could always be stretched out with pins in a dissecting dish, slit longitudinally, and pinned open to reveal its functional surface (Fig. 7). In the dissections shown in Fig. 7, the vas deferens (VD) has been cut and the penial sheath has been cut near its apex in order to stretch out the upper part of the penis, which normally lies tightly coiled within the sheath (Solem, 1985, fig. 243).

The sculpture of the lower part of the penis consists of two smooth, longitudinal pilasters (PP), the left of which—i.e. appearing on the

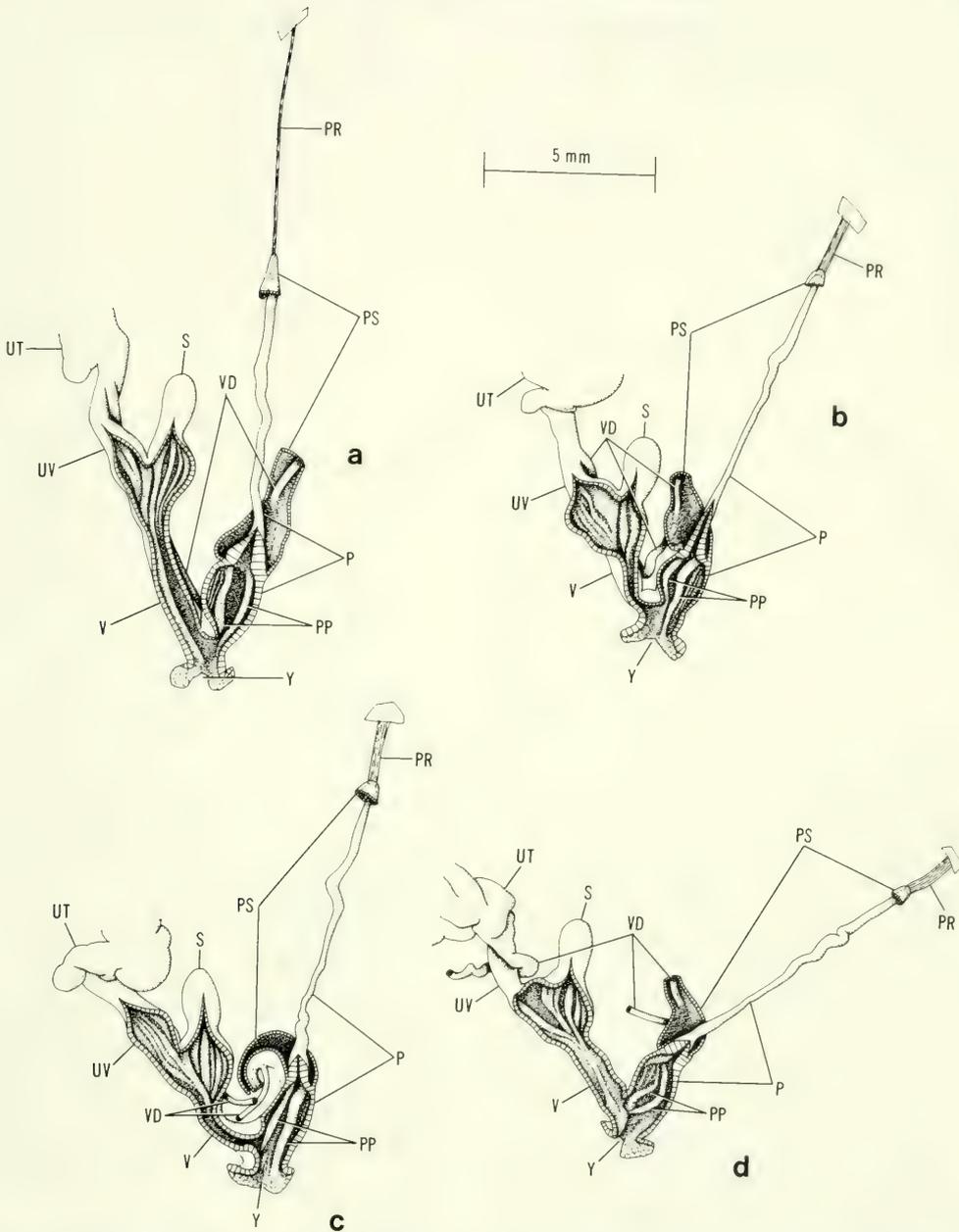


FIG. 7. Four stages in the retraction/extension process: terminal genital tracts, pinned out and dissected open. P = penis, PP = penial pilasters, PR = penial retractor muscle, PS = penial sheath, S = spermatheca, UT = prostate-uterus, UV = free oviduct, V = vagina, VD = vas deferens, Y = genital pore.

left side of the dissection, which is actually on the right side of the everted penis—is narrower than and stands about twice as high as the right. The ventral space between

these two pilasters is smooth, but the dorsal penial wall is sculpted with longitudinal ridges, which are thin and numerous at the penial apex, but which anastomose in various

TABLE 3. Lengths of the terminal genital tracts at four stages of retraction/extension. Means and standard deviations are based on five snails per stage.

Measurement	Stage of Retraction/Extension			
	a	b	c	d
Vaginal Length	4.5 (0.7)	3.3 (0.4)	3.6 (0.3)	3.6 (0.2)
Spermathecal Length	2.7 (0.2)	2.7 (0.4)	2.2 (0.2)	2.0 (0.3)
Penis + Sheath Length	6.4 (0.4)	5.5 (0.9)	5.4 (0.5)	5.7 (0.6)
Penis - Sheath Length	2.1 (0.3)	1.7 (0.2)	1.8 (0.3)	1.9 (0.2)

TABLE 4. Penial sculpture as measured at four stages of retraction/extension.

Retraction/ Extension Stage	Left Pilaster Width (mm)	Right Pilaster Width (mm)	Dorsal Wall Ridges		Width of Central Mid (mm)
			Number		
			Apical	Mid	
a	0.18 (0.05)	0.20 (0.06)	13.6 (2.9)	6.4 (1.3)	0.09 (0.03)
b	0.17 (0.03)	0.20 (0.04)	12.4 (1.1)	5.4 (0.5)	0.08 (0.03)
c	0.18 (0.05)	0.23 (0.03)	12.3 (2.2)	5.8 (2.2)	0.07 (0.02)
d	0.17 (0.03)	0.22 (0.04)	12.6 (3.2)	6.0 (0.7)	0.08 (0.03)

patterns proximally to become thicker and less numerous.

Measurements and counts of these features of penial sculpture (Table 4) show that they are extremely variable within the population and that there is no effect whatever due to the stage of retraction/extension. Averaged over all 20 specimens, the left pilaster width was 0.17 mm, with a coefficient of variation (CV) of 0.2; right pilaster width = 0.21 mm (CV = 0.2); number of apical dorsal ridges = 12.7 (CV = 0.2); number of mid-dorsal ridges = 5.9 (CV = 0.2); and central mid-dorsal ridge width = 0.08 mm (CV = 0.4).

Table 5 gives values of the two indices of measurement precision, along with the means, standard deviations, and ranges of the variables as calculated from the third set of replicated measurements. The mean coefficient of variation (CV Mean) was lowest for shell diameter (0.001), and was 7 × this value for shell height and whorl-count, and 31 × to 344 × this value for the soft-part distances between homologous landmarks.

The second index, the percentage of specimens with zero CVs, indicates the percentage of specimens for which the three repli-

cated measurements were identical. Its value varied from 9% to 70% and the ranges of values were equable between shell and soft-part variables (Table 5).

The precision of the shell measurements is analyzed in more detail in Table 6. Re-measurement of a shell's diameter gave precisely the same result 76% of the time, differed by 0.1 mm in 23% of the cases, and differed by 0.2 mm in only 1% of the cases. The greater imprecision of height measurements is evidenced by both its percentage (55%) and its range (up to 0.3 mm) of deviations. Whorl counts were 70% repeatable, and of the deviations, 93% (0.28/0.30) were off by only one-tenth whorl; no deviation exceeded two-tenths whorl.

The results of variance-partitioning of the lengths of the terminal genitalia are presented in Table 7. In this table, the effects of retraction/extension (four stages), individual variation (5 replicates per stage), and measurement error (three measurements per replicate) are summarized from analysis of variance for each of four genitalic measurements. For vagina length, over half of the total variation was due to retraction/extension, less than half was due

TABLE 5. Shell and soft-part measurements: univariate statistics and two indices of measurement precision.

Variable	Mean (SD)	Range	Precision Indices	
			CV Mean (SD)	CV = 0
Diameter	17.1 (0.5)	15.9-18.3	0.001 (0.002)	64%
Height	8.4 (0.3)	7.7-9.2	0.007 (0.005)	21%
Whorls	5.0 (0.1)	4.85-5.25	0.007 (0.006)	32%
MANTLP	0.05 (0.06)	0.00-0.20	0.344 (0.660)	70%
FOOTIP	0.25 (0.15)	-0.05-0.50	0.121 (0.139)	40%
ANTENN	0.43 (0.16)	0.15-0.80	0.133 (0.152)	13%
PALCAV	0.54 (0.07)	0.35-0.65	0.067 (0.069)	31%
VICMAS	2.72 (0.30)	2.15-3.35	0.031 (0.046)	19%
EMPAPX	1.55 (0.32)	0.9-2.3	0.087 (0.128)	9%

TABLE 6. Deviations of repeated shell measurements from their grand means. Deviation units are 0.1 mm for diameter and height, and 0.1 whorls for whorl-count. The proportion of replicates (and its standard deviation) is given for each deviation unit.

Measurement	Deviation		
	0.0	+ 0.1	+ 0.2 or 0.3
Diameter	0.76 (0.10)	0.23 (0.09)	0.01 (0.01)
Height	0.45 (0.03)	0.45 (0.05)	0.10 (0.03)
Whorls	0.70 (0.04)	0.28 (0.05)	0.02 (0.02)

to individual variation (among the five snails measured for each stage of retraction), and less than a tenth was due to measurement error. For spermatheca length, over half of total variation was due to retraction/extension, about one-fourth was due to individual variation, and about one-fifth was due to measurement error. For penis-plus-sheath length, individual variation accounted for over half the total variation; retraction/extension accounted for one fifth, whereas measurement error accounted for over one fourth, of this variation. For penis-minus-sheath length, measurement error was high, accounting for over one third of the total variation; individual variation accounted for half, and retraction/extension accounted for only about one tenth of the total variation in the length of the penis minus the sheath.

DISCUSSION AND CONCLUSIONS

Body Landmarks During Retraction/Extension

Interpreting the principal components (PCs) of retraction/extension (Table 1, Fig. 1) must allow for the facts that (1) since the six variables used in the analysis differ in their

measurement precisions, their differences may show up as artifacts in the structure of one or more PCs; and (2) the variable ANTENN should, in retrospect, have been measured from the mantle collar rather than from the heart, which causes it to overlap PALCAV and therefore makes its interpretation more difficult in the context of PC structure.

Retraction/extension of the head and the foot (ANTENN and FOOTIP) are strongly correlated (PCs 1 and 2) because of their physical connection, but apparently either end may slightly precede the other (PCs 3 and 4). During head-foot extension/retraction, the visceral mass is either farther or closer to the shell apex (PCs 1 and 2), and the mantle collar is either closer or farther (PCs 1, 3 and 4) from the shell lip (Fig. 1, Table 1). Thus retraction/extension involves a complex interplay of body landmarks. This complexity may be due, at least in part, to confounding the two separate processes of retraction and extension. Thus, for example, the mantle collar may be pulled along with the head-foot during extension, but may lag behind the head-foot during retraction. For this reason, the best single criterion for the state of retraction/extension in preserved specimens is the position of the tip of the foot relative primarily to the body wall, and secondarily to the shell lip.

TABLE 7. Partitioning of the total variance in the lengths of terminal genital tracts.

Measurement	Source of Variation		
	Retraction/ Extension	Individual Variation	Measurement Error
Vaginal Length	52%	40%	8%
Spermathecal Length	55%	26%	19%
Penis + Sheath Length	20%	53%	27%
Penis - Sheath Length	12%	50%	38%

Thus the mantle collar, which is often the most visible landmark through the shell of retracted snails, is unreliable as an indicator (compare Fig. 2c and d).

When I ranked the deshelled specimens according to the position of the foot-tip relative to the body wall (RETRAN), this index was significantly but not strongly correlated with PCs 1, 2, and 3. Thus, only RETRAN is a reliable general measure of retraction/extension state as it distorts systematically important body organs.

Effect of Shell Size

Shell size is no predictor of the state of retraction/extension. This conclusion does not come from canonical-correlation analysis between the sets of shell variables and soft-part variables (Table 2), because the latter were measured as whorl increments and the sum of four of them equals the shell variable "Whorls" (thus the first, and only significant, canonical variate merely reflects this mathematical relationship). The conclusion results rather from the facts that the second and third canonical variates were not only non-significant but also biologically nonsensical, and that the multiple correlation of each soft-part variable with the set of shell variables was zero to negligible (Table 2).

Retraction/Extension and Systematic Characters

The four stages I chose from the continuum of retraction/extension are fairly distinct and easily identified in deshelled specimens: full extension, head invagination, half retraction of the foot, and full retraction of the foot (Fig. 2a-d). The latter stages are difficult or impossible to identify without removing the shell, however, because the transition between the exposed foot and the folded body wall into which it retracts is seldom discernable through the shell and—sometimes—the man-

tle (see Fig. 2c and d). Since the specimens did not fall into discrete categories, the four stages were chosen at equal distances (i.e. numbers of specimens) along the retraction/extension continuum. For this reason, the five "replicates" of each retraction/extension "stage" are actually only five adjacent specimens in one region of the continuum; the similarity of replicates was probably greatest at the endpoints: full extension and full retraction.

Body retraction is effected by the sequential contractions of four muscles that are posteriorly fused—the rhinophoral, ommatophoral, buccal, and pedal retractors. The sequence is the same in *Helix pomatia* (Trappman, 1916; Jones, 1975). It appears that successive muscles are not effective throughout the process of body retraction, but each reaches a limit of contraction, after which it folds as the next muscle(s) continue to contract (Fig. 3). Body retraction is remarkably rapid. For example, several species of polygyrid land snails retract too quickly to be fixed in extended condition by immersion in liquid nitrogen (Emberton, unpublished).

Distortion of internal organs by the retraction process differs widely in both its degree and its nature. The retractor muscles themselves, despite drastic changes in length, shape, and both absolute and relative distances among each other, retain their basic topology throughout retraction. The length of the foot is not greatly altered during body retraction, if measured along the curvature of its sole (Fig. 3). The upper lip is extremely stretched during the final stage of retraction. The size and shape of the buccal mass is virtually unaffected, although this was not studied in detail. The esophagus undergoes extensive shape changes, but its overall length appears stable. Both size and shape of the stomach, however, are sensitive to the stage of body retraction (Fig. 3).

One of the most drastic changes during retraction occurs during its early stages. This is

when the buccal mass is pulled back through the nerve ring. The effects of the size and shape of the nerve ring and its constituent ganglia are major (Fig. 4).

The distal reproductive system undergoes a great deal of distortion during body retraction as it is displaced by both the buccal mass and the foot (Figs. 5 and 6). The lengths of the terminal tracts are often given in systematics accounts, but the recorded variation compounds individual variation, variation due to retraction state, and measurement error.

The results of this study indicate clearly that body retraction contributes a significant amount of variation in the lengths of the terminalia, even when they are dissected free from the body and pinned out straight for measurement. In the case of the lengths of the vagina and the spermatheca, the effect of body retraction actually outweighed individual variation (Table 7). Thus, these tracts are not only bent and folded by retraction, but are also physically shortened. The effect of body retraction is nonlinear (Table 3), and the nature of the nonlinearity is likely to differ among species, so excluding the effect of body retraction on the vaginal and spermathecal lengths for interspecific comparisons would be difficult indeed. This irremedial effect is quite profound: one-fourth retraction can reduce the total length of the vagina by 25% and the spermatheca by 18%. (This caveat probably does not apply, however, to the majority of snails having a long, thin-walled spermathecal duct.) Therefore, interspecific differences can easily be rendered undetectable by employing retracted specimens. Measurement precisions for the vagina and spermatheca were good (approximately 1/10 and 1/5 total variances [Table 6]), so interspecific comparisons using only fully extended specimens should be fairly reliable.

The land-snail penis is frequently of great value in systematics because of its variability. Fortunately, body retraction/extension has no substantial effect on penial characters. For the length of both the total and the basal penis, the effect of retraction/extension was well below measurement error (Table 7). Also, no matter how distorted the penes were in retracted states (Figs. 5 and 6), it was always possible to quantitatively compare the sculptures of their functional surfaces by dissection (Fig. 7). The widths of the two pilasters and of the central ridge of the penial wall and the numbers of dorsal wall ridges, although variable among individuals, were un-

affected by the state of body retraction/extension (Table 4).

Measurement Precision

The differences in precision of the shell measurements depended in part on the problems of orienting the shells for diameter and height measurements, and of locating the zero-whorl notch for whorl counts. *Ningbingia dentiens* has a relatively low-spined shell approximately equal in size to the tip of one of the human fingers used to hold and orient it for measurement with dial calipers. These factors make it difficult to judge the position of the coiling axis. Measuring the diameter requires holding the coiling axis parallel to the jaws of the calipers and rotating the shell on this axis until the maximum diameter is achieved. This rotation—it becomes slight and almost unnecessary with practice—helps locate the coiling axis and ensures that the maximum diameter is measured. The precision of this measurement, therefore, is relatively high: 95% of repeated measurements lay within 0.5% of their mean, and no single error was greater than 1% of the grand mean.

The measurement of shell height is sensitive to any tilt away from the coiling axis. Such tilt is especially difficult to detect and control in the plane perpendicular to the jaws of the calipers. Rotation in this plane does not affect the measurement of the diameter. Because of this additional source of error the precision of height is lower than that of diameter: 95% of repeated measurements lay within 2.8% of their mean, and no single error exceeded 4% of the grand mean.

Accurately locating the origin of the suture (Schindel, 1989)—the apical notch of zero whorls (see Emberton, 1985, fig. 1)—requires a perfectly clean apex and an incidental source of narrow-beam illumination. The result was that 95% of repeated measurements lay within 2.8% of their mean, and no single error exceeded 4% of the grand mean. Thus, for this, on average, 8.4-by-17.1-mm, 5-whorled shell, whorl counts to the nearest 0.1 whorl were just as precise as height measurements to the nearest 0.1 mm, which were 1/7 as precise as diameter measurements to the nearest 0.1 mm.

The applicability of this precision analysis to other gastropod studies is limited, depending both on the size, shape, number of whorls, and ease of detection of the suture origin of the shell, and on the experience and care of

the investigator. On the other hand, its methodology should be broadly applicable to other studies. The indices (Table 5) and categorizations (Table 6) of precision are useful, can be applied to any kind of measurement, and provide the kind of backup necessary to, but too often lacking in, morphometric studies (e.g. Gould & Woodruff, 1986).

The precision of each soft-part distance depends on two main factors: the ease of locating its landmarks, and its size. The mantle collar in this species is easy to see either flush with the shell lip or, when it is retracted up to 0.2 whorl, through the shell. Its distance (MANTLP) from the shell lip, another reliable landmark, is calculable with high precision. Because MANTLP is such a short distance however (mean = 0.05 whorl), the few deviations among replicated measurements are equal to or greater than its mean value. This combination of factors explains why, among all variables, MANTLP shows the highest precision using the $CV=0$ index (70%), but the lowest precision (= highest value) using the CV -mean index (0.34) (Table 1). $CV=0$ is the better index because of its independence from the size of the variable; MANTLP is a variable calculable with high precision.

The tip of the foot is as easy to locate as the mantle collar, but the distance between these two landmarks (FOOTIP) has a lower precision ($CV=0$ value = 40%) than MANTLP for two reasons. First, the mantle collar is a slightly less reliable landmark than the shell lip. Second, and most importantly, the everted foot—unlike in retracted foot—rarely follows the contour of the body whorl as it is depicted diagrammatically in Fig. 1. Instead, it is more or less straight (Fig. 2a and b), so imprecision enters in estimating its curved distance. Nonetheless, FOOTIP is the second most precise soft-part distance.

Slightly less precise ($CV=0$ value = 32%) is the distance between the mantle collar and the auriculo-ventricular junction of the heart, used as a truncated measurement of the pallial cavity (PALCAV). Although the mantle collar is a good landmark, the position of the heart, as mentioned in the Materials and Methods section, can be difficult to pinpoint, depending on its chromatic differentiation from surrounding tissues, its size (state of contraction? degree of distention by haemocoelic pressure changes at death?), and the opacity of the overlying shell.

Finding the retracted ommatophore was almost always easy—it is very dark gray and

shows well through the shell—but judging its anterior-most point involved error. Measuring the base of the ommatophore on an extended snail suffered from either guessing its position on an invaginated head, or estimating its curved distance (as for the everted foot), or both. Combining this imprecision with that of the heart made the distance between these two landmarks (ANTENN) fairly imprecise, with a $CV=0$ index value of 13%. In retrospect, a better measurement of antennal retraction (ANTENN) would have been the distance between the ommatophore and the mantle collar (instead of the heart); this would have been more precise.

There is apparently no way to improve the low precisions ($CV=0$ values = 19% and 9%) of measurements of the visceral mass (VICMAS) and the apex of the shell empty of (unoccupied by) body tissue (EMPAPX). The landmark common to these two variables, the apex of the visceral mass, is often quite difficult to pinpoint. As mentioned in the Materials and Methods section, it can be obscured both by denatured fluid within the empty apex and by opacity of the shell, the apex of which receives the earliest and heaviest abrasion. Finding this landmark is aided by thoroughly cleaning the umbilical pit and by manipulating the light source. The imprecision index of VICMAS (the distance between the heart and the apex of the viscera) reflects—as do the indices of all soft-part distances, to a lesser degree—my learning process in locating the landmarks. The least precise of all soft-part distances, EMPAPX, combines the discriminatory problem of the visceral apex with that of its other landmark, the suture origin, which was discussed above.

In sum, soft-part distances (Table 5, Fig. 1) varied greatly in precision depending on their size and on the difficulty of locating and measuring their landmarks. The “ CV mean” index was an indicator of size-related imprecision, and the “ $CV=0$ ” index was an indicator of landmark-related precision. Both indices also include my improvement in discriminating difficult landmarks.

Relative Sources of Variation

The results indicate clearly that body retraction/extension contributes a significant amount of variation to the lengths of the terminal genital tracts, even when they are dissected free from the body and pinned out straight for measurement. In the case of the

lengths of the vagina and the spermatheca (including duct), the effect of body retraction actually outweighed individual variation (Table 7). Thus, these tracts were not only bent and folded by retraction, but are also physically shortened.

The penis is frequently of great value in systematics because of its variability, probably due to sexual selection (e.g. Cain, 1982; Eberhard, 1985). Measuring the length of the penis of *Ningbingia dentiens* requires straightening the upper region that is tightly coiled within the penial sheath (Fig. 7). This doubtless contributed to the large error of measurement, which accounted for over one fourth of total variance in the total length of the penis (Table 7). Nevertheless, the measurement error for the basal penis, exclusive of the sheath, was even more imprecise, accounting for over one third of total variance in length. These are substantial components of variation that could easily interfere with any attempts at meaningful comparisons among populations or species. Fortunately, none of this measurement error affected the penial sculpture, as viewed by dissecting open the unverted penial tube (Fig. 7), which can be a valuable source of systematic characters (e.g. Schileyko, 1978; Solem, 1985; Emberton, 1988). However, this study has shown quantitatively that intrapopulational variance in these characters can be quite high (Table 4).

ACKNOWLEDGMENTS

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BIOLOGY AND COMPARATIVE ANATOMY OF *DIVARISCINTILLA YOYO* AND *D. TROGLODYTES*, TWO NEW SPECIES OF GALEOMMATIDAE (BIVALVIA) FROM STOMATOPOD BURROWS IN EASTERN FLORIDA

Paula M. Mikkelsen¹ & Rüdiger Bieler²

ABSTRACT

Two new galeommatid bivalves, *Divariscintilla yoyo* and *D. troglodytes*, are described as commensals in burrows of the stomatopod *Lysiosquilla scabricauda* from central eastern Florida. They are remarkable in their snail-like appearance and behavior, due to elaborately ornamented pallial layers enclosing the shell, and their ability to actively crawl on a highly mobile foot. Both are simultaneous hermaphrodites, brooding their larvae in the suprabranchial chamber prior to release of straight-hinged veligers. The two new species differ from one another in shell morphology, the number of secretory "flower-like organs," and the nature and ornamentation of the mantle. They differ from the type and only other described species in this genus, *D. maoria*, primarily in shell characters, namely in anterior (rather than posterior) prolongation, and in the absence of a ventral cleft. The genus *Divariscintilla*, previously known only from New Zealand, is redefined with the following diagnostic characters: incompletely internalized shell with anterior or posterior prolongation, species-specific numbers of pallial tentacles and papillae, a two-part foot used in active crawling and "hanging" utilizing both byssus- and byssus adhesive glands, secretory "flower-like organs" on the anterior surface of the visceral mass, eulamellibranch ctenidia with interlamellar and interfilamentary junctions, and simultaneous hermaphroditism with larval brooding.

Key words: *Divariscintilla*, Galeommatidae, Galeommatodea, systematics, anatomy, Stomatopoda, commensalism, Florida.

INTRODUCTION

A wide variety of mollusks are known to associate with other invertebrates in symbiotic relationships. Galeommatodean [= galeommatacean] bivalves are among the best known symbionts (Boss, 1965, as Erycinaea), and are interesting in the anatomical and behavioral modifications associated with their specialized mode of life. These include (1) internalization of the shell by the middle pallial fold, (2) elaboration of this pallial layer by tentacles and papillae, (3) snail-like locomotion on a highly extensible foot, and (4) the occurrence of hermaphrodites or dwarf males. Anatomical data are available for species in less than 30 of the approximately 110 Recent, presumably valid genera (Vokes, 1980; Chavan, 1969).

Within the family Galeommatidae Gray, 1840, the monospecific genus *Divariscintilla* Powell, 1932, was originally based on empty shells of the New Zealand species *D. maoria* Powell, 1932. Distinguishing shell characters

include a deep ventral notch, a strongly oblique posterior prolongation, and dentition limited to a small conical tooth in each valve. The anatomy and biology of *D. maoria* were subsequently described by Judd (1971) from specimens found living in the burrows of the stomatopod crustacean *Heterosquilla tricarinata* (Claus).

A study of organisms associated with the sand-burrowing stomatopod *Lysiosquilla scabricauda* (Lamarck) in shallow waters in eastern Florida has yielded a number of undescribed or poorly known molluscan species. Data on the two species of vitrinellid gastropods in the burrows have appeared elsewhere (Bieler & Mikkelsen, 1988). Five previously undescribed species of galeommatid bivalves were also encountered, and two, assignable to *Divariscintilla*, are here described. The data presented here identify anatomical characters of value at the generic level and represent a step toward clarification of the taxonomic disorder in this superfamily.

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MATERIAL AND METHODS

Stomatopod burrows in shallow-water sand flats in the Indian River lagoon just inside the Ft. Pierce Inlet, St. Lucie County, eastern Florida (27°28.3'N, 80°17.9'W), were sampled using a stainless steel bait pump ("yabby pump") and sieves of 1–2 mm mesh. Depths during extreme low water ranged from less than 0.5 m to supratidal, wherein the water level lay several centimeters below the level of the sand.

Living clams were maintained in finger bowls of seawater at room temperature (24°C). Behavioral studies were aided by video recordings taken of the living animals in aquaria using a standard commercial 1/2-inch-format video camera equipped with a macro lens.

Carmine and fluorescein sodium particles aided observation of ciliary action and currents produced by the animals. Relaxation prior to dissection or preservation was most effectively accomplished with menthol crystals, floated on the seawater surface, or with crystalline magnesium sulfate, added directly in small, gradual amounts. Methylene-blue/basic-fuchsin and neutral red were used to delineate tissues and organs in gross dissections.

For histological serial sections, animals were fixed in either a glutaraldehyde-formalin solution (4% formalin, 2.5% glutaraldehyde in 0.1M phosphate buffer, pH 7.2) or in 5% buffered formalin (Humason, 1962: 14). Shells were decalcified using either dilute hydrochloric acid (complete decalcification within minutes, however, with bubble production presenting technical histological difficulties) or a 1% solution of ethylene diamene tetraacetic acid (EDTA, adjusted to pH 7.2; decalcification complete over a period of 5–6 days). Specimens were embedded in paraffin, sectioned at 5–7 μ m and stained with alcian blue/periodic-acid-Schiff (PAS), counterstained with Harris' hematoxylin/eosin (Humason, 1962: 125, 269, 298), hereafter referred to as APH. Staining reactions described in the text refer to this method unless otherwise noted. Colors referred to in the text are supplied for future use, e.g., to infer homologies of the various glands. Other similarly prepared specimens were stained with hematoxylin/eosin. The section in Fig. 23 was fixed in Karnovsky's fixative (Karnovsky, 1965), post-fixed in 1% osmium tetroxide in a phosphate buffer, dehydrated through an ethanol propy-

lene oxide series, embedded in Epon-812, sectioned at 1 μ m and stained with Richardson's stain (Richardson, et al., 1960). Photomicrographs of sections were taken either with a Zeiss Photomicroscope-3 or an Olympus BH-2 stereomicroscope fitted with an Olympus OM-2 camera.

For scanning electron microscopy (SEM), partially dissected preserved specimens were passed through an ethanol-to-acetone series and critical-point dried. These and air-dried shells were coated with gold/palladium and scanned using a Zeiss Novascan-30.

All cited anatomical measurements were taken from specimens of average size (approximately 10–15 mm mantle length). Because of the extreme expansivity and contractility of the mantle, it is difficult to accurately measure "length" of a living animal of this type. Approximate mantle length was measured along an anteroposterior axis from an animal in normal crawling or hanging posture; throughout the text, this is expressed as "relaxed" and does not refer to any chemical treatment of the animals. Measurements of type specimens refer to preserved mantle lengths. Shell length is expressed as the maximum dimension, i.e. an oblique anteroposterior length.

Cited institutions are (* indicates location of type and other voucher material):

- AMNH— American Museum of Natural History, New York
- *DMNH— Delaware Museum of Natural History, Wilmington
- HBOI— Harbor Branch Oceanographic Institution, Ft. Pierce, Florida
- *IRCZM— Indian River Coastal Zone Museum, HBOI
- *MCZ— Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
- SMSLP— Smithsonian Marine Station at Link Port, Ft. Pierce, Florida
- *USNM— National Museum of Natural History, Smithsonian Institution, Washington, D.C.

TAXONOMIC DESCRIPTIONS

Family GALEOMMATIDAE GRAY, 1840

Gray (1840: 154) introduced the family name Galeommidae for *Galeomma* Turton, 1825 (erroneously spelled "Galeomidae" by

Gray, 1842: 78). It has been used in that form by various authors (e.g. H. & A. Adams, 1857; Tyron, 1872; Kisch, 1958). Dall (1899: 875) emended the spelling without explanation to Galeommatidae, and it is this form that is now in common use (e.g. Thiele, 1934; Popham, 1939; Vokes, 1980; Chavan, 1969; B. Morton, 1973; Abbott, 1974; Boss, 1982). Dall's action was a justified emendation of an incorrect original spelling [ICZN, 1985: Art. 29(b)(i), 32(c)(iii)] because the Greek noun *ὄμμα* provides the stem *ommat-* for the formation of the family name. As a justified emendation, Galeommatidae bears Gray, 1840, as authority and date [ICZN, 1985: Arts. 11(f)(ii), 19(a)(i)]; the name of the superfamily is accordingly Galeommatoida [= Galeommatacea] Gray, 1840. The nominal superfamilies Leptonoidea Gray, 1847; Erycinoidea Deshayes, 1850; and Chlamydoconchoidea Dall, 1889, are here considered junior synonyms.

DIVARISCINTILLA POWELL, 1932: 66.

Type species: *Divariscintilla maoria* Powell, 1932 (by original designation). Recent, New Zealand.

DIVARISCINTILLA YOYO, SP. NOV. (FIGS. 1, 3, 5, 6, 8–11, 26)

Material examined: Holotype: 5.3 mm [preserved mantle length], USNM 860036. Paratypes (8): 5.8, 4.7 mm, USNM 860037; 8.3, 7.5 mm, MCZ 297406; 6.0, 5.2 mm, IRCZM 064:01721; 5.7, 4.7 mm, DMNH 175516. Total material: 83 specimens: FLORIDA: Ft. Pierce Inlet: March 1987, 4; 2–3 May 1987, 19 (including MCZ paratypes); 24 June 1987, 4; 03 August 1987, 6; 14 August 1987, 7; 31 August 1987, 17 (including USNM, IRCZM, and DMNH type specimens); 28 December 1987, 1; 11 March 1988, 2; 12 April 1988, 13. —Sebastian Inlet: 30 December 1987, 10.

Type locality: Ft. Pierce Inlet, St. Lucie County, Florida, 27°28.3'N, 80°17.9'W, in *Lysiosquilla scabricauda* burrows on intertidal sand flats with patches of the seagrass *Halodule wrightii* Ascherson.

Diagnosis

Animal translucent white. Mantle thick, surface granular, falling into large creases. Two long "cephalic" pallial tentacles; one very short mid-dorsal tentacle just anterior to ex-

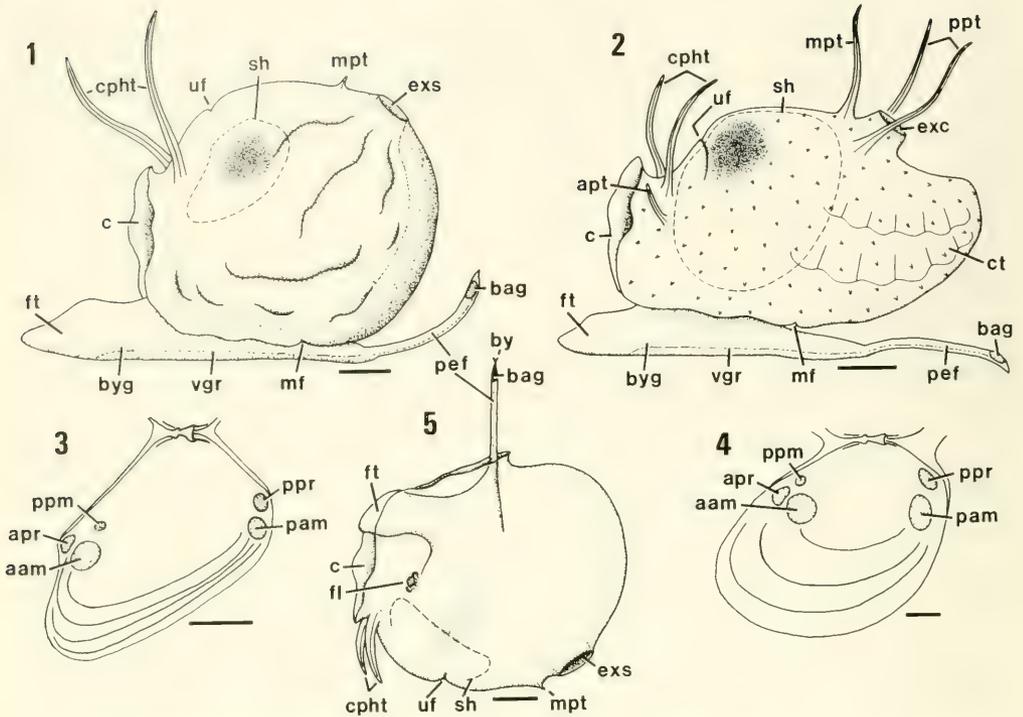
current siphon. Shell wedge-shaped, elongate-pointed anteriorly, with weak internal ribs, length approximately 40% of extended mantle length. "Flower-like organs" on anterior surface of visceral mass ventral to labial palps, numbering 3–7 (usually 5).

Description

External features and mantle: Living extended animal (Fig. 1) 10–15 mm in length, globular in general shape, entirely translucent white, except for dark upper portion of digestive gland. Shell nearly completely enclosed by thick mantle with granular external surface (Fig. 6; formed by middle pallial fold) falling into large creases, and with sparse, minute papillae; mantle thinner, more translucent, and with scattered, relatively larger papillae in smaller (approximately 7 mm) specimens. Anteropodal pallial opening wide, forming extensive anterior cowl (Fig. 1, c). Two long, retractable, "cephalic" tentacles (Fig. 1, cpht) anterodorsally just behind cowl. Very short (< 1 mm) median pallial tentacle (Fig. 1, mpt) on dorsal midline anterior to excurrent siphon (Fig. 1, exs). Each tentacle with central core of longitudinal muscle and nerve fibers, visible as an inner thread under low magnification. Mantle fused dorsally from edge of cowl to excurrent siphon located posterodorsally and often on conspicuous rounded protuberance (dependent on degree of pallial expansion); fusion interrupted only by small circular (approximately 2 mm diameter) foramen (Fig. 1, uf) just over umbo of shell. Mantle fused posteroventrally from excurrent siphon to mid-ventral point (Fig. 1, mf) at posterior end of anteropodal opening. Inner pallial fold highly muscular; fibers continuous with muscles of central "core" of tentacles.

Preserved animals characterized by general globular appearance, with retracted cephalic tentacles, mantle-covered shell (with small foramen over umbo), contracted cowl and excurrent siphon. Foot usually completely withdrawn into pallial cavity.

Shell (Figs. 8–11). Thin, transparent to translucent white except for yellow prodissococonch and network of opaque white coloration on early portion; equivalve, showing fine growth lines; oval initially, changing to anteriorly elongate-pointed with angulate corners anteriorly and posteriorly near attachment points of adductor muscles; weak internal radial ribs corresponding in placement to weak

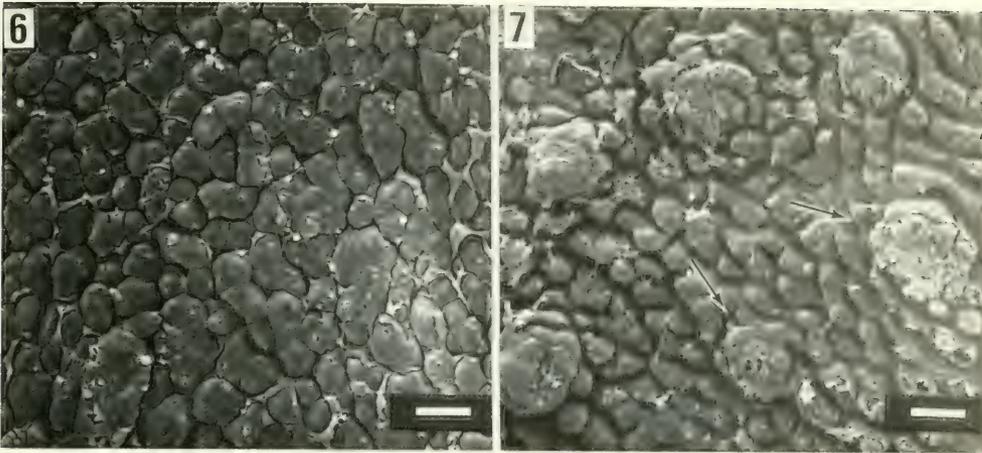


FIGS. 1–5. External appearance and internal shell morphology. 1. *Divariscintilla yoyo* in crawling position, from left side. 2. *D. troglodytes*, same as Fig. 1. 3. *D. yoyo*, internal surface of right valve, showing approximate location of muscle insertions. 4. *D. troglodytes*, same as Fig. 3. 5. *D. yoyo*, in hanging position, from right side. Scale bars: 1, 2, 5 = 2.0 mm; 3, 4 = 1.0 mm. (aam, anterior adductor muscle; apr, anterior pedal retractor muscle; apt, anterior pallial tentacle; bag, byssus adhesive gland; by, byssus; byg, byssus-gland; c, cowli; cpht, cephalic tentacles; ct, ctenidium; exs, excurrent siphon; fl, flower-like organ; ft, foot; mf, point of ventral mantle fusion; mpt, median pallial tentacle; pam, posterior adductor muscle; pef, posterior extension of foot; ppm, pedal protractor muscle; ppr, posterior pedal retractor muscle; ppt, posterior pallial tentacles; sh, shell; uf, umbonal foramen; vgr, ventral groove).

external grooves. Muscle scars indistinct. Hinge (Fig. 10) primarily internal, with weak external ligament, stronger internal resilium and two rudimentary, non-interlocking cardinal teeth; lateral teeth absent. Shell nearly completely enclosed in chamber formed by pallial layers, communicating with exterior via small umbonal foramen (Fig. 1, uf). Periostracal groove lying between inner and outer pallial folds. Size small in relation to body, extending only over dorsal portion of visceral mass; length approximately 40% of relaxed mantle length. Permanently gaping at 110–120° angle while relaxed, incapable of closure more than 50°. Periostracum colorless, most evident as periostracal webbing extending between valves, anterior and posterior to hinge, and at periphery of shell. Shell microstructure (Fig. 11) cross-lamellar, with thin homogeneous layer on either side.

Prodissoconch (Fig. 16) approximately 350 μm in length, having distinct prodissoconch I and prodissoconch II stages; prodissoconch I approximately 140 μm in length, with “granulated” surface sculpture and marginal radial ridges; prodissoconch II stage relatively large, sculptured with distinct concentric ridges. Abrupt demarcation between prodissoconch and dissoconch.

Organs of the pallial cavity: Foot (Figs. 1, 5, 18–19, ft, pef) highly extensible, with hatchet-shaped anterior crawling portion and elongated tubular posterior extension. Anterior portion internally with dorsal haemocoel, sparse longitudinal musculature, and with extensive lateral and ventral external ciliation and accompanying mucous glands (staining turquoise to dark blue in APH). Ventral groove (Figs. 1, 18, 21, vgr) extending from approx-



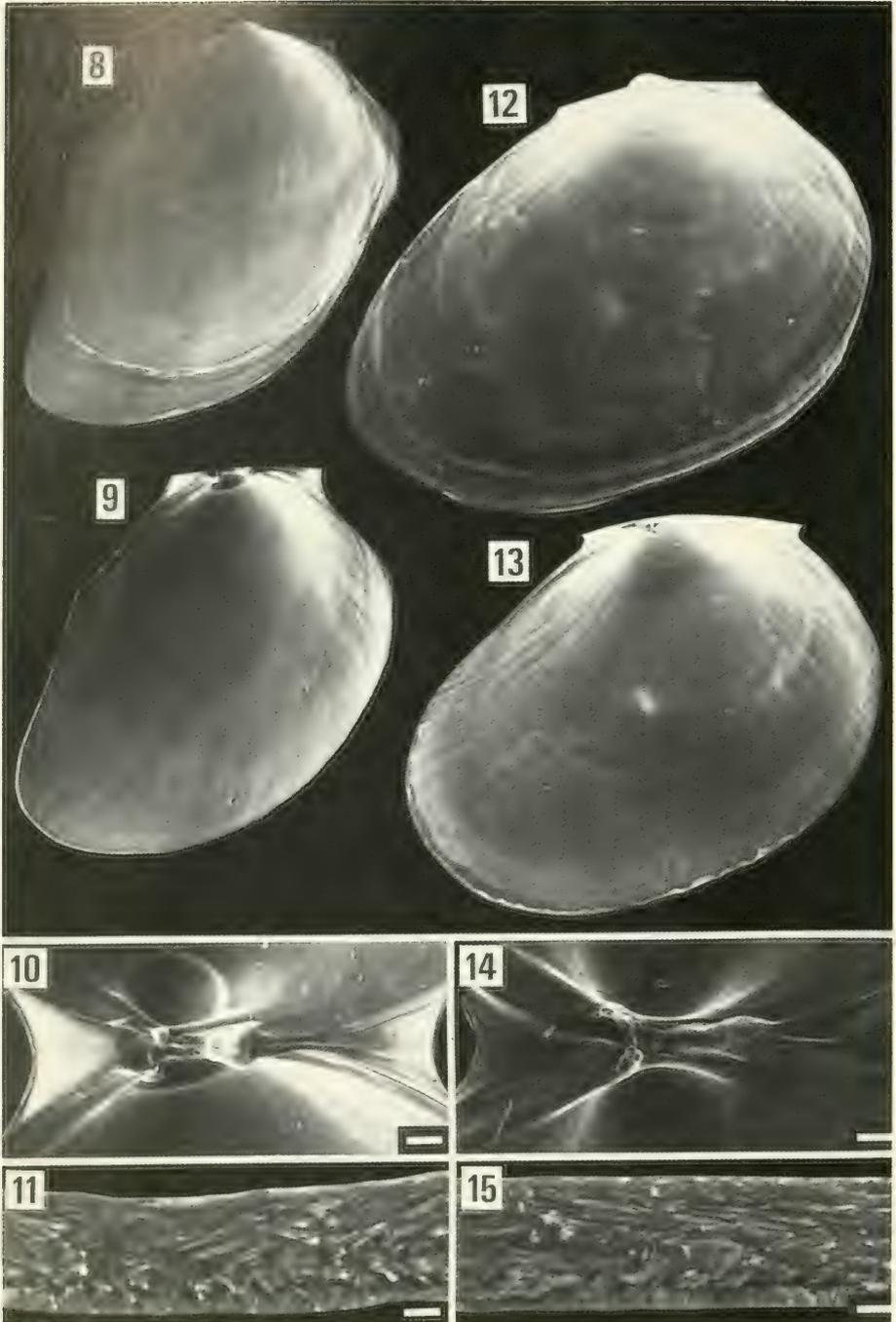
FIGS. 6–7. Exterior pallial surfaces (SEM). 6. *Divariscintilla yoyo*. 7. *D. troglodytes*; arrows indicate enlarged pallial papillae. Scale bars = 50 μ m.

imate midpoint of anterior tip to terminus of posterior extension, heavily ciliated interiorly along entire length. Byssus-gland (Figs. 1, 21, byg) restricted to very small area on either side of ventral groove, a short distance behind anterior end of groove in vicinity of pedal ganglia (see below); closely associated with numerous blood spaces; faintly whitish in living animal, staining dark blue in methylene blue, purple in APH. Posterior extension terminally pointed (Fig. 19), consisting internally largely of longitudinal muscle fibers and connective tissue; proximal half with free edges of ventral groove heavily ciliated externally; external ciliation and accompanying mucous glands disappearing abruptly to leave distal half of posterior extension with ciliation restricted to interior of groove. Byssus adhesive gland [Figs. 1, 22, bag; see Ecology and Behavior (below) for explanation of term] just short of terminus of posterior extension, with internal lamellae surrounding a common lumen; opaque white in living animal, staining dark blue in methylene blue, light purple in APH.

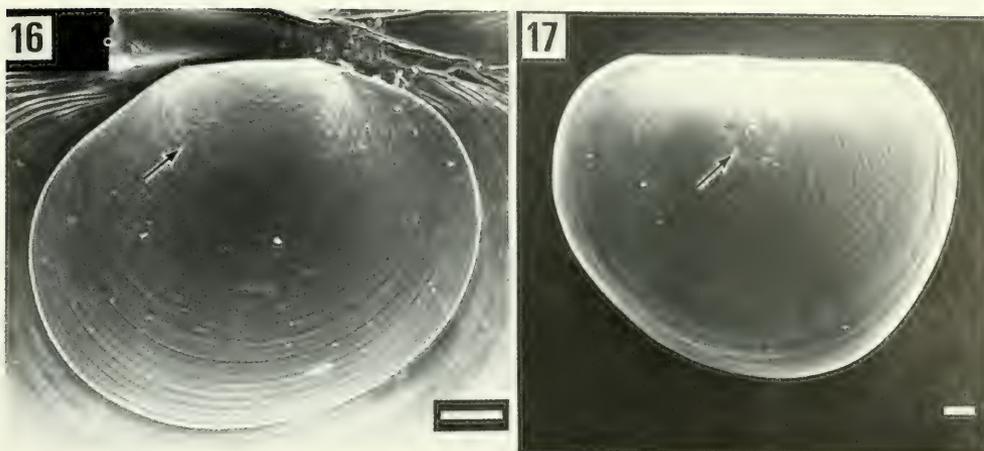
Anterior and posterior adductor muscles subequal, long, of moderate diameter. Attachment ends oval, subequal. Anterior pedal retractor slightly smaller in diameter than, and attaching to shell anterior to, anterior adductor; posterior pedal retractor smaller than, and attaching to shell posterodorsal to, posterior adductor. Very small pedal protractor attaching to shell dorsal to anterior adductor. Integument of visceral mass with numerous

longitudinal muscle fibers, most highly concentrated posteriorly; these continuous with anterior and posterior pairs of pedal retractor muscles, only slightly smaller in diameter than adductor muscles. Small anterior pedal protractor originating ventral to anterior adductor muscle within anterior tissues of digestive gland, passing posterodorsally to insert on shell, dorsal to anterior adductor. Muscles leaving no visible attachment scars on shell; approximate insertion locations shown in Fig. 3.

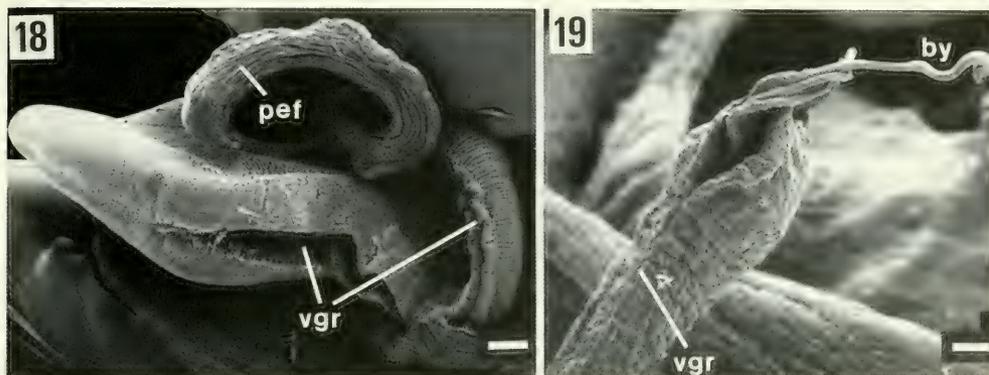
Labial palps (Fig. 28, lp) large, oval, each with 10–14 lamellae each side; each pair fused at midline near mouth. Outer palps attached laterally by elongated strip of tissue to inner surface of mantle lining shell; inner palps similarly attached to surface of visceral mass. Ciliary currents moving particles oralward on inner palp surfaces, laterally toward ctenidia on outer palp surfaces. Ctenidia (Fig. 25) eulamellibranch, homorhabdic, hanging in loosely pleated folds, with numerous filaments; inner and outer demibranchs on each side with both ascending and descending lamellae. Both demibranchs with well-developed, numerous interfilamentary junctions (Fig. 24, ifj; Fig. 25, arrow), and evenly distributed, albeit few, interlamellar junctions (Fig. 24, ilj). Inner demibranch approximately 50% larger, extending farther ventrally and anteriorly than outer, with food groove (Fig. 25, fg) at free edge; anterior end (with terminus of food groove) extending between labial palps. Ventral tips of anterior filaments of in-



FIGS. 8–15. Shells and shell structure (SEM). 8. *Divariscintilla yoyo*, left valve, external view, 3.9 mm [maximum dimension]. 9. *D. yoyo*, right valve, internal view, 3.0 mm. 10. *D. yoyo*, hinge, anterior to left. 11. *D. yoyo*, microstructure, with internal surface at top. 12. *D. troglodytes*, same as Fig. 8, 5.9 mm. 13. *D. troglodytes*, same as Fig. 9, 5.3 mm. 14. *D. troglodytes*, same as Fig. 10. 15. *D. troglodytes*, same as Fig. 11. Scale bars: 10 = 100 μm ; 11, 15 = 5 μm ; 14 = 200 μm .



FIGS. 16–17. Prodissococonch and larval shell morphologies (SEM). 16. Prodissococonch (*Divariscintilla yoyo*); arrow indicates boundary between prodissococonch I and II. 17. Shell of newly hatched larva (*D. troglodytes*); arrow indicates zone of initial shell formation. Scale bars: 16 = 50 μm ; 17 = 10 μm .



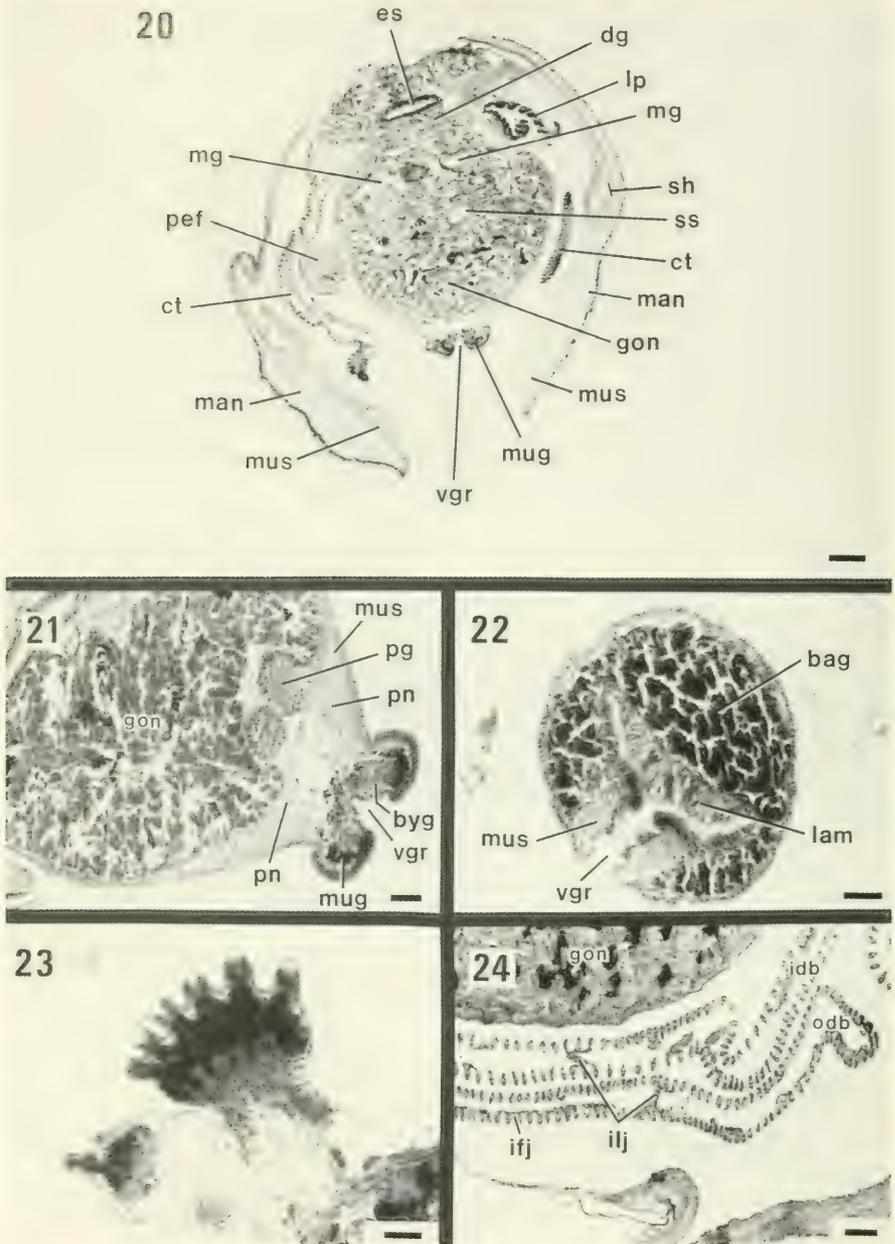
FIGS. 18–19. Foot (SEM). 18. Ventral view of entire foot, showing ventral groove (*Divariscintilla troglodytes*). 19. Terminus of posterior foot extension, showing byssus-threads (*D. yoyo*). Scale bars: 18 = 200 μm ; 19 = 50 μm . (by, byssus; pef, posterior extension; vgr, ventral groove).

ner demibranch "not inserted into a distal oral groove" (Stasek, 1963, Category III); antero-ventral margin of inner demibranch fused to inner palp lamella. Outer demibranch shorter, without food groove; margins inserting between inner and outer labial palps, along upper portion of visceral mass, and on inner surface of mantle to posterior end of pallial cavity. Ciliary currents as in Fig. 30, moving food particles in food groove and in groove between demibranchs oralward. Tract on inner surface of cowl anterior to palps as exit point for removal of waste particles. No cilia

currents evident on inner pallial surface or surface of visceral mass.

Visceral mass of brownish digestive gland anterodorsally, whitish granular-appearing gonad posteriorly, distally, and, in ripe specimens, overlapping digestive tissue laterally and dorsally; red pedal ganglia visible at distal end of gonad in base of foot.

Cluster of 3–7 (most often 5; \bar{x} = 4.7, n = 31) nonretractable "flower-like organs" (Figs. 23, 26) originating on anterior surface of visceral mass just ventral to labial palps. Usually arranged as single organ closest to palps,



FIGS. 20–24. Internal structure, histological sections. 20. Cross-section at level of esophagus and anterior edge of ctenidia (*Divariscintilla yoyo*). 21. Cross-section through foot at region of byssus-gland (*D. yoyo*). 22. Longitudinal section through byssus adhesive gland at terminus of posterior foot extension (*D. yoyo*). 23. Longitudinal thin section through two "flower-like organs" (*D. yoyo*). 24. Cross-section of ctenidium showing interlamellar and interfilamentary junctions (*D. troglodytes*). Scale bars: 20 = 300 μm ; 21, 24 = 100 μm ; 22, 23 = 50 μm . (bag, byssus adhesive gland; byg, byssus-gland; ct, ctenidium; dg, digestive gland; es, esophagus; gon, gonad; idb, inner demibranch; ifj, interfilamentary junctions; ilj, interlamellar junctions; lam, lamellae of byssus adhesive gland; lp, labial palp; man, mantle; mg, midgut; mug, mucous glands; mus, muscle fibers; odb, outer demibranch; pef, posterior extension of foot; pg, pedal ganglia; pn, pedal nerve; sh, shell; ss, style sac; vgr, ventral groove).

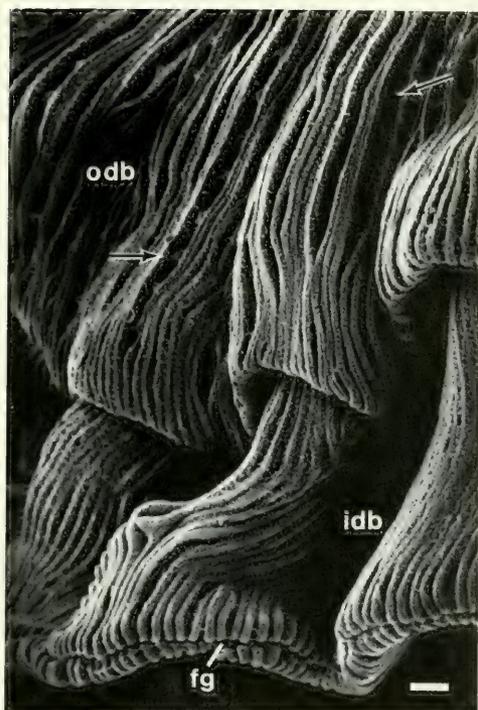


FIG. 25. Ctenidia of *Divariscintilla yoyo* (SEM). Arrows indicate interfilamentary junctions. Scale bar = 100 μm . (fg, food groove of inner demibranch; idb, inner demibranch; odb, outer demibranch).

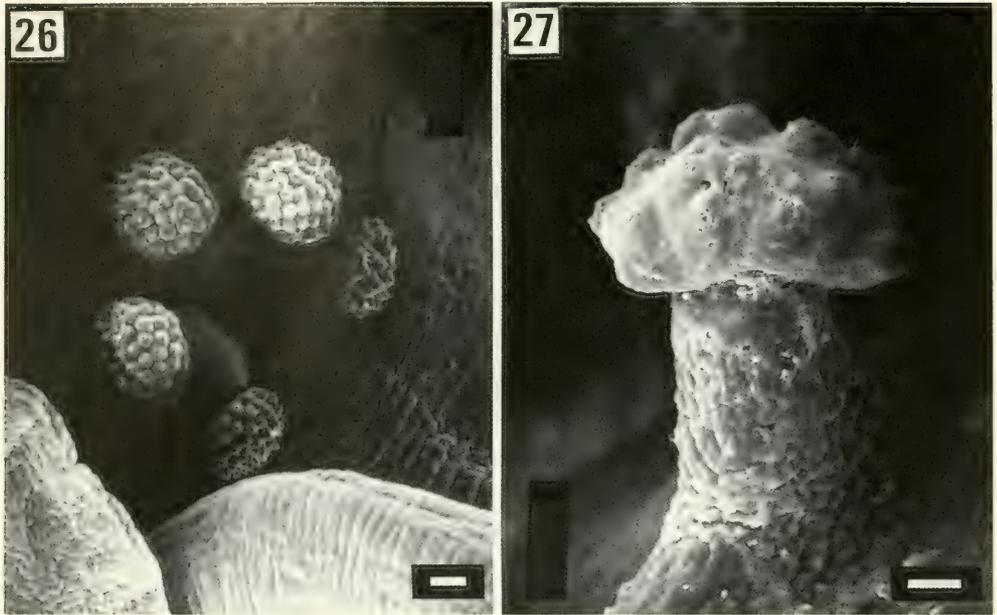
with successive organs commonly originating in pairs, ventral to first; more ventral pairs often slightly smaller. Tendency for more numerous "flower-like organs" in larger specimens (≤ 5 in specimens of shell length < 4.0 mm; ≥ 5 in specimens of shell length > 4.0 mm), but highly variable (smallest specimen = 2.1 mm shell length with 5 organs; largest specimen = 5.8 mm shell length with 5 organs; specimens of 2.6 and 4.7 mm shell length with 7 organs each). Each organ 0.3–0.7 mm in diameter, 0.5 mm in height (including "head" plus stalk); head composed of numerous (80–90), onion-shaped subunits, each opening to exterior via large pore (Fig. 23); homogeneous stalk of blood-filled spongy connective tissue, without lumen and without obvious nervous connection.

Digestive system: Mucous glands embedded in bases of labial palps surrounding mouth and anterior esophagus. Short esoph-

agus leading from mouth into stomach at dorsal center of visceral mass. Stomach (Fig. 28, st) round or oval, slightly elongated antero-posteriorly. Major openings into stomach include those from: (1) esophagus (eso), opening anteriorly, (2) right and left digestive ducts (dd), opening posteroventral to esophageal opening, (3) left pouch (lpch), adjacent to left digestive duct, and associated with shallow dorsal pocket [dorsal hood (dh)], (4) style sac (ss), opening posteroventrally, and (5) midgut (mg), opening just anterior to, but morphologically separate from, style sac. Major typhlosole (ty) on mid-ventral surface of stomach as wide loop extending from midgut and style sac to right digestive duct. Faintly ridged areas (?sorting areas) present, adjacent to esophageal opening and between edge of gastric shield and major typhlosole. Many small ducts to digestive gland opening into right and left digestive ducts and left pouch. Gastric shield (Fig. 28, gs and A) with thickened knob-shaped dorsal projection (upon which crystalline style rotates) attached to tissue flap between left digestive caecum and left pouch; remainder of gastric shield thin, wrapped around dorsal end of crystalline style with dorsal extension forming narrow channel into dorsal hood.

Style sac extending nearly entire length of visceral mass, with ventral tip visible externally within gonadal tissue on left side of foot; internally with typhlosole on anterior wall continuing into stomach and communicating with major typhlosole; crystalline style (Fig. 28, cs) extending entire length of style sac, sharply tapered at distal end. Midgut (mg) with 2–3 loops within anterior part of visceral mass, often visible just below surface of integument on either side; typhlosole initially large, decreasing in size rapidly; extending to distal end of visceral mass on right side, near tip of style sac, where it loops back to pass directly dorsal [as hindgut (hg)] near surface along posterior right side of gonad, leaving visceral mass near region of heart. Rectum (re) passing posteriorly through heart and kidney; rectal glands absent. Anus (Figs. 28, 29, an) positioned just inside excurrent siphon. Fecal strands of irregular length and varying width.

Suprabranchial chamber (Fig. 29). Receives openings of gonad, kidneys and digestive system. Two oval, whitish, glandular patches [?hypobranchial glands (hgl)] on roof of suprabranchial chamber, flanking rectum.

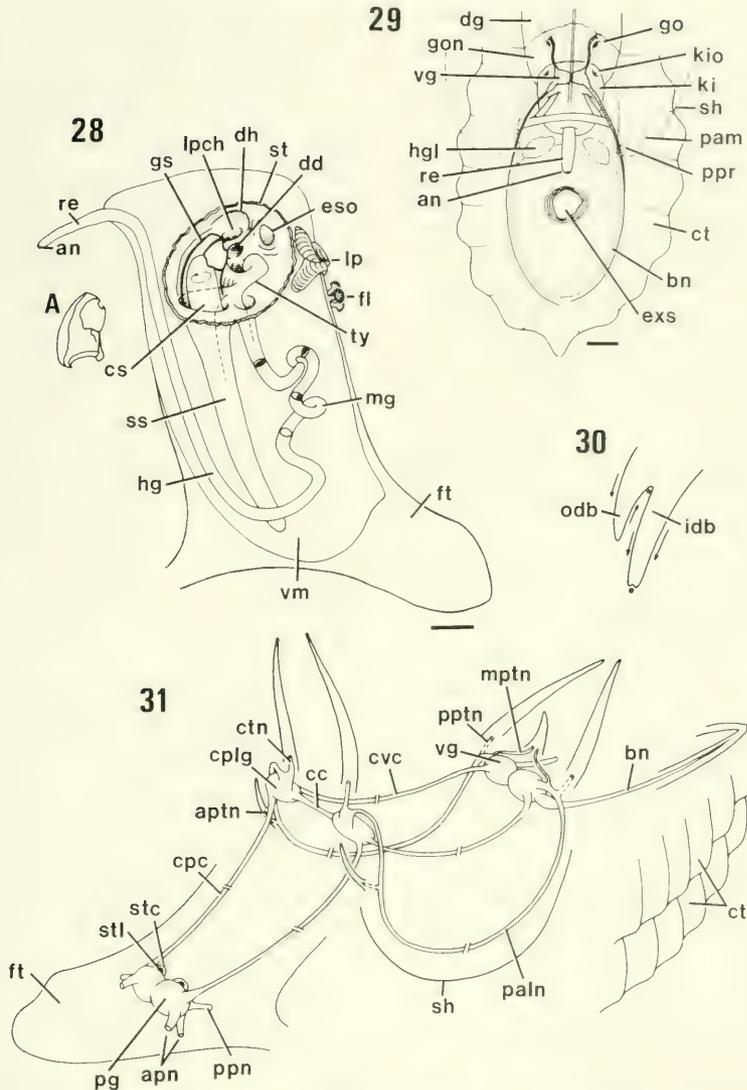


FIGS. 26–27. Flower-like organs (SEM). 26. of *Divariscintilla yoyo*, showing typical number of five, of subequal size. 27. of *D. troglodytes*, in lateral view. Scale bars: 26 = 100 μm ; 27 = 50 μm .

Nervous system (Fig. 31). Nervous system of typical bivalve organization with three pairs of ganglia, red in living animal, connected by long commissures. Ganglia relatively large, subequal (length approximately 0.4 mm), cerebropleural ganglia more elongate than others. Cerebropleural ganglia (cplg) lying just anteroventral to anterior adductor muscle, dorsal to esophagus; cerebral commissure (cc) short; each ganglion giving rise to three additional major branches: (1) dorsally, common trunk giving rise to cephalic tentacular nerve (ctn) leading to cephalic tentacle, and pallial nerve (paln) leading to ventral shell edge as a continuous cord (to visceral ganglion) with numerous smaller nerves extending into mantle tissue; (2) ventrally, cerebropleural-pedal commissure (cpc) passing between visceral mass and integument along anterior face of foot, penetrating gonadal tissue distally to join with pedal ganglion; and (3) laterally, cerebrovisceral commissure (cvc) passing through upper portion of visceral mass to visceral ganglion. Pedal ganglia (Figs. 21, 31, pg) closely fused at midline; showing through integument of foot in living animal as red organ at extreme distal end of gonad; each dorsally receiving cerebropedal commissure from cerebropleural ganglion;

each ventrally giving rise to two anterior and one posterior pedal nerves. Statocyst (Fig. 31, stc) on posterodorsal face of each pedal ganglion; each with one spherical statolith (stl) 50 μm in diameter. Visceral ganglia (vg) joined together at midline (but not as closely fused as pedal ganglia), lying ventral to heart, posteroventral to posterior adductor muscle; each receiving cerebrovisceral commissure (anterolaterally) and pallial nerve (dorsolaterally) from cerebropleural ganglion; each giving rise ventrolaterally to branchial nerve (with somewhat swollen base), which extends along common axis of inner and outer demi-branches of ctenidium.

Reproductive system: Simultaneous hermaphrodite. Ototestis white, encompassing most of volume of visceral mass, extending from small portion in umbonal area, down posterior surface of digestive gland, and expanding to surround pedal ganglia and ventral extensions of style sac and intestinal loops. "Spent" appearance sparse, with pedal ganglia fully exposed at terminus, and with silvery ducts clearly visible, packed with mature spermatozoa. Common genital ducts with large ciliated openings, emptying into supra-



FIGS. 28–31. Anatomical structures in *Divariscintilla* species. 28. Visceral mass, from right side, showing stomach, opened laterally. Midgut (mg) with four cross-sections, showing reduction of typhlosole. (A) = gastric shield, excised. 29. Roof of suprabranchial chamber, with anterior end up and inner lamellae of right and left inner demibranchs removed. 30. Diagrammatic representation of tentidial demibranchs in cross-section, showing ciliary currents. 31. Nervous system (semi-diagrammatic). Tentacles with nerves drawn as broken lines present only in *D. troglodytes*; remainder identical for both species. Sizes of ganglia and lengths of nerves not drawn to scale. Scale bars = 1.0 mm. (an, anus; apn, anterior pedal nerves; aptn, anterior pallial tentacular nerve; bn, branchial nerve; cc, cerebropleural commissure; cpc, cerebropleural-pedal commissure; cs, crystalline style; cplg, cerebropleural ganglion; ct, ctenidium; ctn, cephalic tentacular nerve; cvc, cerebropleural-visceral commissure; dd, right and left digestive ducts; dg, digestive gland; dh, dorsal hood; eso, esophageal opening; exs, excurrent siphon; fl, flower-like organs; ft, foot; go, gonadal opening; gon, gonad; gs, gastric shield; hg, hindgut; hgl, ?hypobranchial gland; idb, inner tentidial demibranch; ki, kidney; kio, kidney opening; lp, labial palps; lpch, left pouch; mg, midgut; mptn, median pallial tentacular nerve; odb, outer tentidial demibranch; paln, pallial nerve; pam, posterior adductor muscle; pg, pedal ganglion; ppn, posterior pedal nerve; ppr, posterior pedal retractor muscle; pptn, pallial tentacular nerve; re, rectum; sh, shell; ss, style sac; st, stomach; stc, statocyst; stl, statolith; ty, major typhlosole; vg, visceral ganglion; vm, visceral mass).

branchial chamber just anterior to visceral ganglia (Fig. 29, go).

Ova small, approximately 20 μm in diameter (maturity not determined, measured in paraffin sections, in posterodorsal region of gonad). Spermatozoa approximately 7 μm in head length (acrosome + nucleus + middle piece); nucleus cylindrical, asymmetrical; acrosome subterminal, dish-shaped with central "papilla," tilted approximately 45° from long axis of nucleus; middle piece short; tail long. Gametes and gametogenesis to be described in detail in a paper currently in preparation.

Brooding large number of small larvae for an undetermined period (longest time observed 14 days). Larvae held primarily within outer demibranch, and in suprabranchial chamber where they are circulated via pallial expansions and contractions. During brooding, excurrent siphonal opening constricted by sphincter-like muscles around plug formed by free end of rectum (often expanded into bulb by haemocoelic pressure), allowing digestive processes to continue during brooding and preventing loss of larvae through excurrent siphon. Larvae initially white, turning pink with shell development; released as straight-hinged veligers with apical flagella, 122–138 μm in shell length (\bar{x} = 131.8 μm , n = 20; Fig. 17). Larval shell with distinct zone of initial shell formation (Fig. 17, arrow). Larvae expelled through excurrent siphon via strong contractions of shell and pallial muscles. Adults brooding larvae collected in May and June 1987, and April 1988.

Circulatory system: Heart just posterior to umbones, within pericardium lined by brownish pericardial gland. Doughnut-shaped ventricle traversed by intestine; auricles lateral to ventricle, inconspicuous. Blood vessels not evident; major haemocoelic spaces present within foot, tentacles and main axes of demibranchs.

Excretory system: Kidney yellow, ventral to heart, dorsal to visceral ganglia, surrounding pedal retractor muscles on roof of suprabranchial chamber. Paired ciliated renopericardial apertures opening anteriorly into ventral wall of pericardium. Paired renal openings into the suprabranchial chamber large, funnel-shaped, adjacent to visceral ganglia.

Distribution: Known only from the type locality, Ft. Pierce Inlet, St. Lucie County, and

one other location approximately 45 km north, Sebastian Inlet, Brevard County, Florida.

Etymology: A noun in apposition from the English vernacular "yo-yo," a child's toy originating in China about 1000 B.C., referring here to the periodic up-and-down motion of the bivalve as it hangs from its byssus-thread. The word "yo-yo" is in Tagalog, an Indonesian language, for a similarly constructed, sixteenth-century hunter's weapon made of large wooden disks and twine.

DIVARISCINTILLA TROGLODYTES, SP.
NOV. (FIGS. 2, 4, 7, 12–15, 27).

Material examined: Holotype: 7.7 mm [preserved mantle length], USNM 860038. Paratypes (9): 6.7, 4.5 mm, USNM 860039; 6.8, 6.6 mm, MCZ 297407; 7.0, 5.0 mm, IRCZM 064:01722; 4.9, 4.8, 4.5 mm, DMNH 175517. Total material: 87 specimens: FLORIDA: Ft. Pierce Inlet: 10 March 1987, 1; 2–3 May 1987, 12 (including MCZ paratypes); 24 June 1987, 12; 03 August 1987, 4; 14 August 1987, 7; 31 August 1987, 13 (including USNM and IRCZM type specimens); 28 December 1987, 6; 11 March 1988, 6; 12 April 1988, 13. — Sebastian Inlet: 30 December 1987, 13 (including DMNH paratypes).

Type locality. Ft. Pierce Inlet, St. Lucie County, Florida, 27°28.3'N, 80°17.9'W, in *Lysiosquilla scabricauda* burrows on intertidal sand flats with patches of the seagrass *Halodule wrightii* Ascherson.

Diagnosis

Animal translucent yellowish-white. Mantle thin, surface granular with numerous evenly distributed short papillae. Two long "cephalic" tentacles; two short anterior pallial tentacles; three long posterior pallial tentacles surrounding posterodorsal excurrent siphon. Shell oval, elongate-rounded anteriorly, with weak internal ribs, length approximately 50% of extended mantle length. A single "flower-like organ" on anterior surface of visceral mass ventral to labial palps.

Description

External features and mantle: Living extended animal (Fig. 2) 10–15 mm in length, globular to oval in general shape, translucent white to yellowish, except for dark upper portion of digestive gland showing through tis-

sues. Shell nearly completely enclosed by relatively thin mantle, clearly revealing outlines of shell and ctenidia. Extended mantle somewhat posteriorly elongated, with granular surface and numerous, evenly distributed, short papillae (Fig. 7, arrows). Anteropodal pallial opening and cowl as in *Divariscintilla yoyo*. Two long, retractable, "cephalic" tentacles anterodorsally just behind cowl; two shorter, retractable anterior pallial tentacles originating laterally to cephalic pair. Posterodorsal excurrent siphon on prominent rounded protuberance; pallial fusion as in *Divariscintilla yoyo*. Three long posterior pallial tentacles surrounding excurrent siphon: one anterior and mid-dorsal, two lateral. Umbonal foramen (Fig. 2, uf) a transverse slit-like opening, capable of distention during periods of stress to expose nearly entire shell.

Preserved animals with shell nearly completely exposed by retraction of umbonal foramen, retracted pallial tentacles, contracted cowl and excurrent siphon. Foot often anteriorly protruding from pallial cavity.

Shell (Figs. 12–15). Nearly completely enclosed in chamber formed by pallial layers, communicating with exterior via slit-like umbonal foramen (Fig. 2, uf). Shell length approximately 50% of relaxed mantle length, extending over dorsal half of visceral mass, and anterior portion of ctenidia. Permanently gaping at 80–120° angle while relaxed, incapable of closure more than 50°. Shell (Figs. 12–13) thin, transparent to translucent white except for yellow prodissoconch and network of opaque white coloration on early portion; equivalve, oval, roundly elongated anteriorly, showing fine growth lines; weak internal radial ribs strongest at periphery, corresponding in placement to weak external grooves. Slightly scalloped edge formed by ends of radial ribs, also evident on former heavier growth lines. Periostracum, hinge (Fig. 14), internal muscle scars (Fig. 4), prodissoconch, and microstructure (Fig. 15) as in *Divariscintilla yoyo*.

Organs of the pallial cavity: Foot, visceral mass, and ctenidia as in *Divariscintilla yoyo*. Labial palps of same general structure as those of *D. yoyo*, but each with more numerous (14–20) lamellae each side. Adductor, pedal, and internal pallial musculature similar to that in *D. yoyo*. Core muscle bundles of all tentacles continuous with pallial muscle layer; single posterior tentacle receiving muscles

from both sides of midline. "Flower-like organ" (Fig. 27) always single, similar in general size and form to those of *D. yoyo*, head with fewer (approximately 25) subunits.

Nervous system: As described for *Divariscintilla yoyo*. Anterolateral and paired posterior tentacles, as well as single posterior tentacle receiving innervation from branches of the pallial nerve (Fig. 31, aptn, mptn, pptn).

Reproductive system: Simultaneous hermaphrodite. Ovotestis, ova and spermatozoa as in *Divariscintilla yoyo*. Gametes and gametogenesis to be described in detail in a paper currently in preparation.

Divariscintilla troglodytes broods its larvae in the suprabranchial chamber and outer demibranch as in *D. yoyo* for an undetermined period (longest time observed 29 days). Adults brooding larvae were collected in June and December 1987. White larvae with initial stages of shell measured at 68 μm diameter. Newly released straight-hinged veligers 120–130 μm in length (\bar{x} = 126.1 μm , n = 20).

Digestive, circulatory and excretory systems: As described for *Divariscintilla yoyo*.

Distribution: Same as that of *Divariscintilla yoyo*.

Etymology: A noun in apposition from the Greek τρογλοδυτης = troglodytes, a hole- or cave-dweller.

ECOLOGY AND BEHAVIOR

Neither *Divariscintilla yoyo* nor *D. troglodytes* was ever found actually attached to a stomatopod, either in the field or in museum specimens (IRCZM). They are assumed to be free-living within the burrow near the opening(s), although specimens were never visible at the opening prior to pumping. However, in spite of other burrowing invertebrates in the area (callianassid shrimps, polychaetes, sipunculans), neither *Divariscintilla* species has ever been collected in any habitat other than a *Lysiosquilla* burrow. The two species were often collected together [and often also with two species of vitrinellid gastropods (Bieler & Mikkelsen, 1988) and two of another galeommatid genus] from a single *Lysiosquilla* burrow (of 21 burrows with *Divariscintilla*, 12 con-

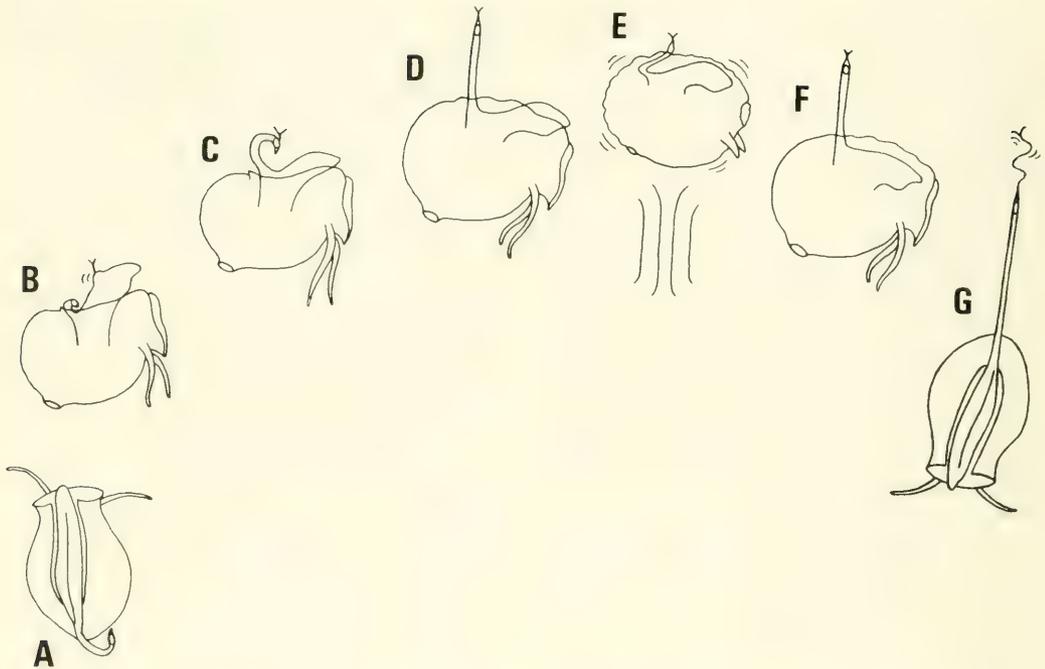


Fig. 32. Diagrammatic representation of (A) crawling, (B,C) byssus-thread production, (D) hanging, (E,F) "yoyo" response to stimuli, and (G) crawling to break byssus attachment.

tained both, 9 contained only one species). Densities were low, frequently of only one or two specimens per species per burrow sample; the highest number of specimens in one burrow was 13 in the case of either species, and not all burrow samples included galeommatodeans. However, it must be noted that in no case was an entire stomatopod burrow excavated and assessed for mollusks; the yabby pump only effectively samples its own length (0.5–1.0 m) of the burrow adjacent to an opening. Estimates of occurrence and/or density of any clams living in the deeper horizontal section of the burrow was not possible using this method.

Small (0.5 mm length) parasitic worms (Trematoda: ?Digenea) were found encased in small tissue pockets on the pallial layer lining the inner shell surface of a specimen of *Divariscintilla troglodytes*. Density per clam and frequency of occurrence were not assessed.

Living animals spend much of their time in the laboratory "hanging" from byssus-threads from the water surface, or, more frequently, on the sides of the aquarium or finger bowl. The hanging sequence is depicted in Fig. 32.

The byssus-threads (usually two) are produced by the byssus-gland located in the crawling portion of the foot (Fig. 19). Strong pulsing of the byssus-gland area during thread production (Fig. 32, b) is probably caused by engorgement of the many blood spaces in the vicinity; this area remains somewhat swollen for a short time after completion. The threads are attached immediately to the substrate, usually with a V-shaped attachment. As they are completed, the threads appear to be "picked up" (Fig. 32, c) by the byssus adhesive gland at the terminus of the posterior elongation so that they are secured within the ventral groove between the two glands; details of this process are unclear. The "hanging" animal thereafter appears to be suspended from the posterior tip of the foot (Figs. 5; 32, d). While relaxed in this posture, the tentacles and posterior siphon are extended, the ventral edges of the cowl are pursed together forming a functional incurrent siphon, and the crawling portion of the foot is partially withdrawn into the pallial cavity. Periodically, and especially in response to external stimuli, the adductor muscles, and muscles of the mantle, tentacles and foot contract

simultaneously producing rapid movement upward toward the byssus attachment point. This is followed by gradual relaxation and return to the resting/feeding posture. This action (Fig. 32, e,f) resembles the up-and-down motion produced with a child's yo-yo toy, and suggested the name for one of the species described here.

During normal "hanging," the posterior foot extension is capable of stretching to a length approximately 1–2 times the mantle length. One specimen of *Divariscintilla troglodytes*, whose byssus adhesive gland was accidentally severed during examination, was able to produce a byssus-thread and hang, although the threads did not lie within the full extent of the ventral groove; the distal half of the posterior extension remained curled at the side of the animal, unextended and unused. These observations lead to the conclusion that the glandular structure at the terminus of the posterior foot extension serves to secure the byssus-threads within the full length of the ventral groove. It is likely that this gland secretes an adhesive substance for this purpose, therefore we refer to it here as the "byssus adhesive gland." The fact that the injured animal could still use part of the ventral groove for hanging suggests that the extensive ciliation and mucous secretion of the proximal part of the groove also serve to secure the threads. This specimen was maintained and observed in the laboratory; two weeks after severing the tip of the posterior extension, the animal was observed to be hanging normally and the tip of the foot with its whitish gland had regenerated and regained function.

When dislodged, the clams actively crawl about, using an even, gliding motion produced by ciliary action on the ventral surface of the foot. Sudden contractions of the shell and pallial muscles frequently occur during crawling, and, although not providing any significant forward propulsion, probably assist the animal in moving its not-so-streamlined body, as well as in cleansing the pallial cavity. The anterior unslit tip of the foot is continually actively "seeking" appropriate substrate. The terminal half of the posterior extension, which is unciliated externally, is not active in crawling, being carried behind either in a trailing curl or with the tip barely touching the substrate behind. The clams were observed to dislodge themselves voluntarily from laboratory substrate via initiation of crawling activity, thus stretching the byssus-threads until breaking occurred (Fig. 32, g). It is assumed

from laboratory observations that the animals spend most of their time in the burrows attached to the smoothly packed walls, and that crawling is utilized only when relocation is necessary or when dislodged by external forces.

DISCUSSION

The two new species described here are remarkably similar to each other in morphology and behavior. Significant differences are found in shell morphology, the number of "flower-like organs," and the nature of the mantle, including color, thickness, papillation, and number of pallial tentacles (Table 1). Thus far, both species are known only from the specimens studied and cited here; shells are unknown from dry collections (AMNH, DMNH, IRCZM, USNM), probably because of their fragile nature.

The two new species agree closely in anatomy, habitat, and behavior with those described for *Divariscintilla maoria* Powell, 1932, type and sole described species of the genus, by Judd (1971). Some of the features reported here (e.g. stomach, nervous system, reproductive anatomy, shell musculature, circulatory and excretory systems) were not discussed for *D. maoria*, and others (e.g. ctenidia, "flower-like organ," byssus apparatus) were described in less detail (Judd, 1971). Differences between our two species and *D. maoria* in shell, pallial, and perhaps ctenidial characters (see below; Table 1) are weak when weighed against the many similarities, and, we accordingly place our new species in *Divariscintilla*.

Shell and musculature: The most distinct difference between the two species described here and the type species of *Divariscintilla* is in the shape of the shell. *Divariscintilla maoria* has a ventral notch in each valve, a character used at the generic level (Chavan, 1969) to treat *Divariscintilla* as a subgenus under *Vasconiella* Dall, 1899, whose members possess a likewise-notched shell. The shell of *Vasconiella jeffreysiana* (P. Fischer, 1873), the type and sole described species of the genus, however, is greatly inequivalve and notched in only the right valve (Kisch, 1958). As noted by Judd (1971: 344), the ventral notch of *Divariscintilla maoria* "does not appear to be functionally important," as it is not associated with a cleft in the mantle nor with the passage

TABLE 1. Distinguishing characteristics of the three described species of *Divariscintilla* (for additional information, see text).

	<i>D. maoria</i> (from Judd, 1971)	<i>D. yoyo</i>	<i>D. troglodytes</i>
Shell:			
General shape	oval	elongate-pointed	oval
Prolongation	ventrally notched	unnotched	unnotched
Sculpture	posterior	anterior	anterior
Length relative to mantle length	unribbed	unribbed	internal radial ribs
Mantle:	68%	40%	50%
Color, thickness	(not given)	whitish, thick	yellowish, thin
Extent covering shell	margins only	entire	entire
Papillae	very small	sparse, very small	numerous, small, evenly-distributed
Anterior tentacles	4 long	2 long	2 short, 2 long
Posterior tentacles	1 long	1 very short	3 long
Defensive appendages	6-8 present	absent	absent
Flower-like organs:			
number	1	3-7 (usually 5)	1
Ctenidia:	smooth	pleated	pleated
Labial palps:			
Lamellae per palp	(not given)	10-14	14-20
Geographical range:	New Zealand	eastern Florida	eastern Florida

of byssus-threads. Therefore, we do not consider the presence of this notch a prerequisite to inclusion in *Divariscintilla* and furthermore do not advocate treatment of *Divariscintilla* as a subgenus of *Vasconiella* on this basis. Claims of a "tendency" within the family for the development of a concave or indented ventral shell margin (Powell, 1932; J.E. Morton, 1957) appear overstated; a cursory survey of the galeommatid shells illustrated by Chavan (1969) show that most are evenly rounded at the ventral margin.

A second conchological difference between *Divariscintilla maoria* and the two new species is the direction of prolongation of the shell. All are skewed, but in opposite directions; *D. maoria* is prolonged posteriorly while *D. yoyo* and *D. troglodytes* are prolonged anteriorly.

Divariscintilla maoria also has a relatively larger shell in relation to its body (maximum shell length approximately 68% of the relaxed mantle length in fig. 1 of Judd, 1971), which also differs by being covered by pallial folds only along its margins. The degree of shell reduction and internalization in members of this superfamily varies widely and is a character which deserves further attention at supraspecific levels.

Divariscintilla yoyo and *D. troglodytes* both possess the full complement of five major

muscles (e.g. two adductors, two pedal retractors, and one protractor). As in *D. maoria* (see Powell, 1932), these leave no muscle scars on the shell, even to the extent, realized during this study, that they do not show under scanning electron microscopy.

Mantle ornamentation: The complement of pallial tentacles and papillae is quite different in *Divariscintilla maoria* and the two new species described here. The two pairs of anterior tentacles and the single posterior tentacle of *D. maoria*, described by Judd (1971), seem homologous to tentacles described in this study. However, *D. yoyo* and *D. troglodytes* do not possess anything resembling the "posterior appendages" described by Judd (1971). They do, however, possess numerous papillae on the exterior portion of the mantle, beyond the shell margins; this area is without papillae in *D. maoria*.

Ctenidia: As shown in Judd (1971: fig. 3) and confirmed here (Fig. 30), the ciliary currents of the ctenidia in *Divariscintilla* can be ascribed to type C(1) as defined by Atkins (1937). This type, in which only the inner demibranch bears a ventral marginal food groove, is known from a great number of genera (e.g., *Galeomma*: B. Morton, 1973; *Ceratobornia* Dall, 1899; Narchi, 1966). Also like

most other galeommatoideans, the outer demibranch is shorter in *Divariscintilla*, and interfilamentary junctions are well-developed and numerous. The presence of interlamellar junctions in *Divariscintilla* (this study; no data available for the type species), contradicting a statement by B. Morton (1973: 142) that the presence of interfilamentary and the lack of interlamellar junctions "is typical of the Leptonacea [= Galeommatoidea] in general and can be correlated with the habit of incubating their larvae within the ctenidia . . ." (see also B. Morton, 1981: 97–99). *Divariscintilla* does show, however, a negative correlation between the number of interlamellar junctions and the incubatory habit (see also Oldfield, 1961: 290).

In gross morphology, the gills of *Divariscintilla yoyo* and *D. troglodytes* contrast with those of *D. maoria* and nearly all other galeommatoideans in being loosely pleated rather than smooth. This may be an adaptation for increasing surface area of the food-gathering structures of animals in habitats (e.g. burrows) that may present reduced food density. Pleating was also observed by Popham (1939) in *Phlyctaenachlamys lysio-squillina* Popham, 1939, another burrow-dwelling commensal, although it was interpreted as an artifact due to preservation.

Flower-like organs: The function of the "flower-like organs" of *Divariscintilla* species is not evident, although the presence of glandular tissues in the flower head plus the lack of nervous connections point to a secretory rather than sensory role. Judd (1971: 352) described a single "small median papilla on the dorsal edge of the anterior part" of the visceral mass of *D. maoria* which is clearly the same structure. No function was suggested by Judd, however, reference to a "mucoid secretion" from subepithelial gland cells agrees with this study that the organs are generally secretory. The "flower-like organs" could possibly emit a pheromone for attracting reproductive partners in conditions of low population densities. If so, their placement at the *incurrent* opening, requiring flow of the attractant *through* the animal prior to release, is indeed peculiar.

"Flower-like organs" have not been reported in any other galeommatoidean genus. However, the pheromone organ and defensive papillae of *Chlamydoconcha orcutti* Dall, 1884 (see B. Morton, 1981), bear at least superficial resemblance. They cannot be con-

sidered homologous, because the structures described for *C. orcutti* arise from the middle pallial fold, while *Divariscintilla*'s "flower-like organs" are from the surface of the visceral mass. Also unlike the organs of *C. orcutti*, the "flower-like organs" of *Divariscintilla* are not retractable.

Stomach and feeding: The structure of the stomach was not discussed by Judd (1971) in the redescription of *Divariscintilla maoria*. Stomach structure in the two species described here agrees well with those of others in this superfamily (e.g. *Phlyctaenachlamys* Popham, 1939; *Galeomma*: B. Morton, 1973), defined as type IV by Purchon (1958). Major common features include complete separation of the midgut from the style sac (exceptions are *Pseudopythina* P. Fischer, 1884: B. Morton; 1972, and *Montacutona* Yamamoto & Habe, 1959; B. Morton, 1980), and an arch-shaped major typhlosole leading toward the openings to the digestive diverticula. Variation occurs in the degree of concentration of these latter openings into caeca or ducts, and in the extent of the typhlosole in the midgut.

Reproduction: Galeommatoideans are frequently cited as having "the most complex reproductive patterns in the Bivalvia" (Ó Foighil & Gibson, 1984: 72). Hermaphroditism, the occurrence of dwarf or "complemental" males, and ctenidial brooding of larvae are common features of this superfamily and have been claimed to be trends associated with a commensal mode of life (B. Morton, 1976; Ó Foighil, 1985). No data were presented on the reproductive biology of *Divariscintilla maoria* by Judd (1971: 349) other than noting the incubation of larvae in the "exhalant chamber." The two *Divariscintilla* species described here were both found to brood their young within the folds of the outer demibranch as well as in the suprabranchial chamber. Both species are simultaneous hermaphrodites. The most unusual reproductive feature encountered was the morphology of the spermatozoa which exhibit rotational asymmetry: the dish-shaped acrosome is tilted approximately 45° from the long axis of the cylindrical nucleus.

Foot and locomotion: All galeommatoideans are capable of active, snail-like locomotion, and most (e.g. *Galeomma* and *Kellia* Turton, 1822: Popham, 1940) possess a blunt, heel-like posterior foot with a ventral

groove and a more-or-less postero-terminal byssus-gland. *Divariscintilla* differs from the typical, but is not unique in having an elongated posterior foot; this feature is also present in *Phlyctaenachlamys*, *Rhamphidonta* Bernard, 1975, and *Ceratobornia*. The foot of *Phlyctaenachlamys* (Popham, 1939) is nearly identical to that of *Divariscintilla*, with an elongated posterior portion and a whitish organ at the terminus. In *Phlyctaenachlamys*, the byssus-gland (although likewise concentrated in the central portion) continues throughout the posterior extension (Popham, 1939); the "opaque white area immediately short of the tip" of the posterior extension (Popham, 1939: 64) may be similar to the byssus adhesive gland of *Divariscintilla*, although "hanging" behavior has not been described for *Phlyctaenachlamys*.

The byssus-gland in the elongated posterior foot of *Rhamphidonta retifera* (Dall, 1899) was vaguely described by Bernard (1975) as centrally located; this posterior extension is very different from those discussed above in being dorsoventrally flattened and wider than the anterior portion. "Hanging" behavior was not mentioned by Bernard (1975) for *Rhamphidonta*.

Members of both described species of *Ceratobornia*, *C. longipes* (Stimpson, 1855) and *C. cema* Narchi, 1966, are capable of hanging from a highly extensible posterior foot; the byssus-gland has been described at the extreme posterior tip in both [for *C. longipes*, see Dall, 1899: 889, pl.88, figs. 10, 11, 13 (previously unpublished figures of Stimpson); for *C. cema*, see Narchi, 1966: 515, 517–518, text-figs. 2, 5]. However, the byssus apparatus in *Ceratobornia* may deserve reinvestigation in light of the structures found in *Divariscintilla*. Narchi (1966: 518, fig. 5) provided confusing statements about the midventral "main mucous gland" and byssus-gland of *Ceratobornia cema*, with the latter both at the extreme posterior in a text-figure and "extend[ing] along the groove throughout the posterior portion, excepting for the tip" in the text. The "byssogenous [sic] lamellae" described for the byssus-gland of *C. cema* bear greater resemblance to *Divariscintilla*'s byssus adhesive gland than to the byssus-gland proper. Stimpson (1855: 112) reported that, in *C. longipes*, "there is no true byssus" although a "glutinous substance" secreted by the "opaque byssal gland" at the posterior terminus "may be slightly drawn out"; this material was re-interpreted by Dall (1899: 889) as a "single byssal thread."

In *Divariscintilla maoria*, the white organ at the end of the posterior extension was interpreted as the byssus-gland, secreting a single thread by which the animal "hangs." In view of the present interpretation of the foot of the two new species, this seems in need of re-investigation.

The members of *Divariscintilla*, *Phlyctaenachlamys*, and *Ceratobornia* have all been described as inhabiting the holes of burrowing invertebrates (Stimpson, 1855; Popham, 1939; Narchi, 1966); although the location of the byssus-gland apparently differs, the ability to hang from an extensible, thread-like foot may be an advantage in attachment to vertical walls. [However, other galeommatoids that lack this feature also inhabit holes, e.g. three species referable to *Scintilla* Deshayes, 1856, from these same *Lysiosquilla* burrows (Mikkelsen & Bieler, pers. obs.).] *Ceratobornia cema* was also reported to attach "temporarily to the body of the shrimp [*Callinassa major* Say]" (Narchi, 1966: 522), although details of this attachment were not given.

The byssus apparatus of *Kellia suborbicularis* (Montague, 1803) and of *Montacuta substriata* (Montagu, 1808) described by Oldfield (1961: 269–270, figs. 5, 7), each consist of a "subsidiary" byssus-gland dorsal to the ventral groove of the foot, plus a "main" byssus-gland with "byssogenous lamellae" equipped with a duct to the posterior "heel." These bear superficial resemblance to the foot of *Divariscintilla*, but need behavioral observations and more detailed histological examination for proper comparison.

The supportive "chondroid wedge" described for *Ceratobornia cema*, *Rhamphidonta retifera*, and several other galeommatoids (Narchi, 1966; Bernard, 1975) is not present in *Divariscintilla*.

Although extremely similar in gross morphology, the anterior foot of *Divariscintilla* is not the "compact mass of muscle" described for *Phlyctaenachlamys* by Popham (1939). Longitudinal muscle fibers are sparse in the anterior foot of *Divariscintilla*, being more concentrated in the posterior extension. Extension of the anterior tip is apparently accomplished by haemocoelic pressure.

The crawling activity of many galeommatoids (e.g. *Montacuta* Turton, 1822; Gage, 1968a; *Mysella* Angas, 1877; Gage, 1968b) has been described roughly as an extend-attach-pull forward sequence. *Divariscintilla*, in contrast, relies primarily on ciliary action for

forward crawling movement. Propulsive shell and pallial muscle contractions assist locomotion in *Phlyctaenachlamys* (Popham, 1939) and *Galeomma* (B. Morton, 1973), and at least to some extent in *Divariscintilla*. During these contractions in *Divariscintilla*, the relatively large adductor muscles partially close the shell, reducing the shell angle by about 50%. This is in contrast to the "poorly developed" adductor muscles of *Phlyctaenachlamys*, contraction of which causes "little movement of the shell valves" (Popham, 1939: 67). Retention of well-developed adductor muscles in *Divariscintilla* may have been favored by providing additional water-propelling force for locomotion and cleansing of the pallial cavity.

Commensalism: The nature of the association between these bivalves and their stomatopod "host" is unclear. Although apparently more dependent upon the burrow habitat than on the resident stomatopod, collection records suggest a strongly obligatory association with *Lysiosquilla* for both new *Divariscintilla* species. The large-diameter burrows of this particular stomatopod, with their smooth, hard-packed walls, are well suited for byssus attachment by the clams and provide a well-maintained, protective habitat. Furthermore, strong respiratory currents produced in the burrow by the stomatopod are undoubtedly beneficial to these more-or-less confined, filter-feeding clams. Ockelmann & Muus (1978) have suggested that this type of association is dependent upon the bivalves' responses to chemical/host, rather than physical, stimuli. Indeed, neither *Divariscintilla* species described here has ever been found in any other habitat, protective or otherwise.

Redescription of the genus: This work redefines *Divariscintilla* and identifies the following generic characters: Shell thin, prolonged anteriorly or posteriorly, incompletely internalized within pallial tissues; hinge teeth reduced, possessing only small cone-shaped cardinals. Mantle ornamented with species-specific numbers of tentacles and papillae. Byssus-gland communicating by ventral groove with posterior byssus adhesive gland. Two-part foot, consisting of extensible anterior crawling portion and tubular posterior extension, used in active crawling and "hanging." Secretory "flower-like organs" on anterior surface of visceral mass, situated ventral to labial palps. Eulamellibranch

ctenidia with interlamellar and interfilamentary junctions. Simultaneous hermaphroditic reproduction with ctendial incubation of larvae.

The known range of the genus is extended from New Zealand alone (type species, *Divariscintilla maoria*) into the western Atlantic (*D. yoyo* and *D. troglodytes*, described here).

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KARYOTYPIC EVOLUTION IN PLEURO CERID SNAILS. I. GENOMIC DNA ESTIMATED BY FLOW CYTOMETRY

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ABSTRACT

Total genomic DNA was measured in 16 species of North American pleurocerids, representing all six living genera. A constant value of 2.1 pg DNA/haploid genome was obtained, consistent with values from other mesogastropods and other mollusks with similar chromosome number. The relationship between DNA content and evolutionary radiation is called into question.

Key words: Snails, freshwater, Pleuroceridae, cytogenetics, flow cytometry, DNA.

INTRODUCTION

Few groups of North American mollusks are as common, diverse, important, or poorly understood as the pleurocerid snails. They are the most conspicuous element of the macrobenthos in many rivers and streams, and as such have figured prominently in a number of ecological investigations (e.g. Elwood & Nelson, 1972; Sumner & McIntire, 1982; Hawkins & Furnish, 1987; Dillon & Davis, in review). Their occurrence in numerous, isolated populations, easily sampled year round, has made them ideal models for evolutionary research (Chambers, 1980, 1982; Dillon, 1984, 1988a, 1988b). Yet their systematics are so confused that the specific identity of the populations inhabiting much of the United States is problematic.

The first monographic treatment of the family was given by Tryon (1873). He catalogued about 500 nominal species, which he placed in nine genera. The currently accepted system of classification is due to a series of papers by Goodrich (e.g. 1940, 1942). Goodrich recognized somewhat over 100 species and subspecies, and his revision formed the basis of the classification by Burch & Tottenham (1980) and Burch (1982) that I use here. Burch recognized six living genera: *Io*, *Juga*, *Leptoxis* (including Goodrich's *Anculosa*, *Nitocris*, and *Eurycaelon*), *Lithasia*, *Pleurocera*, and *Elimia*. Burch resurrected "*Elimia*" on the strength of Pilsbry & Rhoads' (1896) type designation, failing to note that Pilsbry subsequently reversed himself (Walker, 1918:149).

Elimia is a composite group, and thus I use the much more familiar name favored by Tryon and Goodrich, *Goniobasis*.

Very little distinguishes many of these genera. *Pleurocera* is distinguished from *Goniobasis* by a short "canal" on the anterior lip of the shell, a feature that is inconspicuous or absent in many species. Detailed comparisons of morphology, anatomy, life history, and ecology failed to find any other distinctions (Dazo, 1965). *Juga* is distinguished from *Goniobasis* by being from western North America, not eastern or central. It seems clear that the systematic relationships of pleurocerid snails need to be re-examined.

Analysis of karyotype has proven to be a powerful tool in evolutionary studies (White, 1973). But very little is known about the cytogenetics of any pleurocerid species. In a review of molluscan karyotypes, Patterson (1969) found two reports for North American pleurocerids: $n = 18$ for *Goniobasis laqueata* and $n = 20$ for *G. livescens*. Dillon (1982) reported $n = 17$ in *G. proxima*. The most thorough study to date has been made by Chambers (1982), who found $n = 18$ in Florida *Goniobasis* and described striking variation in arm length ratios. So the evidence available suggests that karyotypic variation does occur in the Pleuroceridae. In this series of papers, I will survey the six genera to see whether karyotype may be used to elucidate the systematics and evolution of this important family of freshwater snails.

Karyotypes are traditionally compared by constructing idiograms for each species, re-

producing the relative sizes and centromeric positions of the chromosomes. Idiograms are generally standardized to unit length, so that each species is assumed to have the same amount of genetic material. An increase in chromosome number is viewed as a centric fission. This is a reasonable assumption—many convincing examples of such “Robertsonian” events are known. But an increase in chromosome number could also represent additional genetic material. Additional chromosomes may be incorporated into a genome by coincident nondisjunction in the parents, or by large-scale gene duplication (Ohno, 1970). Thus it is of great value to determine the total genomic DNA content of each species to be karyotyped. In this first paper of the series, I estimate the genomic DNA content of a variety of pleurocerid snails using flow cytometry.

Flow cytometry is one of the most sensitive techniques available for quantifying cellular DNA. The technique has been used to discriminate between human chromosomes (Gray et al., 1975) and identify structural abnormalities in the chromosome complements of cell lines (review by Arkesteijn et al., 1987). The technique has been thoroughly reviewed by Melamed et al. (1979), Van Dilla et al. (1985), and Shapiro (1988).

Briefly, tissues in an aqueous suspension are stained with a dye that intercalates into double-stranded nucleic acid. I used propidium iodide, after treatment with ribonuclease to eliminate double-stranded RNA. Then the suspension is channeled at high speed through a narrow aperture, using mechanics similar to those of the familiar Coulter counter. Each individual particle passes through a laser, which excites a red-fluorescent emission proportional to its DNA content. The degree to which the laser beam is scattered by each particle provides an estimate of the particle's size. The emissions of the individual particles are captured by photosensors and displayed in a scatter plot, which enables the operator to distinguish individual, whole cells from debris and clumped cells. Then the red fluorescence of the whole-cell fraction is plotted in a histogram, with fluorescence measured in arbitrary units called “channel numbers.” Since the relationship between channel number and DNA content is effectively linear, a flow cytometer calibrated with known samples can be used to estimate the DNA content of an unknown.

The contribution of mitochondrial DNA to total red fluorescence has generally been

found to be negligible (Melamed et al., 1979). Correction for any background mtDNA levels can be made by using a single tissue type for both the unknowns and the calibration standards.

METHODS

The following populations were sampled:

Goniobasis acutocarinata (Lea)—Small creek flowing into the Powell River at Virginia Highway 662 bridge, 0.5 km E of Stickeys, Lee County, Virginia. Goodrich (1940) synonymized this species under *G. clavaeformis* (Lea).

Goniobasis alabamensis (Lea)—Coosa River at tailwater of Mitchell Dam, 20 km E of Clanton, Chilton County, Alabama.

Goniobasis catenaria dislocata (Reeve)—“Intermittent” tributary of Big Poplar Creek at South Carolina Highway 6 bridge, 3 km SE of Elloree, Orangeburg County, South Carolina.

Goniobasis floridensis (Reeve)—Blue Spring at Florida Highway 6, Madison County, Florida. Site 8 of Chambers (1980).

Goniobasis livescens (Menke)—Portage Creek at Toma Road bridge, 5 km S of Pinckney, Washtenaw/Livingston County line, Michigan. Station 2 of Dazo (1965).

Goniobasis proxima (Say)—Mitchell River at North Carolina Highway 1330 bridge, 2.8 km N of Mountain Park, Surrey County, North Carolina. Site MTCH of Dillon (1982, 1984).

Goniobasis simplex (Say)—same site as *G. acutocarinata*.

Io fluvialis (Say)—Powell River by small road just S of Virginia line, Hancock County, Tennessee.

Juga hemphilli (Henderson)—Oak Creek 11 km W of Corvallis, Benton County, Oregon.

Leptoxis (Mudalia) carinata (Brug.)—Pratts Run at U.S. Highway 340 bridge, Waynesboro, Augusta County, Virginia.

Leptoxis praerosa (Say)—same site as *Io fluvialis*.

Lithasia duttoniana (Lea)—Duck River at Tennessee Highway 11 bridge, 10 km N of Farmington, Marshall County, Tennessee.

Lithasia verrucosa (Raf.)—French Broad River at Cement Shoals, 1 km downstream from Kimberlin Heights, Knox County, Tennessee.

Pleurocera acuta Raf.—Dazo's (1965) station 2, same as *G. livescens*.

Pleurocera canaliculatum (Say)—Elk River



FIG. 1. From left, *Lithasia duttoniana*, *Goniobasis catenaria dislocata*, *G. alabamensis*, *G. acutocarinata*, *Juga hemphilli*.

at bridge 8 km W of Fayetteville, Lincoln County, Tennessee.

Pleurocera unciala (Reeve)—same site as *lo fluvialis*.

The shell morphology of many of these species is quite variable, as are the species concepts of many prior workers in pleurocerid taxonomy. Typical shells from several of the less common taxa are shown in Fig. 1. Voucher specimens for all populations are deposited in the Academy of Natural Sciences of Philadelphia.

Techniques for sample preparation were based on Allen (1983), Buzzi (1989), and standard clinical methods. Foot muscle was excised from living snails and ground, with powdered glass, in a clear polystyrene tube with 600 μ l of phosphate buffered saline. This buffer was modified from Allen (1983): NaCl 8.0 g/l, KCl 0.20 g/l, $MgCl_2$ 0.10 g/l, Na_2HPO_4 1.15 g/l, KH_2PO_4 0.20 g/l. Drops of cold absolute ethanol were added, while vortexing, to bring the final ethanol concentration up to 70%. Samples fixed in this manner were held at least overnight at 3°C, and sometimes as long as two weeks.

An RNase solution was prepared by dissolving 50 mg ribonuclease A (Sigma type III-A) in 50 ml 1.12% trisodium citrate and heating at 80°C for 10 minutes. The solution was frozen in 2 ml aliquots. On the morning of flow cytometric analysis, fixed tissue samples were centrifuged, aspirated, and resuspended in a several ml of a solution containing 47 ml phosphate buffered saline, 1 ml 1.2% (v/v) Nonidet P-40, and one aliquot of RNase solution. Since the lot of ribonuclease III-A that I received had 105 units of activity per ml, the

final RNase activity in phosphate buffered saline was approximately 4 units/ml. Tubes were incubated at room temperature for 30–60 minutes.

Each sample was vortexed, drawn into a 1 ml tuberculin syringe, and forced through a 52 μ m Nytex screen. Then 20 μ l of a 0.10% (w/v) propidium iodide solution was added per ml of tissue suspension, and incubated at room temperature for 30–60 minutes prior to analysis on an Ortho Spectrum III flow cytometer.

In collaboration with W. Buzzi, a calibration curve was constructed using human leukocytes and tissue samples from four mollusk species of known genomic content. We analysed four *Crassostrea virginica* (Gmelin), five *Mercenaria mercenaria* (L.), and two *Ilyanassa obsoleta* (Say), all collected from the Charleston, South Carolina, area. We obtained four *Mytilus edulis* L. from Milford, Connecticut. The total genomic DNA of *C. virginica* is given by Swanson et al. (1981:134), and values for the remaining mollusks are from Hinegardner (1974). Three individuals of *G. catenaria dislocata* were included as unknowns.

Goniobasis catenaria dislocata served as the standard in all subsequent analyses. Several fresh *G. catenaria* were analysed first, followed by four to six individuals of a second pleurocerid species. The peak red fluorescence for each sample was noted, as well as the concentration of countable cells. Aliquots from samples of the two species were combined into a third tube such that cell concentrations were equalized. The combined sample was then re-analysed and the resulting histogram of red fluorescence inspected for

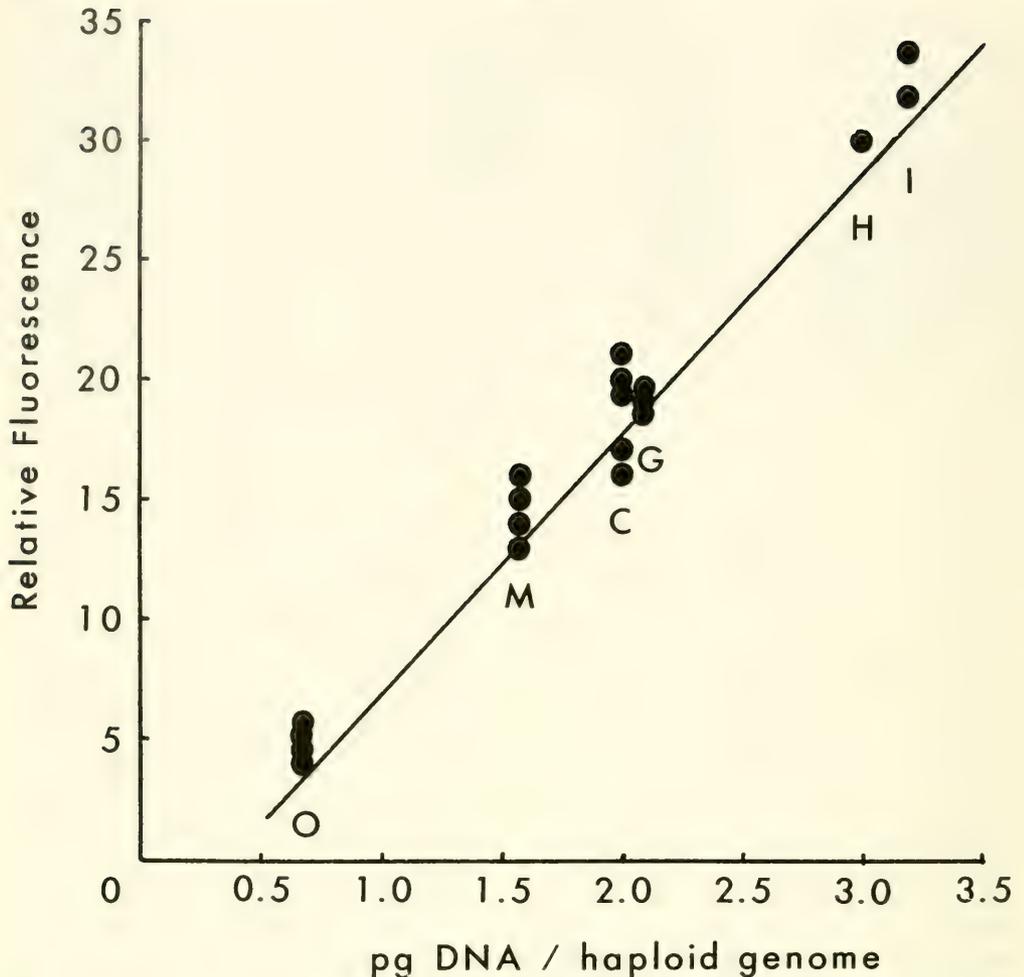


FIG. 2. Calibration curve. O—*Crassostrea*, M—*Mytilus*, C—*Mercenaria*, G—*Goniobasis catenaria dislocata*, H—human, I—*Ilyanassa*.

evidence that the two peaks were non-overlapping.

RESULTS

The calibration curve is shown in Fig. 2. An excellent fit to the linear hypothesis $y = 10.8x - 3.76$ was obtained, with $r^2 = 0.98$. So given a mean relative fluorescence of 17.3, I estimated that *G. catenaria dislocata* has 2.1 pg DNA/haploid genome.

A typical comparison between *G. catenaria dislocata* and an unknown (*G. proxima* in this case) is shown in Fig. 3. This particular sample of *G. catenaria* tissue came from a snail

collected the previous day, and shows two peaks—a strong gap 1 peak and a lower gap 2/mitosis peak with twice the fluorescence. Only snails freshly collected in warm weather generally showed a gap 2 peak. Even if temperature and photoperiod were controlled and the snails fed commercial fish food *ad lib*, gap 2 peaks generally disappeared after only a day or so in captivity, as shown in the *G. proxima* sample. In fact, it is evident that DNA synthesis has already been discontinued in the *G. catenaria* individual analysed, since no S-phase cells, with DNA contents intermediate between G1 and G2, are apparent in Figure 3. So although the snails in my aquaria always appeared healthy, cell division in foot

muscle tissue was apparently disrupted almost immediately.

The rapid loss of cells at gap 2 and mitosis in captive snails did not affect the accuracy of sample comparisons. The much stronger, sharper gap 1 peaks were used as the basis for comparison in all cases.

No difference was detected between the peak red fluorescence of *G. catenaria dislocata* and that observed in any other species of pleurocerid examined. Figure 3 shows that an equal mixture of *G. catenaria* cells and *G. proxima* cells shows no evidence of two gap 1 peaks. This result was obtained in all comparisons.

DISCUSSION

It would appear that all 16 pleurocerid species in my sample, representing six genera, have a uniform genomic DNA content of 2.1 pg DNA/haploid genome. Hinegardner (1974) found that seven species of mesogastropods range from 0.67–2.4 pg DNA/haploid genome. A vermetid was the only cerithiacean examined, with 1.5 pg DNA/haploid genome. So the value I have obtained for pleurocerids is consistent.

From a broad comparison of gastropod orders, Hinegardner suggested that high amounts of DNA appear to be associated with evolutionary radiation. But in spite of their rather average-sized genome, the Pleuroceridae have radiated extensively. Hinegardner's generalization may not hold for freshwater groups, where dispersal is generally much more restricted and the potential for differentiation greater.

Across the five kingdoms, there is a general relationship between genome size and degree of organismal complexity or "evolutionary advancement" (Hinegardner, 1976). The "C-value paradox" arose when it was noted that some organisms, such as some flowering plants and amphibians, have amounts of DNA ("C-values") much greater than more advanced eukaryotes. But the pleurocerid genome size is rather typical for mollusks, and for invertebrates in general.

Hinegardner (1974) reported a correlation between chromosome number and DNA content in gastropods significant at the 0.01 level. Extrapolating from his graph, a chromosome number of $n = 13$ to 18 would be predicted from the DNA content of North American pleurocerids. This is consistent with the lim-

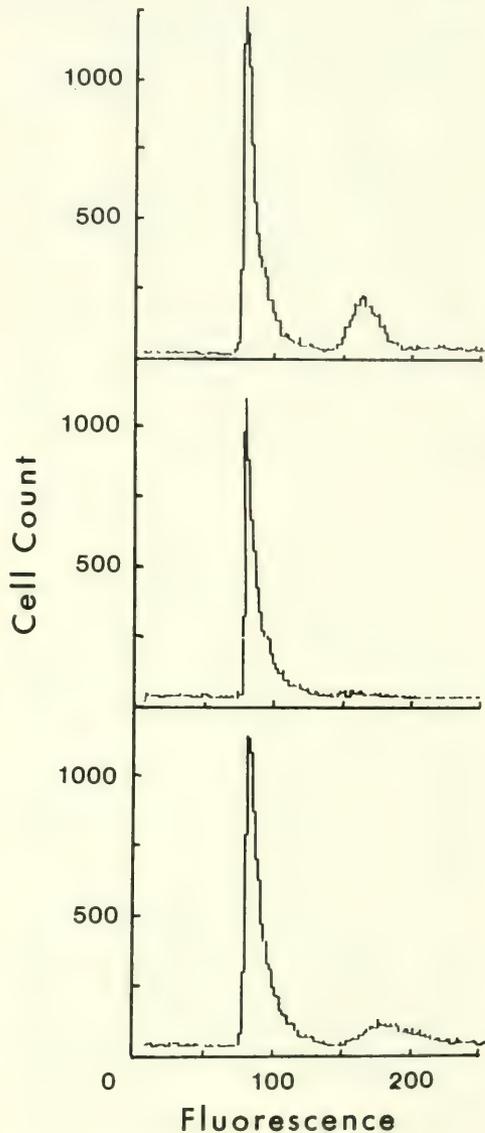


FIG. 3. Example comparison of unknown and standard. Top—fresh *G. catenaria dislocata* standard, showing gap 1 and gap 2 peaks. Middle—the unknown (*G. proxima*), showing gap 1 peak only. Bottom—equal mixture of standard and unknown, demonstrating complete overlap of gap 1 peaks.

ited information available on pleurocerid karyotypes. Ongoing studies will more thoroughly address the degree to which uniformity in genomic DNA content reflects karyotypic conservation in this family. Any variation in chromosome number among pleurocerids can be

viewed with some confidence as originating in Robertsonian fusion or fission.

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HABITAT SELECTION BY A FRESHWATER MUSSEL: AN EXPERIMENTAL TEST

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ABSTRACT

Two groups of the freshwater mussel *Lampsilis radiata siliquoidea* (Barnes, 1823) were collected in Inner Long Point Bay, Lake Erie. The first group of mussels was collected from sandy, turbulent areas of the bay, while the second group was collected from soft-bottomed, muddy areas. The sand-collected mussels were larger and thicker-shelled than the mud-collected group, which is consistent with previously observed correlations between shell form and habitat in this and other Unionidae species. I placed 50 individuals from each of these two groups into each of two artificial ponds. Each pond contained equal areas of sand and mud in "checker-board" fashion, and each mussel was placed at random coordinates on the bottom of the ponds. After four months, two-thirds of the mussels were found in the mud sediment. About 80% of the mussels initially placed in mud stayed there, while about half of the mussels initially placed in sand moved to mud. Sand-collected mussels had a stronger tendency, relative to the mud-collected group, to either stay in mud if they started there or move to mud from sand. The results support the hypothesis that habitat selection has evolved in this unionid species, but are not consistent with the hypothesis that the two groups of mussels represent specialists for the habitats from which they were collected.

Key words: habitat selection; Unionidae; shell morphology; specialists; sediment preference.

INTRODUCTION

As discussed by both Kat (1982) and Huehner (1987), there has been more observational and anecdotal evidence than detailed, experimental study of habitat selection in freshwater mussels. This has led to a remarkable lack of understanding of their ability (or lack of ability) to select habitat. Clearly this knowledge is important in understanding the relative niche breadths of each species, as well as the degree of niche overlap among species.

Short-term (three-hour) experiments in the laboratory by Huehner (1987) indicated that most populations of *Anodonta grandis* Say, 1829, and *Lampsilis radiata* (Gmelin, 1791) show a preference for sand over gravel. The other species tested, *Elliptio dilatata* (Rafinesque, 1820), showed no substrate preference. Huehner (1987) commented on the behavioural and morphological plasticity of *Lampsilis radiata*. In his laboratory experiments, one population of *L. radiata sili-*

quoidea showed a preference for sand, while another had no preference. In this study, I tested the ability of two *Lampsilis radiata siliquoidea* forms to select substrate over a relatively long (four-month) experimental period.

Lampsilis radiata siliquoidea (Barnes, 1823) is one of many freshwater mussels whose shell morphology and growth rate vary with habitat. Bailey & Green (1988) and Hinch et al. (1986) found thicker-shelled, faster-growing *L. r. siliquoidea* in the turbulent, sandy sediment areas of Inner Long Point Bay, Lake Erie, when compared to conspecific mussels from the more quiescent, muddy areas of the bay. Many authors have claimed that correlations between the habitat of freshwater mussels and their shell form are due to differential adaptation resulting in specialist phenotypes. Wilson & Clark (1914) suggested that larger, flatter shell forms are better adapted to burrowing in the coarse substrates of fast current areas in streams, while smaller, more obese (large width-to-length ratio) shells maintain a mussel's buoyancy in

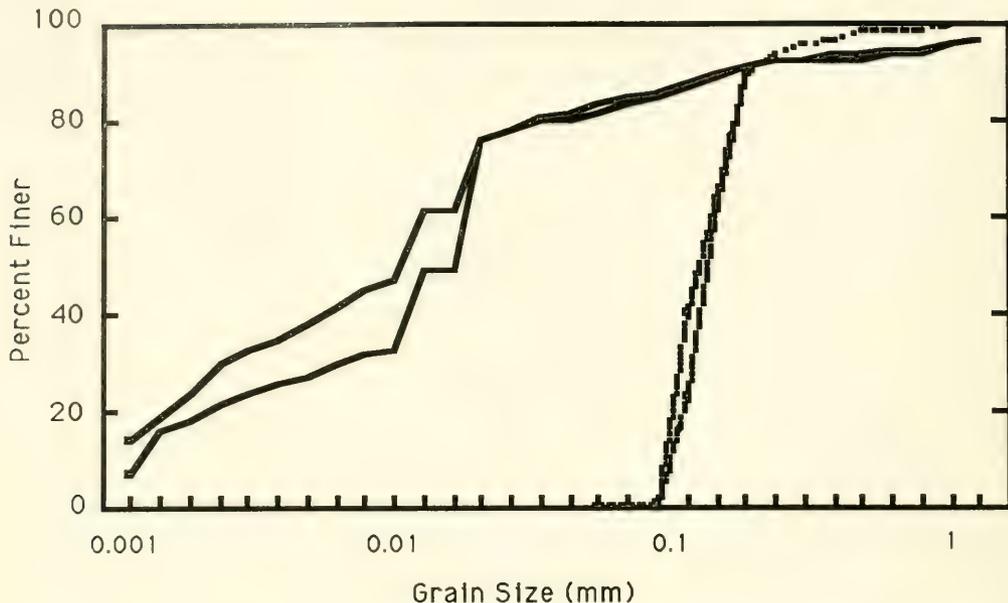


FIG. 1. Particle size distribution of substrates used in the pond experiment (--- SAND, — MUD).

soft substrates. Eagar (1978) claimed that more obese shells allow for a greater volume of soft tissue, thereby improving the "metabolic and functional activity" of mussels in quieter waters. Stanley (1970) considered the functional morphology of the entire Class Bivalvia and drew conclusions similar to those of Wilson & Clark (1914). Although these hypotheses seem reasonable, clear tests of their predictions have not been made.

In the present study, *L. r. siliquoides* from both turbulent and quiescent areas of Inner Long Point Bay, Lake Erie, were used in a substrate selection experiment carried out in artificial ponds. Mussels from the two areas differed morphologically in a manner more or less consistent with the adaptive hypotheses outlined above. I predicted that if these two phenotypes represented specialists for different habitats, the availability of both fine- and coarse-grained sediments in artificial ponds would lead to differential habitat selection by the two groups of mussels.

MATERIALS AND METHODS

On 11 June 1985, 100 similarly aged (8–12-year-old) *L. r. siliquoides* were collected using SCUBA from each of low and high exposure areas in Inner Long Point Bay, Lake

Erie. Inner Long Point Bay is a large (75 km²), shallow ($z = 2.5$ m) bay with a heterogeneous distribution of high, medium, and low exposure areas grading into one another (see Bailey, 1988, for a map of exposure areas). The mussels were collected from well within one high and one low exposure area in the bay, in each case within 50 m of the boat. These mussels were transplanted into two artificial ponds on the campus of The University of Western Ontario. Each pond measured 5 × 9 m and had a depth of about one meter. One week before collecting the mussels, equal areas of "sand" and "mud" sediment, obtained from Southwinds Sand and Gravel (London, Ontario), were spread to a depth of about 15 cm prior to filling the ponds with city water using taps located at the side of each pond. The sediment was added in checkerboard fashion such that there were two rectangular areas of each sediment in each of the ponds. The sand used was "golf course sand"; the mud was from silt deposits created by the wastewater from washing crushed gravel. Percent loss on ignition, determined as described in Bailey (1988), was nil for both substrates. Particle size analysis, using wet sieving and hygrometer analysis (Bowles, 1978), indicate that the mud was finer and more heterogeneous than the sand (Fig. 1).

A number was etched onto each mussel's

TABLE 1. Loglinear model analysis showing the significance of "SOURCE" (area where mussel was collected in Inner Long Point Bay), "INITIAL SUBSTRATE" (substrate in which the mussel was initially planted in the experimental ponds), and the interaction of the two effects in predicting the final substrate of the mussels.

Source	df	X ²	p
SOURCE	1	2.9	0.08
INITIAL SUBSTRATE	1	17.4	<0.001
INTERACTION	1	0.13	0.72

shell and 50 individuals from each exposure area were placed at randomly generated coordinates on the bottom of each of the ponds on 12 June 1985. By 18 June, there was ample evidence of mussel movement within the ponds (i.e. tracks). Because of concern about the use of city water, various physico-chemical and biological parameters were monitored. Chlorine (Hach Model CN-70) and dissolved oxygen (Hach Model AI-33) analyses were carried out throughout the experimental period and showed total chlorine concentrations of 0.2–0.3 mg · L⁻¹ (tap water in London was about 0.6–0.8 mg · L⁻¹) and dissolved oxygen concentrations of 90–100% saturation. Temperature over the experimental period ranged from 16–29°C. Flow rate from the taps into the ponds was checked daily and kept at 125 mLsec⁻¹. Qualitative sampling with a plankton net on 2 July 1985 revealed abundant insect, crustacean zooplankton, Hydracarine, and algal populations in both of the ponds. Four months after planting the mussels in the ponds (9 October 1985), 151 individuals (142 alive) were recovered over a two-day period (using SCUBA) and the ponds were drained. Eight additional (dead) mussels were found the following day, and 23 dead mussels were recovered from the dry ponds the following spring. Because the live and dead mussels did not differ in their distribution patterns, data on all recovered individuals were used in the statistical analyses. Shells of the recovered mussels were cleaned, dried, weighed, and measured (length, height, and width as defined in Bailey & Green 1988), and the morphological differences between those collected in the sand and the mud were consistent with differences observed by Bailey & Green (1988).

The habitat from which each mussel was originally collected in the field ("SOURCE"), the substrate in which the mussel was initially placed in one of the ponds ("INITIAL SUBSTRATE"), and the interaction of these two factors were tested as predictors of the

mussel's final substrate "choice" using a log-linear model (Fienberg, 1980). SAS Proc Catmod (SAS Institute Inc., 1982) was used for the analysis.

RESULTS

Two-thirds of the mussels recovered (124/182) at the end of the experiment were found in the mud substrate. The loglinear model analysis (Table 1) showed that this preference for mud was somewhat influenced ($p = 0.08$) by the "SOURCE" of the mussels and more strongly affected by their "INITIAL SUBSTRATE." There was no interaction between these two effects. Compared to mussels collected in the muddy areas of Inner Long Point Bay, more of the mussels collected in exposed, sandier areas of the bay tended to either stay in mud if they started there, or move to mud from sand (Fig. 2). In both groups, there was a tendency for those initially placed in mud to stay there, but those initially placed in sand had about a 50/50 chance of switching to mud (Fig. 2).

DISCUSSION

Although both the sand- and mud-collected mussels appeared to select habitat, the two forms differed only in the magnitude (rather than the nature) of their habitat selection. A greater proportion of the sand-collected mussels starting in mud stayed in mud, and a greater proportion of sand-collected mussels moved to mud from sand, but both groups showed similar basic patterns of habitat choice (Fig. 2). There are at least two explanations for this: (i) the two phenotypes do not represent specialists for different habitats, and (ii) the two substrate types used in the experiment did not adequately recreate the habitat choices available to these mussels in their natural environment.

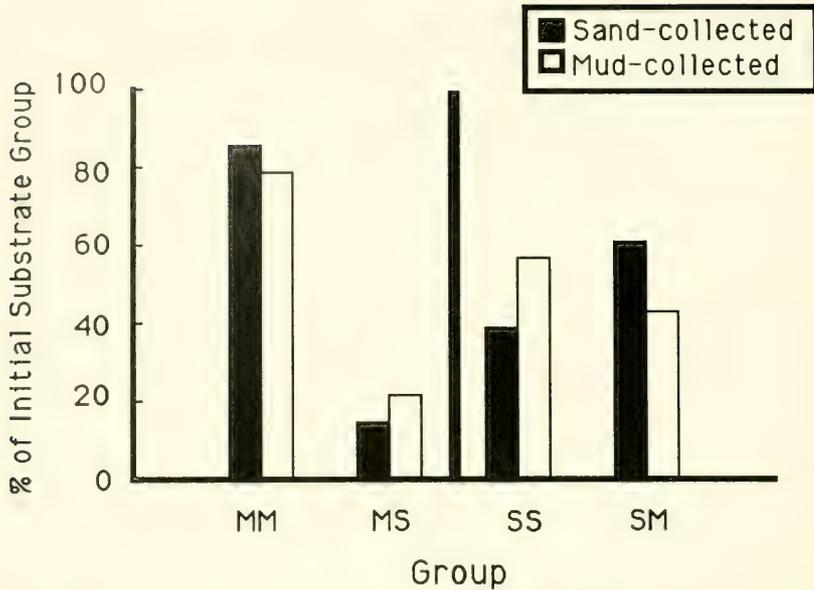


FIG. 2. Initial placement and final substrate of recovered mussels. The percentage of the total for a given SOURCE group (i.e. sand- or mud-collected) is given (MM: initial = mud, final = mud; MS: initial = mud, final = sand; SS: initial = sand, final = sand; SM: initial = sand, final = mud).

It has previously been proposed that the smaller, more obese shells of freshwater mussels living in soft mud habitats simply reflect a non-adaptive response to poorer growing conditions. Food supply may be reduced in these areas (Ball, 1922; Stansbery, 1970; Kat, 1982), but this hypothesis has never been tested. Feeding behavior may also differ in soft sediment habitats. Ellis (1936) observed that mussels in muddy water had their valves closed 75–90% of the time, while those in silt-free water were closed less than 50% of the time. He also found that heavy silting killed most of the mussels kept in experimental tanks. Kat (1982) argued that the net intake of energy would be reduced on muddy substrates because the mussels would require more energy to maintain proper filtering position. As in the case of the “adaptive hypotheses” (see Introduction), little direct evidence has been collected to reject either the “adaptive” or “environmental” hypotheses of variation in shell morphology.

Thus, the difference in shell morphology between sand- and mud-collected mussels may indicate different growing conditions rather than differential adaptation to their respective habitats. If this were true, the two phenotypes would not represent specialists for the two habitat areas in Inner Long Point

Bay, and no difference in habitat choice would be expected. Sand-collected mussels may have exhibited a greater degree of pickiness because of size-dependent controls on the proximal mechanism of habitat selection in these mussels. Perhaps differences in short-term fitness of mussels in the two sediments (e.g. filtering efficiency, maintenance of shell position), which would provide the necessary cues for stimulating habitat selection, were not as great for the mud-collected mussels.

The substrate choices available in the pond experiment may not have adequately represented habitat variation in the natural environment. The most obvious evidence supporting this contention is the clear choice of the “mud” sediment in the ponds by mussels collected from the **sandy** area of Inner Long Point Bay. The particle size distribution of “typical” sediment samples from muddy and sandy areas in Inner Long Point Bay (Fig. 3) are clearly more similar to the “mud” than the “sand” sediment in the ponds (Fig. 1), although the “mud” sediment in the ponds was somewhat more heterogeneous than the natural sediments. Also, there were many differences between the sandy and muddy areas in the bay that were not recreated in the experiment, such as macrophyte and fingernail clam communities (Bailey, 1988), organic

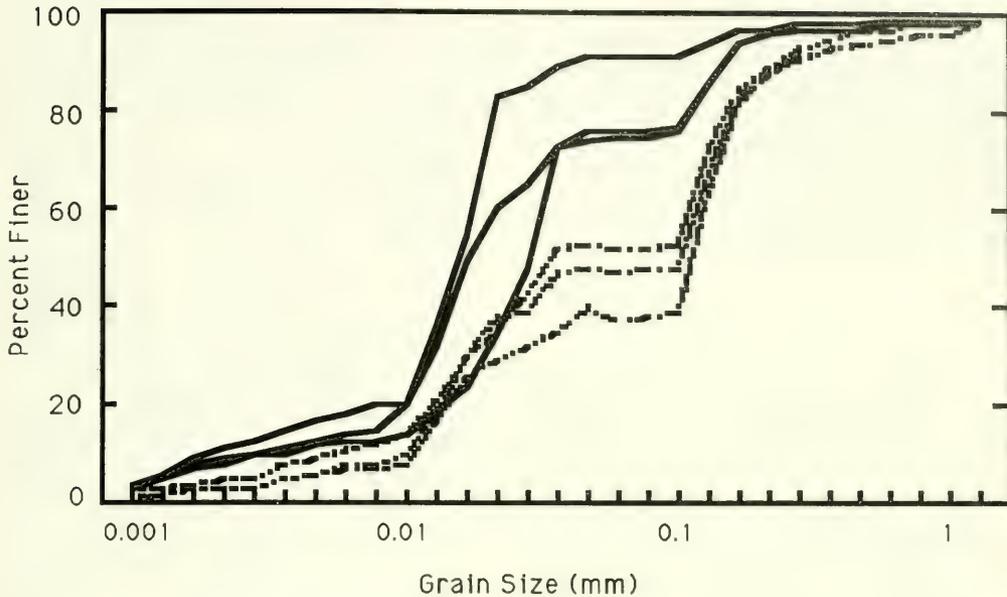


FIG. 3. Particle size distribution of "typical" substrate collected from sandy (---) and muddy (—) areas of inner Long Point Bay, Lake Erie.

content (Bailey, 1988) and penetrability (Bailey, personal observation) of the sediment, and the actual turbulence that created and maintains the sediment variation in the bay. None of these correlated environmental differences were present in the pond experiment, and thus weakened its relevance to the natural environment. On the other hand, the grain size stimulus for habitat selection in *L. r. siliquoides* must have been quite strong to have generated the observed results.

Even though both groups of mussels appeared to select the mud sediment in the ponds, the nature of this and similarly designed substrate selection experiments (e.g. Meier-Brook, 1969; Gale, 1971; Huehner, 1987) allows for another interpretation. The relatively slow-moving bivalves must move **through** the two substrates available. If one of the substrates is considerably harder to move through than the other, the mussels will accumulate in that substrate and appear to have "chosen" it at the end of the experiment. This possibility, which may be likened to a food choice experiment in which one of the diet alternatives makes it physically impossible for the animal to eat anything else, might be called the "stuck in the mud" hypothesis (R. H. Green & S. G. Hinch, personal communication). Although regular observations of

the ponds revealed numerous tracks through both sediment types, detecting any difficulty in movement was beyond the scope of this study.

If one does accept that habitat selection was demonstrated by *L. r. siliquoides*, how relevant is this to the behavior of the mussel in its natural habitat? Many authors have found that juvenile mussels, after finishing a life stage during which they are parasitic on fish, occupy a habitat somewhat different from adults of the same species (e.g. Lefevre & Curtis, 1912; Isely, 1911; Coker et al., 1921). Perhaps at some time between the juvenile dropping from the fish host and the relatively sedentary adult stage (Strayer, 1981; but cf. Salmon & Green, 1983), selection of an appropriate adult habitat should occur. Whether or not habitat selection would evolve would depend on how much would be gained by selecting habitat (i.e. benefits of habitat selection) relative to the time and energy spent searching for the habitat (i.e. costs of habitat selection). The hypothesis that the ability to select habitat has evolved in *L. r. siliquoides* seems credible. This experiment has shown (with the aforementioned reservations) that the ability to select habitat exists in these mussels. This evidence strengthens conclusions from observational, frequency of occur-

rence data and short-term laboratory experiments (e.g. Huehner, 1987). There is no evidence, however, that the sand- and mud-collected mussels from Inner Long Point Bay specialize on different habitat types. Either the difference in shell phenotype between the groups is a non-adaptive, environmentally induced effect or the habitats available in the pond experiment were not suitable for detecting a difference in preference.

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SPERMATOCYTE CHROMOSOMES AND NUCLEOLUS ORGANIZER REGIONS (NORs) IN *TRICOLIA SPECIOSA* (MÜHLFELD, 1824) (PROSOBRANCHIA, ARCHAEOGASTROPODA)

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ABSTRACT

The chromosome complement, $n = 8$ and $2n = 16$, of *Tricolia speciosa* is at present the lowest chromosome number found within the Archaeogastropoda (Mollusca: Prosobranchia). The karyotype consists entirely of bi-armed chromosomes. No heterotypic elements were observed in analyses of meiotic and mitotic chromosomes. An analysis of the nucleolar organizer region (NOR) by silver staining is reported. *Tricolia speciosa* presents an intraspecific variability in Ag-NOR pattern as revealed by differences in the number of Ag-NORs per cell within a cell population.

Key words: *Tricolia*; karyology; nucleous organizer regions.

INTRODUCTION

Three thousand living species distributed in 22 families are currently recognized by Franc (1968) within the prosobranch order Archaeogastropoda. Because karyological information is only available for 76 species from nine families (Vitturi et al., 1982; Nakamura, 1982, 1983, 1986), it is clear that many archaeogastropod species and families remain completely unexplored.

Previous studies on mitotic chromosomes morphology in 46 of the 76 examined species (Nakamura, 1986) revealed that 10-20 percent of the chromosome complements of archaeogastropods consist of sub-telocentric (ST) and acrocentric (A) chromosomes, with higher values of metacentric (M) and sub-metacentric (SM) elements in the karyotypes of those species characterized by a low number of chromosomes, such as Patellidae and Acmaeidae. Moreover, within this order, the haploid chromosome number varied from $n = 9$ (Patellidae) to $n = 21$ (Trochidae), with intermediate values as briefly summarized in Table 1. Nakamura (1986) noted, however, that chromosome numbers were quite constant within each family, except for the Haliotidae and Fissurellidae, in which there was some variation.

The location of nucleolar organizer regions has been reported mainly for mammalian species (Goodpasture & Bloom, 1975; Pardue & Hsu, 1975; Markovic et al., 1978; Traut et al.,

1984), and for a relatively few species of fish (Kligerman & Bloom, 1977; Foresti et al., 1981; Thode et al., 1983, 1985; Thode, 1987).

With regard to Mollusca, results with silver staining have been described for the genera *Bulinus* and *Biomphalaria* (Mollusca, Planorbidae) (Goldman et al., 1983).

In the present paper, we describe spermatocyte chromosome of the species *Tricolia speciosa*, which belongs to the family Phasianellidae (Archaeogastropoda) previously unexplored at a karyological level. Additionally, we report here our findings concerning the distribution and behaviour of nucleolar organizer regions (NORs) in this species.

MATERIALS AND METHODS

Thirty sexually mature male specimens of *Tricolia speciosa* collected in February 1987 in the Gulf of Palermo were employed. Taxonomic identification of the specimens was made according to the guidelines of Parenzan (1970), and voucher shells of ten specimens were deposited at the Museum of the Institute of Zoology of the University of Palermo.

Meiotic chromosomes were obtained by treating testes according to the squashing technique described for other molluscan species (Vitturi et al., 1982). In order to obtain mitotic chromosomes, testes of ten specimens were treated before squashing with

TABLE 1. Haploid chromosome numbers in Archaeogastropoda; (1) including one species reported to have various chromosome numbers

Family	number of species with n =													Total examined species
	9	10	11	12	13	14	15	16	17	18	19	20	21	
Acmaeidae	—	14	—	—	—	—	—	—	—	—	—	—	—	14
Patellidae	5	—	—	—	—	—	—	—	—	—	—	—	—	5
Neritidae ⁽¹⁾	1	1	1	22	—	1	—	—	—	—	—	—	—	23
Haliotidae	—	—	—	—	—	2	—	2	—	4	—	—	—	8
Fissurellidae	—	—	—	—	1	1	1	3	—	—	—	—	—	6
Trochidae ⁽¹⁾	—	—	—	—	—	—	—	—	—	13	—	1	1	14
Turbinidae	—	—	—	—	—	—	—	—	—	3	—	—	—	3
Stomatellidae	—	—	—	—	—	—	—	—	—	1	—	—	—	1
Helicinidae	—	—	—	—	—	—	—	—	—	3	—	—	—	3
Total	6	15	1	22	1	4	1	5	0	24	0	1	1	76

0.025% colchicine in double distilled water for 20 minutes.

The same slides, after removal of the cover-glass, were then stained with silver nitrate following the procedure of Howell & Black (1980).

Acetic-orcein slides were photographed with a Wild phase contrast microscope, and NOR-banded slides with a Wild light microscope.

Mitotic chromosomes were interpreted on the basis of the arm ratio, following the nomenclature proposed by Levan et al. (1964)

OBSERVATIONS

Acetic-orcein slides

At the pachytene stage, all bivalents were tightly paired and their outlines were irregular (Fig. 1).

The analysis of 64 diakinetik plates gave the haploid number of 8 chromosomes (Fig. 2a). When disparate chromosome counts occurred (one plate with 6 chromosomes, three plates with 7, and four plates with 9 chromosomes), the discrepancy was usually attributed to either loss or breakage of bivalents. Almost all bivalents homogeneously stained appeared chiasmatic (Fig. 2b), and their lengths ranged from 2 μm to 3 μm .

At the spermatogonial metaphase stage (Fig. 3a), all 16 elements showed no achromatic area, with the exception of a pale medial zone corresponding to the centromere region, and thus appeared randomly distributed on the squashing plane. From an analysis of the idiogram (Fig. 3b, one plate is represented) combined from the chromosomes of

five metaphase plates and arranged on the basis of their decreasing size and centromere position (Fig. 4, Table 2), it appears that all pairs were metacentric except for one (Figs. 3b, 4, arrows) that was sub-metacentric.

NOR-banding slides

Analysis of nuclei stained by the silver method revealed a variability in the number of nucleoli/nucleus, and the frequencies appear in Table 3.

In Figure 5, the two areas showing an intense silver deposit were of larger dimensions than the six areas observed in Figure 7.

In Figure 6, a nucleus with three nucleoli is visible.

A summary of the state at diakinesis is as follows: 60% of analysed spreads show a completely NOR negative appearance (Fig. 8), 30% have 2–3 elements with NORs represented by minute dots (Fig. 9, arrows), and 10% have almost all elements with Ag granules (Fig. 10, arrows).

Mitotic chromosomes at the prophase stage often show NOR positive areas not associated with the chromosomes (Fig. 11, arrow). In the same figure, the element indicated by two arrows has a large telomeric NOR-band. Variability in the number of NOR positive elements and the size of Ag-NORs was also observed.

At the metaphase stage, spreads with either three Ag-NOR chromosomes (Fig. 12, arrows) or with five or six NOR-elements were present (Fig. 13, arrows).

DISCUSSION

From our observations, it seems that the course of spermatogenesis in *Tricolia spe-*

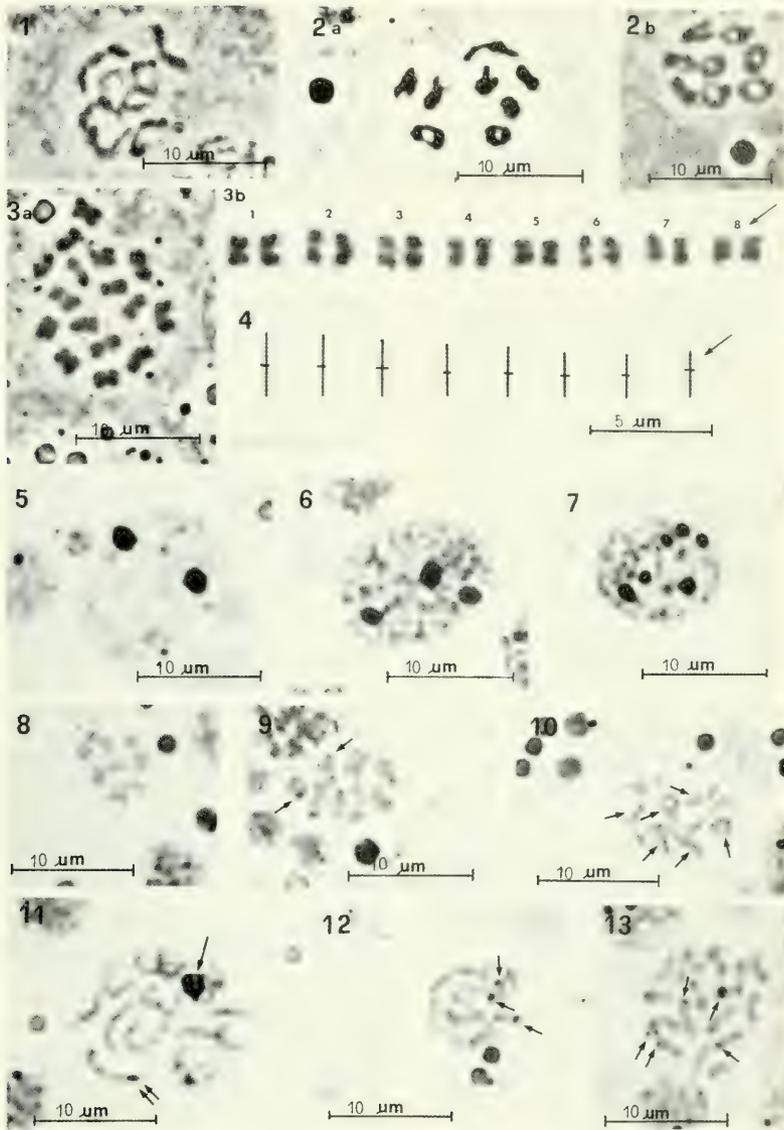


FIG. 1. Pachytene chromosomes in male gonads of *Tricolia speciosa*.
 FIG. 2. (a) and (b) diakinetid bivalents of *T. speciosa*.
 FIG. 3. (a) spermatogonial metaphase chromosomes and (b) karyotype of *T. speciosa* (arrow indicates sub-metacentric pair).
 FIG. 4. Idiogram constructed from five metaphase plates of *T. speciosa* (arrow indicates sub-metacentric pair).
 FIG. 5. Ag-nucleus with two nucleoli.
 FIG. 6. Ag-nucleus with three nucleoli.
 FIG. 7. Ag-nucleus with six nucleoli.
 FIG. 8. NOR-negative diakinetid plate of *T. speciosa*.
 FIG. 9. NOR-positive diakinetid plate of *T. speciosa* (arrows indicate Ag-positive elements).
 FIG. 10. NOR-positive diakinetid plate of *T. speciosa* (arrows indicate Ag-positive elements).
 FIG. 11. Mitotic chromosomes at prophase stage of *T. speciosa* (arrows indicate Ag-NORs).
 FIG. 12. Mitotic metaphase chromosomes of *T. speciosa* (arrows indicate Ag-NORs).
 FIG. 13. Mitotic metaphase chromosomes of *T. speciosa* (arrows indicate AG-NORs).

TABLE 2. Mean length and arm ratio of the chromosomes of five metaphase plates of *Tricolia speciosa*.

Chromosome pairs	Mean length, $\mu \pm SD$	Arm ratio mean	Centromere position
1	2.6 \pm 0.58	1	M
2	2.5 \pm 0.50	1	M
3	2.4 \pm 0.54	1	M
4	2 \pm 0.45	1	M
5	2 \pm 0.44	1	M
6	1.9 \pm 0.36	1	M
7	1.9 \pm 0.36	1	M
8	1.8 \pm 0.34	1.4	SM

TABLE 3. Frequency of nucleoli/nucleus in *Tricolia speciosa*.

	No. of nucleoli/nucleus					
	1	2	3	4	5	6
Nuclei	32	40	107	51	28	5
Frequencies	12	15	41	19	11	2
%						

ciosa does not differ from that of other molluscan species (Patterson, 1969). Cytological characteristics such as pachytene chromosomes with irregular outlines and chiasmatic bivalents, constantly reported within the Mollusca (Vitturi et al., 1982; Vitturi & Catalano, 1984; Vitturi et al., 1985b; Vitturi et al., 1986), were observed.

Distant somatic pairing between homologous chromosomes at the metaphase stage has been described for *Haliotis tuberculata* (Prosobranchia, Archaeogastropoda) (Colombera & Tagliaferri, 1983a) and *Acanthochiton crinitus* (Polyplacophora) (Colombera & Tagliaferri, 1983b) but was not seen in our preparations. In fact, a random distribution of the mitotic metaphase chromosomes on the squashing plane was observed.

The absence of heterotypic elements among spermatocyte bivalents, and of heteromorphic pairs among male mitotic chromosomes, allowed us to exclude a XY sex-determining mechanisms in *Tricolia speciosa*. At present, within the Archaeogastropoda only species included in the family Neritidae show a male XO sex-chromosome system (Nakamura, 1983; Vitturi & Catalano, 1988). However, a chromosome value of 8 bivalents observed for *Tricolia speciosa* suggests that this species has the lowest chromosome number within the Archaeogastropoda (Table 1).

If we accept the idea that evolution in general (Mayr, 1970; Colombera & Lazzaretto-Colombera, 1978), and within the phylum Mollusca in particular (Vitturi et al., 1982; Rastotto & Cardellini, 1983; Vitturi et al., 1985a), proceeds via a decrease of chromosome number, although exceptions are certainly known (Vitturi et al., 1983), then the specialization of *Tricolia speciosa* is apparent. Moreover, it is held that evolved karyotypes are more symmetrical than those observed in the generalized species (Ohno, 1970; Colombera & Vitturi, 1978; Vitturi et al., 1987). If so, the specialization of *Tricolia speciosa*, which is remarkable in having all bi-armed chromosomes, would be further supported.

Data obtained from this study suggest that the Ag-staining pattern was, in this species, variable, as shown by the differences in the number of nucleoli/nucleus and in the number of chromosomes involved in the nucleolar organization. This variability, previously reported in fish (Howell & Black, 1979; Foresti et al., 1981; Thode et al., 1983) and in mammals (Goodpasture & Bloom, 1975; Henderson et al., 1976; Dev et al., 1977; Mikelsaar et al., 1977a,b; Winking et al., 1980), is currently interpreted as a differential transcriptional activity of the ribosomal DNA (Miller et al., 1976). Our results showing a correlation between the number of nucleoli and their dimensions seem to be consistent with the idea that nucleoli in interphase tend to fuse (Goldman et al., 1983).

Because chromosomes stained with acetic-orcein showed no achromatic zones, NORs are in our opinion unrelated to any satellite region in the species under study. In *Gobius fallax* (Pisces, Gobiidae) (Thode et al., 1983) and in other fish species (Almeida Toledo et al., 1981), the same conclusion was reached.

Comparatively small Ag dots in the chromosomes of diakinesis involving from zero to almost all bivalents, were observed. This fact leads us to speculate that in this species, as in human cells (Schwarzacher et al., 1978), a decrease in the NORs activity at meiotic metaphase-I occurs. However, in *Tricolia speciosa* it seems that a higher number of elements are involved in this activity at meiotic metaphase-I rather than at mitotic stages.

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FEEDING EXPERIMENTS ON AND ENERGY FLUX IN A NATURAL POPULATION OF THE EDIBLE SNAIL *HELIX LUCORUM* L. (GASTROPODA: PULMONATA: STYLOMMATOPHORA) IN GREECE

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ABSTRACT

Energy flux in *Helix lucorum* was studied using as food *Lactuca sativa*, *Urtica dioica* and *Petasites albus*. The highest daily consumption and assimilation rates were observed in newly hatched snails and the lowest rates in adult snails. Assimilation efficiency, mean monthly production, as well as the growth (Pg/I%) and ecological (Pg/A%) efficiencies, fluctuated with season, the generation and with the physiological state of the snails. Snails fed on *L. sativa* showed higher assimilation efficiency than those fed on *U. dioica* or *P. albus*. Ingestion rate was found equal to 19.7% if snails were fed on *U. dioica* and 14.6% if they were fed on *P. albus*. Energy flow through *H. lucorum* population was 51.7 Kcal/m²/year if snails were fed on *U. dioica* and 29.2 Kcal/m²/year if they were fed on *P. albus*.

Key words: feeding experiments; energy flux; consumption; nutritional budget; *Helix lucorum*.

INTRODUCTION

Ingestion and assimilation are two essential phases of energy transport from one trophic level to another, and thus they compose an important part of ecosystem functioning. Terrestrial gastropods, as primary consumers, play an important role in matter and energy transport from producer level to upper trophic levels.

Studying the role of terrestrial molluscs in dynamics of woodland ecosystems, first Lindquist (1941) and then Mason (1970b) stressed the need for quantitative studies on food consumption and assimilation. Many studies have been published since on terrestrial pulmonates, such as those of Stern (1968, 1975) on *Arion rufus* and *Agriolimax reticulatus*, of Jennings & Barkham (1976) on *Arion ater*, of Zeifert & Shutov (1978, 1981) on *Bradybaena fruticum* and *Eobania vermiculata*, of Lazaridou-Dimitriadou & Daguzan (1978) on *Euparypha pisana*, of Charrier & Daguzan (1980) on *Helix aspersa*, and of Lazaridou-Dimitriadou & Kattoulas (submitted) on *Eobania vermiculata*. Similarly, many studies on population bioenergetics of freshwater pulmonates and prosobranchs exist, such as those of Aldridge et al. (1986) on *Viviparus georgianus*, of Russell-Hunter et al.

(1983, 1984) on *Helisoma trivolvis* and *Lymnaea palustris*, and of Aldridge (1982) on *Lepidoxis carinata*, etc.

The present study forms part of a wider investigation into ecophysiology of the edible snail *Helix lucorum* in Greece. Reported here are the results concerning the experiments on food consumption and assimilation in the laboratory, and estimates of population metabolism in the field.

METHODS AND MATERIALS

The experiment lasted from April 1984 to March 1985. The snails used in the experiment were collected from a natural habitat of *Helix lucorum* in the Logos region of Edessa, northern Greece, where its ecology and biology have been studied. Every month, nine snails from each generation present in the field at that time were collected and transferred to the laboratory. The number of generations was known from the demographic analysis of the populations of *Helix lucorum*. Adult snails have a wide overlap of generations that could not be distinguished; therefore, the assumption that adults of different ages (snails with an age of three years or more) belong to the same cohort was taken

into account (Staikou et al., 1988). During winter months, that is December, January and February, no experiments were done because the snails hibernated.

The experiments were carried out in the laboratory under semi-natural conditions. Lighting followed the natural cycles, and temperature coincided with natural temperature at the given month. Snails were kept in individual glass chambers (40 × 20 × 15 cm), and high humidity (~ 85%) was supplied by a piece of sponge soaked with water and a small pot of water. Three different kinds of food were used: (a) *Lactuca sativa*, which in general is considered as "good" food for snails, and (b) *Urtica dioica* and *Petasite salbus*, which were the most abundant food resources in the study site of *Helix lucorum*. There were three replicates for each kind of food, that is nine replicates for each generation. Each month, 36 to 54 chambers were used depending on the number of generations that existed in the field.

The methodology followed was that of Lazaridou-Dimitriadou & Daguzan (1978). The amount of excrement produced daily was determined by means of a marker technique (Phillipson, 1960). Before the experiment, snails were fed carrot slices, which resulted in colour-marked faeces. Then the snails were weighed, measured and exposed to the experimental food, which was presented in pieces of specific surface area (4 cm × 4 cm). Food was replaced every 24 hours. The amount of food consumed was estimated as the area grazed by the individual snails, measured by the surface area of the remnant with a planimeter. This method was used as it gave the best results after preliminary experimentation with other methods, such as the difference of live weight between the food given to the snails and control food material kept under the same conditions (Bogucki & Helczyk-Kazecka, 1977). The method of drying food material, weighing, then rehydrating, giving it to the snails, and then drying and weighing again, which has been shown useful in feeding experiments with aufwuchs as food for fresh-water snails (Tashiro et al., 1980), could not be used, as our snails would not feed on food treated this way. The dry weight of food consumed was calculated for each kind of food by using the regression equations of leaf surface on leaf dry weight (16 cm² of *L. sativa* is equal to 0.043 ± 0.0064 g dry weight, 16 cm² of *U. dioica* is equal to 0.0518 ± 0.0095 g dry weight, and 16 cm² of *P. albus*

is equal to 0.0379 ± 0.0037 g dry weight). The above equations were obtained by using 60 pieces of 16 cm² from each kind of food; 30 pieces were collected during spring (April) and 30 more during autumn (October); their dry weight was obtained after drying *in vacuo* in the presence of CaCO₃. The faeces of each snail were collected, dried and weighed.

After the experimental period, which lasted seven days, the snails were again measured, weighed and given carrot food. The faeces were collected until the coloured marker faeces appeared. At the end of each experiment, the snails were killed, the shell was separated from the body and both were dried *in vacuo* at room temperature in the presence of CaCO₃. Dry weights of shell and body were taken seven days later.

To quantify the daily consumption and assimilation rates as well as the growth and ecological efficiencies, the same formulae as Lazaridou-Dimitriadou & Kattoulas (submitted) and the I.B.P. global productivity symbols listed by Petruszewicz & Macfayden (1970) were used.

$$\text{Daily consumption rate} = \frac{C(\text{mg})}{L.W.(\text{g})}$$

$$\text{Daily faecal production rate} = \frac{FU(\text{mg})}{L.W.(\text{g})}$$

$$\text{Daily assimilation rate} = \frac{C(\text{mg}) - FU(\text{mg})^*}{L.W.(\text{g})}$$

$$\text{Assimilation efficiency} = \frac{C(\text{mg}) - FU(\text{mg})}{C(\text{mg})}$$

Production (Pg) or GP = the amount of dry tissue elaborated in the snail body and shell per unit of time (mg/month)

$$\text{Growth efficiency (or gross growth efficiency)} = \frac{Pg(\text{mg})}{I(\text{mg})} \times 100$$

$$\text{Ecological efficiency (or net growth efficiency)} = \frac{Pg(\text{mg})}{A(\text{mg})} \times 100$$

*C (mg)—FU (mg) stands for TA (total assimilated) according to conventional component labels (Russell-Hunter & Buckley, 1983)

[where C^{**} = dry weight of food consumed daily, FU^{***} = dry weight of faeces produced daily, L.W. = mean snail live weight (body + shell), I = dry weight of food ingested per month ($C(\text{mg}) \times 30$), A = dry weight of food assimilated per month ($C(\text{mg}) \times 30 - F(\text{mg}) \times 30$).

Monthly production, that is dry-weight gain of each snail could not be directly measured. It was extrapolated by the regressions of the dry body and shell weight in relation to the largest shell diameter (D) and the calculated organic content of the shell. Different regressions were used for juvenile and adult *H. lucorum*, because it was known from the study of the relative growth that their growth rate differs (Staikou et al., 1988):

For $D < 22$ mm the following regressions, where W_b = dry body weight and W_s = dry shell weight, were used:

$$\text{Log } W_b = 2.592 \text{ Log } D - 3.884 \quad (N = 123, r^2 = 0.884)$$

$$\text{Log } W_s = 3.16 \text{ Log } D - 4.7 \quad (N = 123, r^2 = 0.835)$$

for $21 \text{ mm} \leq D \leq 36 \text{ mm}$ there were used:

$$\text{Log } W_b = 2.801 \text{ Log } D - 4.11 \quad (N = 163, r^2 = 0.754)$$

$$\text{Log } W_s = 3.865 \text{ Log } D - 5.527 \quad (N = 163, r^2 = 0.802)$$

and for $D \geq 36$ mm there were used the following:

$$\text{Log } W_b = 3.338 \text{ Log } D - 4.945 \quad (N = 118, r^2 = 0.319)$$

$$\text{Log } W_s = 3.114 \text{ Log } D - 4.408 \quad (N = 118, r^2 = 0.398)$$

For the determination of the shell organic matter, a known quantity of homogenated shell material was treated with 5 N HCl solution, the remainder was treated with distilled water six to seven times to wash away the calcium chloride (CaCl_2) left and then dried at 65°C . The shell organic matter was determined as the residual weight of dry shell weight left after the above-described treatments. The replicability of these measures was checked by burning a known quantity of

homogenated shell material, after drying it to constant weight, in a muffle-furnace at 560°C to obtain by difference an ash-free dry weight.

The best method of computing organic growth is microbomb calorimetry, that is assessment of energetic equivalents of organic biomass, or analyses of fat, protein and carbohydrates at all stages (Russell-Hunter et al., 1968). Another widely used method is estimating organic carbon by wet oxidation (Russell-Hunter et al., 1968), and the C/N ratio at all stages. In this study, bomb calorimetry was used mainly to produce comparable results with most of the existing studies on terrestrial snails. Thus, all rates of consumption, egestion and assimilation, as well as production and growth and ecological efficiencies, were computed in terms of both dry weight and energetic values. The energy content of *H. lucorum* body, shell organic matter, and faeces, as well as the energy content of the three food materials, was determined on a Phillipson microbomb calorimeter. For each sample, two subsamples were burnt and whenever a difference greater than 0.05 appeared a third and sometimes a fourth subsample was used.

Appendices with detailed calculations of all the rates and efficiencies used can be obtained by the Department of Zoology, School of Biology, Aristotelion University of Thessaloniki, 54006 Thessaloniki, Greece.

RESULTS

The percentage of organic matter in the shell of *H. lucorum* was found to equal 1.7%. The caloric value of the organic material of the shell was 4.797 ± 0.24 cal/mg ash free dry weight.

A comparison between dry weight of food eaten and dry weight of faeces produced revealed a positive correlation between the above two parameters for all food materials used. Coefficient correlation was very high for animals fed on *Lactuca* ($r = 0.951$, $N = 43$) and *Petasites* ($r = 0.907$, $N = 43$) and somewhat lower for animals fed on *Urtica* ($r = 0.751$, $N = 43$).

The highest values for daily consumption rate were observed in newly hatched snails, aged one month for animals fed on *Lactuca* (89.55 mg/g) and *Urtica* (61.73 mg/g), and in juveniles aged three months for animals fed on *Petasites* (28.26 mg/g). Values of this parameter declined with age and became very

**C(mg) stands for TI (total ingested) according to conventional component labels (Russell-Hunter & Buckley, 1983)

***FU stands for NA (not assimilated) according to conventional component labels (Russell-Hunter & Buckley, 1983)

low in mature animals with a largest shell diameter greater than 35 mm. For animals fed on *Lactuca*, the lowest value observed was 2.63 mg/g. For those fed on *Urtica*, 1.11 mg/g, and for those fed on *Petasites*, 0.07 mg/g. Values of daily faecal production rate and daily assimilation rate followed the general pattern of daily consumption rate for all kinds of food used.

The values of the above parameters of the individual nutritional budget of the snails were also influenced by the time of the year or by the physiological state of the animals. Thus, high values appeared during spring, especially in May, and autumn (September, October). Also, high values in adult snails were shown in June before the reproductive period.

Overall assimilation efficiency was higher and more constant in animals fed on *Lactuca* (82%) than in animals fed on *Urtica* (73%) and *Petasites* (59%) (Table I). Values of this parameter calculated for the different generations showed that young snails prefer *Lactuca* and *Urtica* and show a smaller preference for *Petasites*. Mature snails show a marked preference for *Lactuca* while their assimilation efficiency was almost the same, ranging from 30%–80% when fed on *Urtica* or *Petasites* (Figs. 1–3).

Values of mean monthly production (Pg), growth (Pg/l) and ecological (Pg/A) efficiencies varied with the season and/or the physiological state of the snails, becoming highest in June irrespective of the kind of food. Also, high values were observed in September or November and sometimes in March and April (Figs. 1–3).

In general, values of growth and ecological efficiencies were higher in snails fed on *Petasites* and lower in snails fed on *Urtica* or *Lactuca* (Table I). It has to be stressed, though, that these values were underestimated because mucus production was not taken into consideration (Lamotte & Stern, 1987).

Using the values of the calorific content of the body and the excrement of the snails at the end of each experiment, it was possible to convert the parameters of the individual nutritional budget of *H. lucorum* in caloric values (Table II).

Values of monthly ingestion (EI) and monthly assimilation (EA) fluctuated according to the season or/and the physiological state of the animals. Highest values were always observed in late spring (May) and in autumn (September, October) (Figs. 1–3).

Snails fed on *L. sativa* also showed high values in June and July (Fig. 1).

Fluctuations in production (EPg), gross growth (EPg/EI) and net growth (EPg/EA) efficiencies follow the same pattern as when these parameters are calculated in terms of dry weight (Figs. 1–3).

Ingestion rate, which shows the populations' impact on the environment, was estimated from the values of annual turnover ratio ($P/B = 1.24$) (Staikou et al., 1988) as well as the values of growth efficiency EPg/EI (which were 0.65 and 0.85 when snails were fed on *Urtica* or *Petasites* respectively). Ingestion rate was found equal to 19.7% if snails were fed on *Urtica* and 14.6% if they were fed on *Petasites*.

Energy spent for egg production was calculated by: (a) the caloric content of eggs (Table II), (b) the mean number of eggs laid (50.5 ± 21.3), and (c) their mean weight (0.43 ± 0.12 g.). By multiplying the eggs laid per snail per year by their mean weight, and then this number by the caloric content of eggs, the mean reproductive output in terms of energy values for any adult snail was assessed. Knowing the duration of life of *H. lucorum* (14 years) and the number of eggs laid by an individual the first and following years (Staikou et al., 1988), the reproductive output in energetic values was calculated for the life span of *H. lucorum*.

It was known by the feeding experiments the energy ingested and assimilated by an individual till its maturity, as well as the energy assimilated during a year of an adult's life. Multiplying the last value, which corresponds to an adult's life, by the number of years an adult snail may live after the attainment of its maturity, it was possible to compute the individual energy budget of *H. lucorum* during its life time (Table I). It was found that of the total assimilated energy a snail spends 14.8% for growth, 2.3% for egg production, and 82.9% in metabolic energy when fed on *Urtica*, and 22.5%, 3.7% and 73.8%, respectively, when fed on *Petasites*. It was also found that the reproductive output was equal to 13.6% and 14.3% of the non-metabolic assimilated energy when snails were fed on *Urtica* and *Petasites* respectively.

DISCUSSION

As stated by Russell-Hunter et al. (1968), the organic material in the shell represents

TABLE 1. The principal parameters of the individual nutritional and energy budget of *Helix lucorum* during its life time, that is 14 years.

Data	In 168 months (mg)			In 168 months (cal)			In one day (mg)			In one day (cal)		
	<i>Lactuca</i>	<i>Urtica</i>	<i>Petasites</i>	<i>Lactuca</i>	<i>Urtica</i>	<i>Petasites</i>	<i>Lactuca</i>	<i>Urtica</i>	<i>Petasites</i>	<i>Lactuca</i>	<i>Urtica</i>	<i>Petasites</i>
Ingestion	376974	174134	87831	1540762	558011	375409	74.8	34.6	17.43	305.7	110.7	74.5
Assimilation	308231	127844	51484	1132202	347736	214894	61.2	25.4	10.20	225.0	69.0	42.6
Growth	10590	11246	7520	64560	51466	48305	2.1	2.2	1.50	12.8	10.2	9.6
production												
Energy spent	432	432	432	1674	1674	1674	—	—	—	—	—	—
for egg												
production the												
first year												
Energy spent	2087	2087	2087	8089	8089	8089	—	—	—	—	—	—
for egg												
production												
Metabolic	295554	114510	41879	1061552	288181	158500	58.7	22.8	8.30	210.6	57.2	31.4
energy												
EA/EI %	82	73	59	74	62	57	—	—	—	—	—	—
EP/EI %	2.8%	6.5%	8.6%	4.2%	9.2%	12.9%	—	—	—	—	—	—
EP/EA %	3.4%	8.8%	15.0%	5.7%	14.8%	22.5%	—	—	—	—	—	—

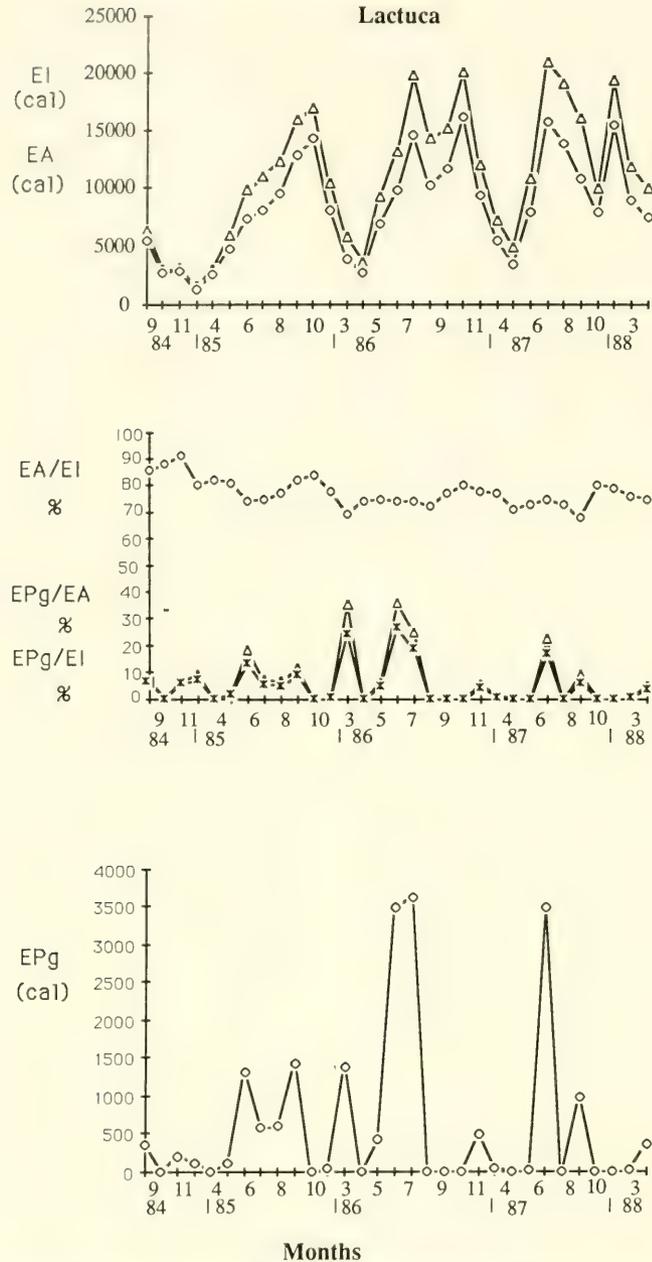


FIG. 1. Mean monthly ingestion (cal) (EI), mean monthly assimilation (cal) (EA), mean assimilation efficiencies (%) (EA/EI), ecological efficiencies (%) (EPg/EA), growth efficiencies (%) (EPg/EI), and mean monthly production EPg (cal) during the life cycle of *Helix lucorum* fed on *Lactuca sativa*.

[For the construction of Figure 1, the feeding experimental results of each generation (G1, G2, G3 or G4) known to be present in the field each month from April 1984 to March 1985 (according to the already published life-cycle data of Staikou et al., 1988) were combined in computations assuming that the first generation (G1) is followed by G2 at the end of the first year and G2 is followed by G3 at the end of the second year and G3 by G4 at the end of the third year. So feeding and growth parameters could be followed monthly from hatching till the maturity of the snails (except during winter time when the snails hibernate) that is for 3.5 years from September 1984 to March 1988, although feeding experiments lasted one year.]

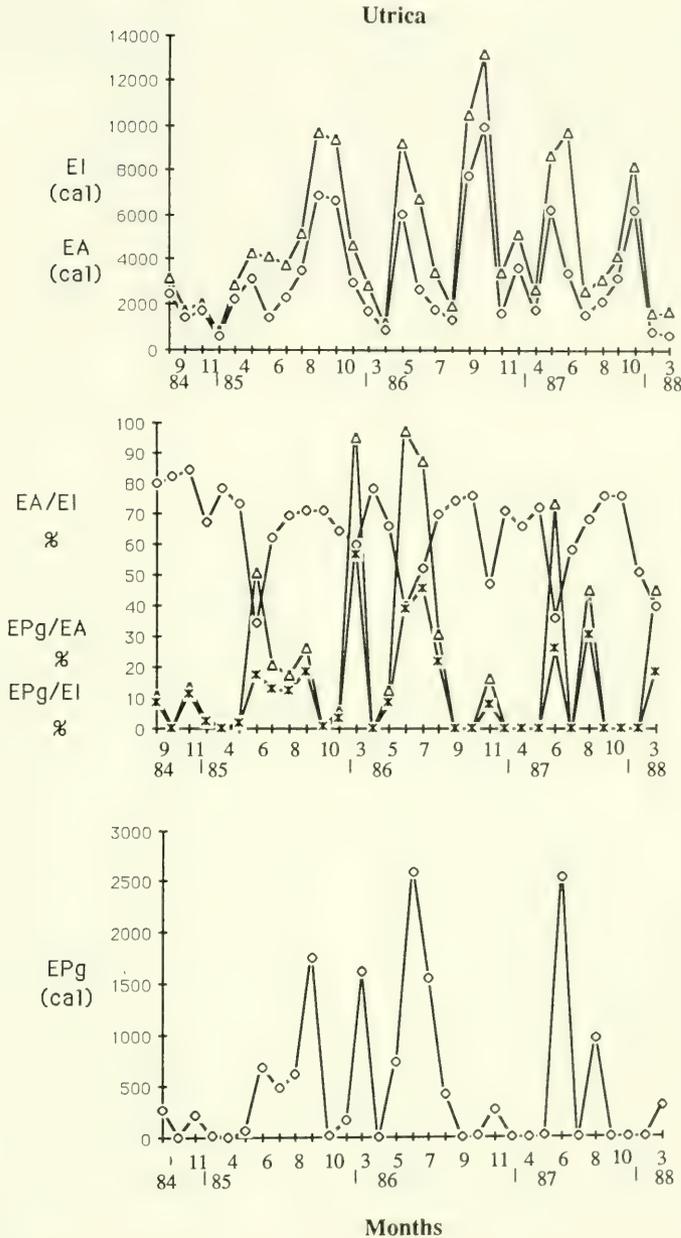


FIG. 2. Mean monthly ingestion (cal) (EI), mean monthly assimilation (cal) (EA), mean assimilation efficiencies (%) (EA/EI), ecological efficiencies (%) (EPg/EA), growth efficiencies (%) (EPg/EI) and mean monthly production EPg (cal) during the life cycle of *Helix lucorum* fed on *Urtica dioica* [For the construction of Figure 2, the feeding experimental results of each generation (G1, G2, G3 or G4) known to be present in the field each month from April 1984 to March 1985 (according to the already published life-cycle data of Staikou et al., 1988) were combined in computations assuming that the first generation (G1) is followed by G2 at the end of the first year and G2 is followed by G3 at the end of the second year and G3 by G4 at the end of the third year. So feeding and growth parameters could be followed monthly from hatching till the maturity of the snails (except during winter time when the snails hibernate) that is for 3.5 years from September 1984 to March 1988, although feeding experiments lasted one year.]

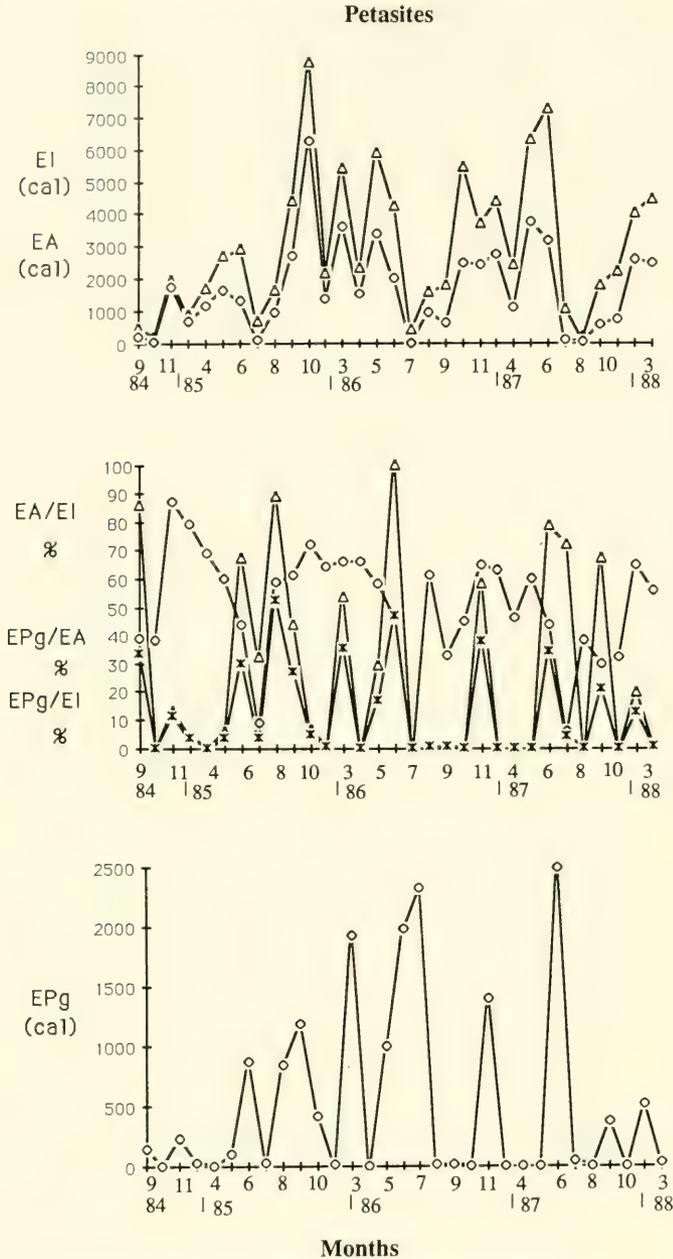


FIG. 3. Mean monthly ingestion (cal) (EI), mean monthly assimilation (cal) (EA), mean assimilation efficiencies (%) (EA/EI), ecological efficiencies (%) (EPg/EA), growth efficiencies (%) (EPg/EI) and mean monthly production EPg (cal) during the life cycle of *Helix lucorum* fed on *Petasites albus*.

[For the construction of Figure 3, the feeding experimental results of each generation (G1,G2,G3 or G4) known to be present in the field each month from April 1984 to March 1985 (according to the already published life-cycle data of Staikou et al; 1988) were combined in computations assuming that the first generation (G1) is followed by G2 at the end of the first year and G2 is followed by G3 at the end of the second year and G3 by G4 at the end of the third year. So feeding and growth parameters could be followed monthly from hatching till the maturity of the snails (except during winter time when the snails hibernate) that is for 3.5 years from September 1984 to March 1988, although feeding experiments lasted one year.]

TABLE 2. Calorific content, of *Lactuca sativa*, *Urtica dioica* and *Petasites albus* leaves, as well as of shell and egg matter of *Helix lucorum* (where N = number of trials, s = standard deviation)

Data	Mean cal/mg \pm s with ash	Mean cal/mg \pm s without ash	Mean ash weight % \pm s	Mean water weight % \pm s
<i>Lactuca sativa</i> (N = 60)	3.7689 \pm 0.2116	4.0040 \pm 0.2813	7.55 \pm 0.51	92.00 \pm 0.006
<i>Urtica dioica</i> (N = 60)	2.4093 \pm 0.2584	3.2705 \pm 0.2383	26.50 \pm 1.11	72.20 \pm 0.009
<i>Petasites albus</i> (N = 60)	3.9119 \pm 0.0933	4.2741 \pm 0.0882	8.14 \pm 0.19	89.00 \pm 0.008
Mean shell organic matter (N = 9)	4.2143 \pm 0.2830	4.7973 \pm 0.2452	18.40 \pm 0.12	75.20 \pm 5.30
Mean egg matter (N = 4)	3.1325 \pm 0.0482	3.8750 \pm 0.0799	20.52 \pm 0.42	82.40 \pm 3.20

stored energy that is never turned over until death, except where external erosion or internal shell resorption takes place. The percentage of the organic matter in the shell of *H. lucorum* was found lower than that reported for *H. aspersa* by Charrier & Daguzan (1980) and for *Eobania vermiculata* by Lazaridou-Dimitriadou & Kattoulas (submitted). It was somewhat similar to that reported by Lazaridou-Dimitriadou & Daguzan (1978) for *Euparypha pisana*. The calorific content of the shell was similar to that reported by Hughes (1970) for the bivalve *Scrobicularia plana*, by Lazaridou-Dimitriadou & Daguzan (1978) for *E. pisana*, and by Charrier & Daguzan (1980) for *H. aspersa*. It was slightly lower than that reported by Lazaridou-Dimitriadou & Kattoulas (submitted) for *E. vermiculata*.

High values of daily consumption rate, daily faecal production rate and daily assimilation rate in newly hatched snails may be due to their higher metabolic rate in relation to older ones. The same phenomenon has been observed in *Arion ater* (Jennings & Barkham, 1976), in *Agriolimax laevis* (Stern, 1979), in *Eobania vermiculata* (Zeifert & Shutov, 1978; Lazaridou-Dimitriadou & Kattoulas, submitted), in *Euparypha pisana* (Lazaridou-Dimitriadou & Daguzan, 1978), and in many non-marine prosobranch gastropods (Aldridge et al., 1986). The season of the year seemed to influence the values of the above parameters. The peaks observed in spring (mainly in May) were probably related to the fact that this is the period of maximum activity for *H. lucorum* in the field (Staikou et al., 1988). Minor peaks observed in autumn (e.g. September or/and October) were probably due to the fact that snails are less active than in May but accumulate food reserves prior to hibernation.

Seasonal fluctuations in values of these parameters have been also reported by Lazaridou-Dimitriadou & Kattoulas (submitted) for *E. vermiculata*. Seasonal degrowth has been shown in freshwater pulmonate gastropods (Russell-Hunter, 1983, 1984).

High assimilation efficiencies in animals fed on *Lactuca* have been reported by Bogucki & Helczyk-Kazecka (1977) for adult *H. pomatia* and by Charrier & Daguzan (1980) for *H. aspersa*. Mason (1970a) and Richardson (1975a) also found that snails show higher assimilation rates when fed on *Lactuca* and much lower when fed on *Urtica*. Assimilation efficiency drops in October or November just before hibernation and in May or June when snails are fed on *Urtica* and in July-August when fed on *Petasites* when higher temperatures occurred in 1984 (Staikou et al., 1988, fig. 2). The less constant assimilation efficiency when snails are fed on *Urtica* and *Petasites* might be attributed to their different quality each month, because they were collected from the field, whereas *Lactuca* came from cultivations throughout the year. The effects of food quality on assimilation and differential catabolism have been shown in non-marine gastropods (Aldridge et al., 1986). Assimilation efficiency in animals fed on *Urtica* is somewhat similar to that reported by Jennings & Barkham (1976) for *Arion ater* (69%) and by Lazaridou-Dimitriadou & Kattoulas (submitted) for *E. vermiculata* (81%). It is higher than that reported by Mason (1970a) for *Hygromia striolata* (52.40–8.78%) and *Discus rotundatus* (47.70–8.89%) feeding on *Urtica*. The low efficiencies in the latter case may be due to the fact that Mason ran his experiments at 10°C.

The peaks observed in the values of mean

monthly production (Pg), growth (Pg/l) and ecological (Pg/A) efficiencies correspond to the months after the most rapid growth (March, April and mainly in June), or prior to hibernation (September to November) when food reserves are accumulated. The above differences were also assessed as changes in overall efficiencies or in physiological rates in non-marine prosobranch gastropods (Aldridge et al., 1986).

Ingestion rate when snails are fed only on *Urtica* accords with the value mentioned by Lazaridou-Dimitriadou & Kattoulas (submitted) for *E. vermiculata* and by Richardson (1975b) and Williamson (1975) for *Cepaea nemoralis*.

The calorific content of the snail's body is comparatively low in relation to that of other animals (Slobodkin & Richman, 1961; Slobodkin, 1962; Golley, 1961), and this is probably due to the low quantity of lipids in the snail's body (Hughes, 1970). Knowing the difference in the calorific content of the bodies of the mature snails before and after the reproductive period (June: 12896.2 cal—August: 11647.3 cal = 1248.9 cal.) and the total reproductive output (1674 cal) (Table I), it was possible to calculate that 25.4% of the energy spent for egg production comes from concurrent trophic input.

Estimates of reproductive output as proportion of total assimilated energy (when snails were fed on *Urtica* or *Petasites*) accord well with the values given by Calow (1978) for some iteroparous fresh-water gastropods, whereas they were much lower than the values given for the semelparous species. Estimates of reproductive output as a proportion of non-metabolic assimilated energy were lower than all the values reported by the same author for the iteroparous species, such as *H. lucorum*, and this may be related to the longer life span of *H. lucorum*.

Knowing the mean number of snails in every size class/m² (Staikou et al., 1988), as well as the quantity of food consumed by them per month, it was possible to estimate the annual consumption and the annual faecal production of the snails in the field. If snails would feed only on *Urtica*, annual consumption would equal 15.81 g/m², and annual faecal production, 3.54 g/m² (equivalent values in calories were 51.7 Kcal/m²/year and 17.3 Kcal/m²/year); mean assimilation efficiency for all size classes was 77.6%. If snails would feed only on *Petasites*, the annual consumption would equal 6.8 g/m², and annual

faecal production, 2.6 g/m² (equivalent values in calories were 29.2 Kcal/m²/year and 13.1 Kcal/m²/year); mean assimilation efficiency for all size classes was 61.8%. The annual consumption values found in this study, are higher than those found by Mason (1970b) for different snail species fed on beech litter, by Jennings & Barkham (1976) for *Arion ater*, and by Zeifert & Shutov (1978) for *Bradybaena fruticum*. These differences may be due to the different density of the snail species in the field or to the different food used for the above studies. The difference in field density may also be another reason for the higher values of annual consumption and energy flow through the population of *E. vermiculata* fed only on *Urtica* (Lazaridou-Dimitriadou & Kattoulas, submitted).

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TIDAL MICROGROWTH BANDS IN *SIPHONARIA GIGAS* (GASTROPODA, PULMONATA) FROM THE COAST OF COSTA RICA

D. J. Crisp,¹ J. G. Wieghehl² & C. A. Richardson³

ABSTRACT

Siphonaria gigas growing on the coast of Costa Rica under a semi-diurnal tidal regime lays down one microgrowth band per tide. This relationship was used to measure the rate of incremental growth at the anterior and posterior margins of the shell. The growth rate was somewhat irregular, and the anomalies at each margin were shown probably to compensate each other. Barnacle cover probably reduced growth rate. An approximate curve of diameter increase against time, assuming the Bertalanffy equation, is given.

Key words: *Siphonaria*, growth rates, microgrowth bands.

INTRODUCTION

Within the calcareous skeletons of many living marine invertebrates occupying the intertidal zone or shallow sublittoral are minute banding patterns, known as microgrowth bands. These may best be seen by making acetate peel replicas of a polished and etched section of the shell cut along the direction in which additional shell is laid down during its growth. These microgrowth bands appear as a series of light and dark bands when viewed under the microscope by transmitted light. The darker bands are usually narrower and have been termed "growth bands" while the lighter intervening areas were termed "growth increments" (Richardson et al., 1979) although both bands and increments represent additions to growth of the shell.

Such tidal banding patterns have been demonstrated in a variety of animal groups, quite independently of their phylogenetic origins. They were first demonstrated by Evans (1972, 1975) in the Pacific cockle *Clinocardium nuttallii*, and are perhaps most clearly expressed in other members of the Cardacea. Richardson and his co-workers' studies that underlie our present understanding of the endogenous and exogenous nature of tidal bands, their relation to other environmental factors, and their interaction with spring and neap tidal changes were carried out with the European cockle, *Cerastoderma edule*, under

the semi-diurnal tidal regime of northwestern Europe (Richardson et al., 1979, 1980a, b, 1981). The few gastropods studied so far contain tidal increments in the coiled whorls of the shell in typical forms or, in the case of limpets, along the corresponding region, viz. outer sides of the shell (Ekaratne & Crisp, 1982, 1984). The evidence for tidal bands in the primitive polyplacophoran molluscs is less certain, but a regular 28-day periodic series of patterns were observed in New Zealand chitons by Jones & Crisp (1985) suggesting a tidal periodicity over the 14-day lunar cycle. Barnacle growth, analysed by Bourget & Crisp (1975a, 1975b, 1985) in *Balanus balanoides*, also was found to show periodic growth with tidal banding in the shell, and similar banding patterns were demonstrated also in *Elminius modestus* (Crisp & Richardson, 1975).

Of particular interest are the marine pulmonates. Pulmonates are believed to have evolved air breathing from the main stock of marine gastropods to fit them to life on land. *Siphonaria* browses on rocks in the littoral zone and has evolved by convergent evolution a shell morphology like that of archaeogastropod limpets and a similar behaviour pattern (Morton, 1968; Barnes, 1982). The question arises whether shell growth occurs in increments separated by tidal bands or whether it grows more or less continuously without reference to tides.

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TABLE 1. Positions of sites and conditions of growth in three groups of *Siphonaria gigas*.

Group no.	Coast	Band-dating technique	Date of marking	Date of collection	No. of days between marking and collection	<i>Chthamalus</i> presence
1	P.M.E.	file-marked identity no.	5.VII.85	17.VIII.85	44	absent
2	P.M.W.	identity no. only	5.VII.85	17.VIII.85	44	absent
3	P.M.W.	identity no. only	5.VII.85	17.VIII.85	44	present

P.M.E.: Punta Mala East; P.M.W.: Punta Mala West

MATERIALS AND METHODS

Siphonaria gigas Sowerby, 1825, was collected from two shores on the west coast of Costa Rica, Punta Mala West and Punta Mala East, Guanacaste Province (Ortega 1985, 1986; Sutherland & Ortega, 1986), from mid to high level of the intertidal zone. The conditions of growth and site details of three groups of animals used in this investigation are summarised in Table 1. The specimens of group 1 only were "file-marked" at the growing edge adjacent to the rock surface at the time of low water on 5 July 1985, without removal from the rock. Simultaneously, a small plastic tag was fixed to the side of the shell with araldite for individual identification. Each individual of groups 1, 2 and 3 were so labelled, but only those of group 1 were also file marked. A file mark in the European archeogastropod limpet *Patella vulgata* causes a cleft to be formed that can be related to a particular growth band, giving it the relevant date of the edge of the shell at that point. Ekaratne & Crisp (1984) described alternative methods of "band dating" shells and found file marking to be one of the more reliable techniques. However, they noted that it usually reduced shell growth rate for a number of days afterwards so that one or two bands immediately after file marking might be lost completely. Similarly, the file marking procedure was found to result in a slight growth check in *S. gigas*, which could be seen as a weak ring running around the surface from the original file mark, and as a cleft seen in section (Fig. 1). Similarly, some of the shells that had been simply given an identity tag also appeared to have been affected by the disturbance, producing a small cleft. Since these individuals had neither been removed from the rock nor filed, the disturbance was minimal and in

some individuals it was not possible to identify such a cleft so that the bands could not be dated.

After having been collected on 17 August 1985, the animals were immediately killed and the tissues removed from the shell. On arrival in the United Kingdom, any adherent barnacles or debris were removed from the outside of the shell, the tag was removed, the shells scrubbed, dried and labelled. The identity number was written in indelible ink on the inside of the shell, and any external ridge associated with the file mark or attachment of the tag was also outlined with an arrow pointing to it (Fig. 2). Thus, the disturbance mark or cleft in the acetate peel could be related to the appropriate band seen in section. Each shell was embedded in "metaset" resin, left for at least 15 h to harden, and cut by hacksaw along its maximum diameter. It was smoothed and polished as recommended by Richardson et al. (1979) using a series of increasingly fine abrasives (340, 120 wet and dry trimite paper), and polished for 30 seconds on cloth soaked in household metal polish "Brasso." It was washed in mild detergent and finally etched for 20 minutes in a 1% "Decal," a formic-acid-based histological decalcifying fluid. After a further rinse in distilled water, it was air dried for 2–3 hours and the section was ready for replication. The appropriate size of acetate sheet (replicating material) was cut out, wetted briefly with ethyl acetate and laid on the section with air bubbles eliminated as far as possible. The section and replica were placed under a plastic box to reduce the rate of evaporation of ethyl acetate. After at least 15 minutes the replica was peeled off and kept flat by holding between coverslip and microscope slide. Peels are best viewed in a low power phase contrast microscope in air, not in mounting medium.

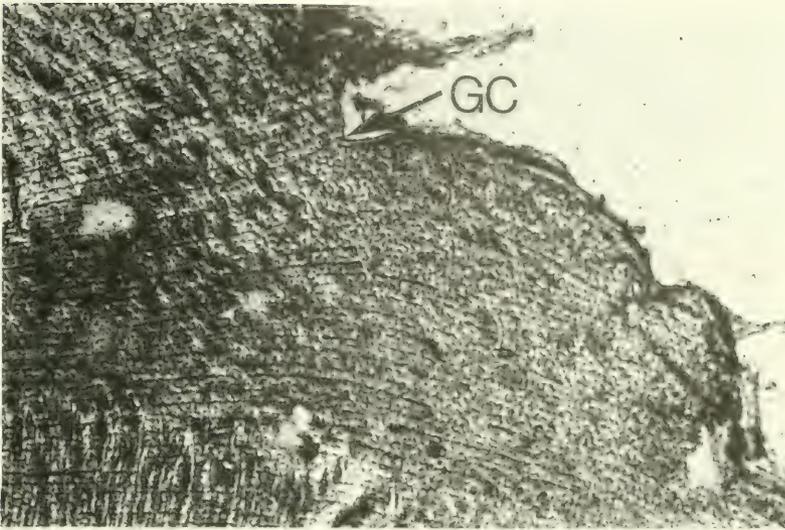


FIG. 1. An enlarged photograph of the acetate peel replica of *Siphonaria gigas* in the region of growth. GC: cleft indicating growth check. Parallel dark lines indicate tidal bands separated by increments. The growth bands are superimposed on light and dark patches caused by varied orientations of crystallites which are generally orthogonal to the direction of the growth bands and increments.

Counting Bands

Where possible the cleft or growth check clearly associated with a file mark or thought to be caused by disturbance through tagging was identified. The first band at this mark was taken as the datum for counting the number of increments between the check and shell edge. As can be seen in Figure 2, growth is not symmetrical around the shell, but the anterior end becomes steeper than the posterior, as in most limpets. Thus, any section in the anterior-posterior plane exposes two growth regions, the anterior being shorter than the posterior. Assuming that the shell increases all round by concurrent increments, the band width should be shorter along the anterior half but the number should be the same. Band counts were made from the growth checks to the anterior (A) and posterior (P) margins of the shell, and each count was repeated. From the band counts and associated statistical tests we sought the answer to the following questions.

1. Did the anterior and posterior profiles manifest the same number of bands?
2. Were the bands laid down at tidal intervals?

3. Were growth rates influenced by spring or neap tidal periods?
4. Did barnacle cover influence growth rate?
5. Did locality influence growth rate?

Measurements

Before embedding the shells in resin, each shell was scrubbed clean, dried and weighed to the nearest 10 mg (W) and its longer diameter (D) and height (H) measured using vernier calipers within 0.1 mm. The total growth between the disturbance mark and the anterior and posterior margins was measured using a calibrated eyepiece graticule to an accuracy of $\pm 1\%$.

Tidal data

The Tidal Institute at Bidston kindly supplied tidal data for the Standard Port of Panama (Balboa) for July 1985. A normal semi-diurnal pattern of tides operates at Punta Mala, with a maximum range of 5 m at springs and a minimum of 2 m at neaps. There were 83 tidal emersions between 5 July and 17 August 1985.

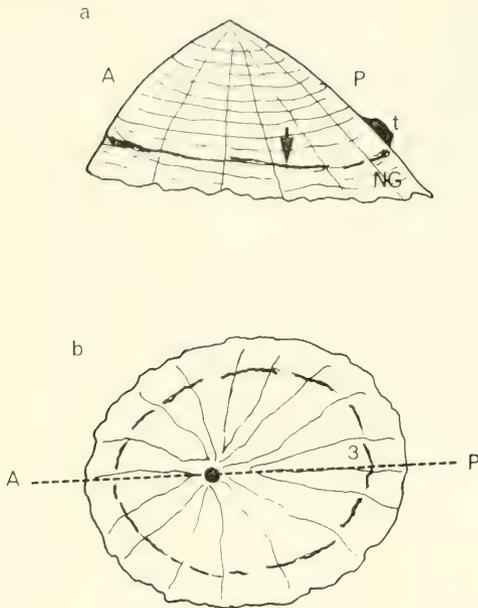


FIG. 2. (a) Side view of *Siphonaria gigas*. Arrow points to disturbance mark. NG: new growth after disturbance, t: marking tag. (b) View of the interior of the shell showing identity (no. 3) and direction of saw cut along the anterior (A) and posterior (P) direction passing through the apex (black dot).

RESULTS

1. Shell Measurements

A comparison of the relationships between shell weight, shell diameter and shell height revealed no significant difference among the three groups of shells described in Table 1. In all cases, volume calculated as $V = \pi D^2 H / 12$ rose with the weight (W), not significantly deviating from isometry (Table 2). The mean values of weight/volume was 0.9248 ± 0.0152 , but shell shape changed significantly with increase in size, as shown in Table 2. The average angle subtended by the shell to the horizontal (θ) was obtained as $\theta = \tan^{-1}(2H/D)$, and $\tan \theta$ increased with size as expected, the shell becoming taller. The mean value of θ over all individuals was 36.6° with 95% confidence limits 35.7° – 37.5° .

2. Microgrowth Bands

In many shells it was far from easy to identify the growth check with certainty. Only in those shells where the distance measured

from the external ridge to the edge of the growing tip corresponded with the distance of the cleft in the replica to the tip of the replica were the observations on numbers of bands included. The number of specimens giving countable bands and fulfilling the above criteria were six with file marks from Punta Mala East, four from Punta Mala West in the non barnacled area, and four from Punta Mala West in the barnacled area. The total number was thus 14, which was sufficient to determine the periodicity of the banding, but insufficient to validate such other questions as differences between sites, influence of barnacle settlement, and effect of spring and neap tidal periods.

Counts of Microgrowth Bands

The bands of the 14 selected shells were each counted along the anterior and posterior margins twice, except for two shells where the posterior margin was not accurately countable (Table 3).

If from all values for first readings (Count 1) are subtracted those of Count 2 an estimate of the reliability of counting can be made. There are 26 values, and the matched pairs t test for 25 degrees of freedom gives $t = 0.64$ (N.S.). There is therefore no significant difference between the two counts ($p = 0.53$).

The standard error of the difference between count 1 and Count 2 is 1.223 so that any count based on the mean of Count 1 and 2 can be relied upon to have a standard error of only ± 0.864 and confidence limits ± 3.7 of the average count observed, when $p = 0.05$.

Similar "matched pairs" t test was applied to the 12 average count differences between the counts at the anterior and posterior margins. The probability that counts at both margins could have come from the same population of values was 0.74, $p = 0.45$, showing that the results were not significantly different and that each margin could be regarded as a replicate count. When all 52 observations were assembled they gave a mean band number of 81.04 with 5% confidence limits lying between 80.31 and 81.77. This result can be compared with the theoretical value for one band per tide of 83.00, or of one band per day of 44.00. Though significantly less than 83.00 ($t = 5.35$, $p = 0.0001$) the deficiency from an exact tidal periodicity is only 2.4%. This is of the magnitude to be expected as a result of the disturbance caused by the

TABLE 2. Changes in shell characteristics with size (33 individuals).

Regression	Derived formula for 33 individuals	Expected index for isometry	Students t value for deviation from expectation	Significance
Log V on Log W	$1.09W^{0.96}$	1.000	-1.29	Not Sig.
Log H on Log V	$7.81V^{0.42}$	0.333	+5.49	Sig. <0.0001
Log H on Log W	$8.11W^{0.41}$	0.333	+4.60	Sig. <0.0001
Log D on Log V	$22.10V^{0.29}$	0.333	-5.48	Sig. <0.0001
Log D on Log W	$22.75W^{0.28}$	0.333	-4.10	Sig. <0.0001
Log H on Log D	$0.117D^{1.3603}$	1.000	+4.09	Sig. <0.0001
Tan θ on W	$0.660 + 0.0537W$	0.000	+5.62	Sig. <0.0001

TABLE 3. Band counts in the anterior and posterior margins of shells of *Siphonaria gigas* specimens grown in two natural environments.

Site and conditions	Specimen number	Number of bands counted in 'A' margin		Number of bands counted in 'P' margin	
		count I	count II	count I	count II
P.M.E. no <i>Chthamalus</i>	G	82	80	80	81
	E	81	82	82	84
	B	83	82	82	79
	O	80	80	79	80
	C	82	81	78	79
	R	83	82	83	83
P.M.E. no <i>Chthamalus</i>	4	78	78	—	—
	5	80	80	77	79
	6	82	83	80	80
	8	81	81	80	81
P.M.W. heavy <i>Chthamalus</i>	T	79	81	83	82
	S	81	82	82	82
	N	82	82	84	83
	F	81	82	—	—

('A') Anterior and ('P') Posterior margins

date marking and is clearly not daily but tidal banding as with many other marine molluscs.

Growth Rates

The longer profile at the posterior end of the shell implies a greater rate of growth than at the shorter anterior profile. The average total increment over 83 tidal cycles was indeed slightly higher at the posterior end 1.46 ± 0.13 mm than at the anterior (1.41 ± 0.12 mm) but not significantly so.

The two sites without barnacles present gave growth rates that did not differ significantly, showing increments in length of each margin at Punta Mala East of 0.0339 and at Punta Mala West of 0.0401 mm day⁻¹. At Punta Mala West in the presence of *Chthamalus* the increment in length averaged at 0.0305 mm day⁻¹. When the growth rates at

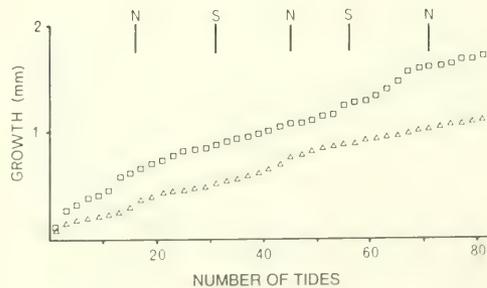


FIG. 3. Details of growth of a single individual *Siphonaria gigas* with very clear microgrowth lines. At anterior border, (Δ) and at posterior border (\square). N: neap tides, S: spring tides.

the two *Chthamalus*-free shores were combined and averaged (0.036 mm day⁻¹) they were not significantly higher than that at

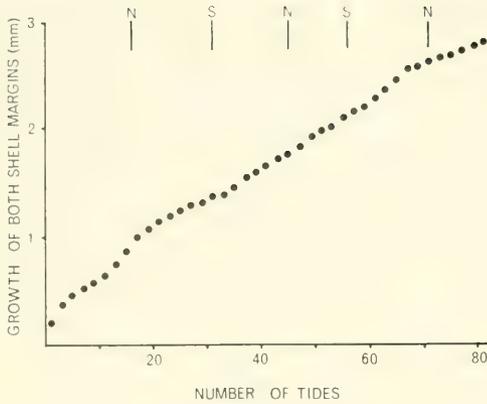


FIG. 4. Sum of growth at anterior and posterior borders of the same individual (Fig. 3) showing deceleration of growth rate with age. N: neap tide, S: spring tide.

Punta Mala West where *Chthamalus* was present ($t = 1.146$, $p = 0.25$). Similarly, a comparison of Punta Mala West shores with and without *Chthamalus* gave $t = 1.37$, $p = 0.20$, again a figure not usually regarded as significant. However, as measured, the growth rate in the presence of *Chthamalus* appears to have been reduced by 24%.

It should be noted that the growth rates of each side of the shell when added together and adjusted for shell slope (Ekaratne & Crisp, 1984) give the growth rate of the shell in height or diameter, which are the measurements usually quoted. However, a detailed measurement of both borders, anterior (A) and posterior (P) of shell N, giving the increment over each of two tidal cycles from the shell edge to 83 bands behind, as reproduced in Figure 3, shows that growth is far from uniform. It will be seen that both borders give sharp increases in length, and then slow down. Although A and P borders are coarsely correlated positively, since both are growing their random fluctuations appear to take place independently and without any common reference to the tidal cycle. Furthermore, if the increments of the A and P borders are summed and A + P is plotted against the number of the tidal event (Fig. 4), the resulting plot appears more regular. In order to test the possibility of compensatory growth, the increments at each border were listed and the mean increment subtracted to give the estimated acceleration or deceleration of growth for that tidal cycle at each border. These

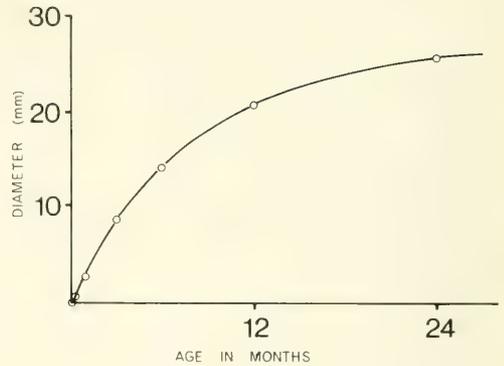


FIG. 5. Growth curve of a sample of four *Siphonaria gigas* in barnacled area based on tidal bands. $L = L_{\infty} (1 - e^{-kt})$, $L_{\infty} = 27.2$ mm, $K = 0.00206$ day $^{-1}$. Rate at 17 mm = 0.047 mm day $^{-1}$.

anomalies were then regressed against each other. They gave a negative correlation coefficient of 0.281 for 39 degrees of freedom and a probability of random variation of only 0.076 in support of compensatory growth. Thus, it seems likely that the apparently random fluctuations at the A and P borders are not entirely random, but negatively correlated. When one border grows rapidly, growth at the other border is suppressed so that the total growth is more regular at either border. After such an episode, the roles reverse and the other border catches up. A similar compensation mechanism was noted by Crisp & Patel (1967) in regard to the growth of the lateral plates of the barnacle *Elminius modestus*.

The general form of the growth curve, if the irregularities are ignored, is asymptotic, probably close to the Bertalanffy model. However, if an attempt is made to determine the constraints of the Bertalanffy equation using the plot of dL/dt against size L (see Crisp, 1985), these irregularities make the differentiation of L by t almost impossible. By using two values of dL/dt from the sum $A + P = L$ over the whole 83 increments for the largest and smallest shells, we obtained a not very approximate equation for *Siphonaria gigas* growth in an area with barnacles present (Fig. 5). By measuring the average angles of the anterior (A) and posterior (P) margins (d) the sum of the growth at each has been converted to diameter (D) increase through the relation:

$$dD = (dA + dP) \cos \theta$$

where $\theta = \tan^{-1} (2H/D)$ and θ , its mean value, was 36.6° , $\cos \theta = 0.803$.

DISCUSSION

Microgrowth bands with a tidal periodicity have been established in certain barnacles (Bourget & Crisp, 1975a, b; Crisp & Richardson, 1975), bivalves (Evans, 1972, 1975; Richardson et al., 1979, 1980a, b, 1981; Richardson, 1987), and probably in Polyplacophora (Jones & Crisp, 1985). All these are marine animals inhabiting the intertidal zone. Crisp (1989), reviewing the phenomenon, gave various lines of evidence to suggest that harder and more perfectly crystalline parts of the shell comprised the bands and that these formed when the body fluids were temporarily at a lower pH due to an accumulation of carbon dioxide and perhaps organic acids during emersion. All shell-secreting invertebrates exposed to the air and closed temporarily to avoid water loss, would be likely to experience acidosis and thus would slow down or prevent secretion of calcium carbonate.

The siphonarian gastropods differ from all the above groups in being regarded as belonging to a group, the subclass Pulmonata, superorder Basommatophora, that has become adapted to terrestrial life. Typically the mantle cavity has reduced external access by a narrow pore, its vascularised roof functions as a lung, the animal has lost the ctenidia and operculum, and it lays a shelled egg. However, *Siphonaria* itself is only partially modified. It retains or re-develops aquatic respiration through the siphon situated on the right side, it has secondary branchial lamellae on the roof or the mantle cavity and has retained a pelagic larval stage. The strong marine affinity has led, in the past, to the Siphonariidae being regarded as evolved from marine opisthobranchs and classified as a family of the tectibranchs.

Whatever the origin of *Siphonaria*, their patelloid form and adherent physiology (Morton, 1968) are so closely similar to those of the patelloid archegastropods that the presence of microgrowth lines in the shell of *Siphonaria* are likely to have been produced by the same factors as in *Patella*. The need to retain water when closely adhering to the rock and the consequent absence of respiratory exchange at the time of low water would similarly give rise to a fall in pH since there is then no ef-

fective air breathing mechanism at work. Thus, it is not surprising that they too should lay down shell bands in synchrony with tidal emersion.

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THE NUMBERS OF FRESHWATER GASTROPODS ON PACIFIC ISLANDS AND THE THEORY OF ISLAND BIOGEOGRAPHY

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ABSTRACT

The freshwater gastropod fauna of the Pacific islands of Beqa, Vanuabalavu, Waya, Rotuma (Fiji), Upolu, Savai'i, Tutuila (Samoa), Tongatapu, Vava'u (Tonga), Rarotonga (Cook Islands), New Georgia (Solomon Islands), Guam, Truk and Ponepe (Micronesia) is described. Thirty eight species were found; 26 species belonged to the Neritidae, 10 to Thiaridae, and one each to Assimineidae and Planorbidae. Using multiple regression analysis, the numbers of species on these and 11 other Pacific islands were shown to be correlated with the water area on the island and the distance the island was from a source of freshwater gastropods (accounting for 92% of the variation). Distance by itself was not a significant contributor. Islands with a small area of water showed a steeper species-water area curve, and the number of species on these islands was more correlated with distance than to water area. This was probably due to a higher extinction rate brought about by the drying up of the limited number of habitats.

Key words: freshwater, gastropods, Pacific islands, island biogeography.

INTRODUCTION

Faunal studies of angiosperms, birds and land snails in the Pacific have documented the ranges and distributions of the species in these taxa and have revealed examples of endemism and of species radiation (Carlquist, 1974; Diamond, 1984; Solem, 1959). These studies have also been used in discussions of the theory of island biogeography developed by MacArthur & Wilson (1967). This theory suggests that because the immigration rate to near islands is greater than that to more distant islands and because the extinction rate is greater on smaller islands than on larger islands, the equilibrium number of species tends to increase with island area. In the past, freshwater snail diversity has been discussed in relation to this theory, with lakes and ponds being considered as islands of water isolated by land barriers (Lassen, 1975; Aho, 1984).

The aims of this work were to establish what species of freshwater gastropods are present on Pacific islands and to find if the island faunas, some of which had already been described (Haynes, 1985, 1988a; Star-mühlner, 1976), supported the theory of island biogeography.

METHODS

Freshwater Gastropod Survey

From 1983 to 1987, freshwater gastropods were collected from the islands of Beqa, Rotuma, Vanuabalavu, Waya (Fiji); Guam; Truk (Federated States of Micronesia); Savai'i (Western Samoa); New Georgia (Solomon Islands); Rarotonga (Cook Islands) (Fig 1). The fauna of these islands is described for the first time. Collections were also made from Ponepe (Federated States of Micronesia); Upolu (Western Samoa); Tutuila (American Samoa); Tongatapu, Vava'u (Tonga) (Table 1). All islands are within the tropics. Guam is the most northerly at 14°N and Rarotonga is the most southerly at 22°S.

Freshwater gastropods were collected by hand from rocks, boulders and vegetation or were sieved with a 1 mm mesh from gravel and mud from streams, rivers and pools. Sampling took place both near the coast and inland to ensure that the gastropods found were representative of the whole fauna. Each site was searched for at least an hour, and all collections were made when the volume of water flowing in each stream was low to normal.

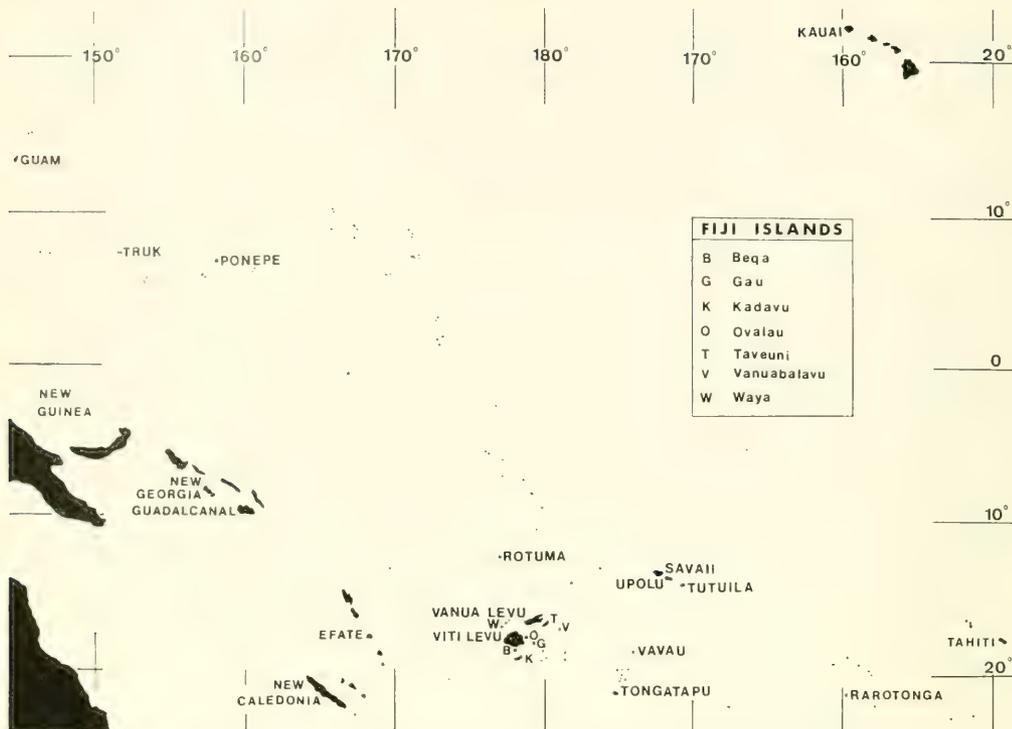


FIG. 1. Pacific islands from which collections of freshwater gastropods have been made.

Identification of the snails followed Riech (1937), Starmühlner (1970, 1976), and Haynes (1984).

Water temperature was recorded, and water samples were collected on New Georgia, Upolu, Savai'i, Tutuila, Tongatapu and Vav'u. These were analysed for pH, total ions ($\mu\text{s cm}^{-1}$) and hardness $\text{mg CaCO}_3 \text{ l}^{-1}$ by the Institute of Natural Resources, University of the South Pacific. Some collections were made on islands that were visited not primarily for collecting gastropods; on these islands no water samples were taken.

All gastropod collections are housed in the Biology Department, University of the South Pacific.

Island Biogeography

Data for the 14 islands investigated are presented in Table 2, along with data already published for other Pacific islands. The islands previously investigated are Viti Levu (Fiji) (Haynes, 1985); Vanua Levu, Ovalau, Gau, Kadavu, Taveuni (Fiji) (Haynes, 1988a); Guadalcanal (Solomon Island), Efate (Vanua

Levu), Tahiti (Starmühlner, 1976); New Caledonia (Starmühlner, 1970); and Kauai (Hawaii) (Burch & Patterson, 1971; Maciolek, 1978).

Stream length was estimated by measuring the length of all streams and rivers on 1:50,000 or 1:25,000 government maps of the islands. The water area was estimated by multiplying the stream length by a mean river or stream width of 10–50 m (depending on the island size) and by adding the area of standing water to it.

The large, geologically old islands of New Guinea, New Caledonia and Viti Levu were considered to be the most likely sources of freshwater immigrants to the islands, so that the distances in Table 2 were measured from the nearest of these three islands to the island in question. The three large islands together with nearby islands form three generally accepted biogeographical subregions of the Pacific islands (Thorne, 1963). The source islands possessed all freshwater gastropod species found on the smaller islands in their regions, with the exception of endemic species. Apart from Kauai (Hawaii), the endemics

TABLE 1. Study Sites

Micronesia

1. GUAM. Largest island in Micronesia. Formed from the union of two volcanoes. Yling River, Cetti and Asafines streams were sampled.
2. TRUK (Moen). Moen is one of the many islands in the Truk Lagoon. Winchen River and several small streams near the Continental Hotel were sampled.
3. PONEPE. A rugged island with high rainfall. Nanepil, Lehnmesi and Pilenkiepu rivers and Enipas Stream were sampled. The collections were made by John Maciolek and John Ford (Maciolek & Ford, 1987), who assisted the author with collections on Guam and Truk.

Solomon Islands

4. NEW GEORGIA. A high volcanic island. Sampled along the length of Puha and Borora rivers.

Western Samoa

5. SAVAI'A. Streams are confined to the south coast because of extensive lava fields on the north coast. Latolo Plantation Stream, Sili Village Stream, Mata'avai Pool, Asago Spring, and Sapavai'i Water Hole were sampled.
6. UPOLU. A high volcanic island. Sampled Fallefa Falls, Le Mafa Pass Stream, Mulivai Stream, and along the Vaisigano River.

American Samoa

7. TUTUILA. Volcanic with short streams. Sampled Alofau, Lemafa Saddle and Le'ele streams, and Pala Lagoon.

Tonga

8. TONGATAPU. A coral island with no running water. Sampled coastal and inland ponds.
9. VAVA'U. An elevated limestone cluster with no running water. Sampled pools and Lake Tuanuku.

Cook Islands

10. RAROTONGA. The only true volcanic island in the Cook Islands. Sampled Avatiu, Vaimanga and Avana streams and taro patches. (Lower courses of all streams were dry in September 1983.)

Fiji

11. BEQA. 14 km offshore from the main island of Viti Levu. Sampled the length of the stream at Naceva and in Naduruvesi Creek.
 12. WAYA. In the Yasawa group. Sampled the two streams in the Yolobe area.
 13. VANUABALAVU. Largest island in the northern Lau group. Northern part uplifted coral, southern part volcanic. Sampled the two streams near Lomolomo.
 14. ROTUMA. An isolated volcanic island 500 km north of Viti Levu. The rock is porous, and there are no permanent streams. Wells and taro patches were sampled.
-

were *Fluviopupa brevior* on Efate and *Melanoides paxa* and *Melanoides peregrina* on Upolu. New Caledonia, the source island for Efate, has three species of *Fluviopupa* that could have given rise to *Fluviopupa brevior*. *Melanoides* is a genus that shows much variation within species, and the isolation on Upolu of one or more of the four *Melanoides* species from the source island Viti Levu could have given rise to Upolu's two endemic species.

The freshwater gastropods on Kauai, like most taxa in the Hawaiian group, show considerable speciation. It has eight endemic

freshwater gastropod species. Four of these, *Neritina granosa* Sowerby, *N. vespertina* Sowerby, *Clithon cariosus* (Wood), *C. neglectus* (Pease), probably arose from species arriving from Southeast Asia or New Guinea. The four Lymnaeidae endemics (*Erinna newcombi*, *E. aulacospira*, *Pseudisidora rubella* and *P. producta*) probably had their origins in America, *Melanoides tuberculata*, *Tarebia granifera* (found elsewhere on Pacific islands), and *Ferrissia sharpi* probably arrived accidentally in recent times whereas *Galba viridis* was introduced from Asia about 1890

TABLE 2. The 25 Pacific islands arranged according to area with the data used in multiple regression analysis.

Island	No. of species y	Area (km ²) X ₁	Height (m) X ₂	Distance (km) X ₃	Stream length (km) X ₄	Water area (km ²) X ₅
New Caledonia	30	16750	1618	source	3320	166
Viti Levu	31	10429	1323	source	2585	136
Vanua Levu	26	5556	1032	60	1230	62
Guadalcanal	24	5302	2330	200	1855	93
Savai'i	11	1709	1856	800	300	16
New Georgia	20	1470	843	200	1080	54
Kauai	12	1432	1598	(6200)	604	83
Upolu	15	1114	1113	840	325	17
Tahiti	15	1042	2241	2440	735	37
Efate	18	887	646	500	370	22
Guam	11	541	406	1800	122	2.00
Taveuni	15	470	864	10	483	11
Kadavu	17	411	838	85	398	6
Ponepe	11	334	772	1400	270	4
Tongatapu	3	259	19	740	0	0.25
Gau	16	140	750	62	197	2
Tutuila	13	137	652	1000	128	1.8
Vava'u	1	118	179	800	0	0.02
Ovalau	20	101	626	17	105	1.5
Rarotonga	3	67	653	2400	87	0.9
Rotuma	1	47	256	500	0	0.01
Vanuabalavu	4	38	290	106	10	0.05
Beqa	13	35	439	14	37	1.9
Truk (Moen)	4	19	369	1300	6	0.03
Waya	9	17	580	46	20	0.20

(Burch & Patterson, 1971; Maciolek, 1978). Therefore, in the case of Kauai, distance from a source island is irrelevant.

It was thought that little bias was introduced by using Starmühlner's figures for New Caledonia, Guadalcanal, Efate and Tahiti. He collected from Upolu and Tutuila (Samoa) in 1985 (Starmühlner, 1986) and reported 23 species (one doubtful), which compares favorably with the 22 species I found in 1987.

Bishop Museum shell collections of freshwater gastropods from Pacific islands were studied in 1985, and I undertook a revision of their nomenclature. The Bishop Museum collections, which are not extensive, contain no species additional to those I found.

The data in Table 2 were the basis of multiple regression analysis using the method described by Bliss (1970). The number of gastropod species on an island was used as the dependent variable and the other factors — island area, island height, island distance from the presumed source of gastropods, stream length and water area — were the independent variables. The four first independent variables

were converted to logs whereas, for convenience, water area was first multiplied by 100 before being converted to logs.

The quantity of calcium ions (hardness) and total ions (conductivity) in the water can determine whether gastropods will be present. However, as the figures for hardness and conductivity for all streams and rivers tested (Table 4) were above 4.3 mg Ca l⁻¹ + 1.2 mg Mg l⁻¹, the amount that limits the presence of gastropods in freshwater (Aho, 1984), they were not used in the multiple regression analysis.

RESULTS

Freshwater Gastropod Survey

Thirty eight species of freshwater gastropods were collected from the 14 islands. Twenty six were Neritidae, 10 Thiaridae, one Planorbidae and one Assimineidae (Table 3).

The species found most frequently was the parthenogenetic thiarid *Melanoides tubercu-*

lata (Table 3). It was present on 11 of the 14 islands investigated. This species is also found in East Africa, the Middle East, Asia and the Caribbean (Starmühlner, 1976).

The stream-dwelling neritids, *Neritina variegata* (on 9 islands) and *Septaria procellana* (on 8 islands), were the next most widespread. These were followed by the brackish-water gastropod *Neritina turrita* on 7 islands.

Twelve of the species were present on both North and South Pacific islands. These were *Melanooides tuberculata*, *Neritina turrita*, *N. variegata*, *N. pulligera*, *N. macgillvrayi*, *N. squamipicta*, *Neritodryas subsulcata*, *Clithon corona*, *Septaria porcellana*, *S. lineata*, *S. sanguisuga* and *Tarebia granifera*.

Although in this study *Thiara cancellata*, *Neritodryas cornea*, *Neritina labiosa*, *N. asperulata* and *Clithon nucleolus* were found only on New Georgia, the first three have been recorded from Papua New Guinea (Riech, 1937; Starmühlner, 1976) and the last two from New Caledonia (Starmühlner, 1970).

The only endemic species recorded were two thiarid species, *Melanooides laxa* and *Melanooides peregrina* on Upolu.

Water temperature, pH, hardness and conductivity for the islands studied and results already published from other Pacific islands are given in Table 4. Gastropods were absent from Lake Tagimaucia, Taveuni where total ions (conductivity) ($14-18 \mu\text{s cm}^{-1}$) and hardness ($0.8-5.0 \text{ mg Ca} + \text{Mg l}^{-1}$) were low (Southern et al., 1986) (Table 4). Hardness and conductivity of other freshwaters were sufficient to support gastropods (Table 4).

Island Biogeography

Because island area (X_1) was correlated with stream length (X_4) ($r = 0.9377$) and with water area (X_5) ($r = 0.8737$), and water area (X_5) was correlated with stream length (X_4) ($r = 0.9522$), each made a similar contribution to the variation in the number of species (y). However, the variable water area correlated best with species numbers ($r = 0.8412$) (Table 2).

Using the stepdown method of reducing the number of variables until only those having significant influence were left (Bliss, 1970), the best correlation obtained was with the variables water area, distance from the source of gastropods (X_3) and island height (X_2). These variables accounted for 93% of the variation in species numbers. When is-

land height was omitted, 92% of the correlation was still accounted for by water area and distance. As the contribution of island height was not significant, the residuals of species numbers ($y - Y$) from the equation $Y = 9.898 + 4.9445X_5 - 3.7935X_3$ were plotted as deviations from the partial regression of species numbers against water area in Fig. 2. They do not depart much from linearity or from uniform scatter about the line. When distance was omitted, the correlation fell to 84%, showing that water area is the major contributor to the correlation, but distance is a significant contributor ($p < 0.001$) when taken in combination with water area. However, distance by itself is not significant ($r = 0.3745$) for 23 islands.

When the eight small islands with least water area (i.e. Ovalau, Rarotonga, Tongatapu, Waya, Vanuabalavu, Truk, Vava'u and Rotuma) were considered separately, distance from source of gastropods was the largest contributing factor to the number of species per island. When combined with water area, the two factors contributed 91% of the correlation, whereas distance alone contributed 81%. Species numbers were plotted against water area for the 25 islands in Figure 3. It is seen that the slope is steeper for the eight islands with small areas of water.

DISCUSSION

The parthenogenetic thiarid *Melanooides tuberculata*, which was found on 11 of the 14 islands, can easily be spread on plant material as it gives birth to live young. One specimen reaching an island can start a new population, and as it inhabits ponds, ditches and taro patches as well as streams and rivers, it can survive on such islands as Tongatapu, Vava'u and Rotuma which have no running water.

The buliniform planorbid *Physastra nasuta*, which inhabits ponds as well as running water, was present on Tongatapu, Rarotonga and Tutuila. It has been found on other Pacific islands, such as New Caledonia (Starmühlner, 1970), Viti Levu (Haynes, 1984) and Vanua Levu (Haynes, 1988a). Walker (1984) suggested that the genus *Physastra* evolved in the Australian region and spread into Southeast Asia and the Pacific through New Guinea. *Physastra nasuta* was collected from Tonga in 1832 (Solem, 1959), and it may

TABLE 4. The comparison of the water chemistry and the number of gastropods present in the streams of Pacific islands.

Island	Temperature °C	pH	Conductivity $\mu\text{s cm}^{-1}$	Hardness $\text{mg CaCO}_3\text{l}^{-1}$	Number of gastropods
Savai'i	25	7.1–7.2	57.8–103.9	11.3–26.1	11
Upolu	26	6.6	78.5	20.3	15
Tutuila	27–30	6.4–7.3	146–152	15.0–33.7	13
New Georgia	25–26	6.9–7.1	181–183	21.5–22.0	20
Vava'u (L. Tu'anuku)	31	7.5	14040	407	0 (1 in pool)
Tongatapu coastal pools	—	7.4	1435–8061	42.9–177	3
Ponepe ¹	—	—	21–104	6–46	11
Viti Levu ²	23–32	5.0–7.5	42.6–231	19.5–99	31
Vanua Levu ³	22–30	6.0–7.0	111.1–915	36–252	26
Ovalau ³	25–26	6.7–7.0	147.1–152.3	56–60	20
Taveuni L. Tagimaacia ⁴ streams ³	— 21–22	5.0–6.5 5.0–5.5	14–18 36.1–66.7	0.8–5.0(Ca+Mg) 9–19.7	0 15
Kadavu ³	25–27	6.5–7.5	36.1–66.7	20–22	17
Gau ³	26–27	7.0–7.7	122–134	52–55	16

1. Maciolek & Ford (1987), 2. Haynes (1985), 3. Haynes (1988a), 4. Southern et al. (1986).

TABLE 5. Freshwater gastropod habitats on Fiji Islands and the gastropods that may inhabit them

Habitats	Gastropods
1. Ponds, dalo (taro) patches, ditches & lakes	<i>Melanoides tuberculata</i> , <i>Physastra nasuta</i> , <i>Ferrissia noumeensis</i> , <i>Gyraulus montrouzieri</i>
2. Brackish water (shaded or mangrove areas)	<i>Neritina turrita</i> , <i>N. turtoni</i> , <i>N. auriculata</i> , <i>Clithon oualaniensis</i>
3. Brackish water (open areas, mouths of streams & rivers)	<i>Neritina turrita</i> , <i>N. turtoni</i> , <i>N. auriculata</i> , <i>Clithon oualaniensis</i> , <i>C. diadema</i> , <i>C. pritchardi</i> , <i>C. rarispinga</i> , <i>C. spinosa</i> , <i>Septaria lineata</i> , <i>Assimineia crosseana</i> , <i>Melanoides arthurii</i>
4. Freshwater (influenced by the tide, lower courses of streams & rivers)	<i>C. pritchardi</i> , <i>C. diadema</i> , <i>S. lineata</i> , <i>Septaria porcellana</i> , <i>Neritina squamipicta</i> , <i>Thiara amarula</i> , <i>T. bellicosa</i> , <i>T. scabra</i> , <i>T. tersichore</i> , <i>Melanoides plicaria</i> , <i>M. arthurii</i> , <i>M. aspirans</i>
5. Fast flowing streams & rivers (substrate pebbles, stones & boulders)	<i>M. tuberculata</i> , <i>M. lutosa</i> , <i>T. scabra</i> , <i>P. nasuta</i> , <i>F. noumeensis</i> , <i>Fluviopupa pupoidea</i> , <i>Fijidoma maculata</i> , <i>Neritina pulligera</i> , <i>N. petiti</i> , <i>N. canalis</i> , <i>N. porcata</i> , <i>N. variegata</i> , <i>N. macgillvrayi</i> , <i>Neritodryas subsulcata</i> , <i>Neritilia rubida</i> , <i>C. pritchardi</i> , <i>C. olivaceus</i> , <i>S. porcellana</i> , <i>S. sanguisuga</i> , <i>S. suffreni</i> , <i>S. macrocephala</i>
6. Cascades (substrate boulders & rocks)	<i>S. porcellana</i> , <i>S. sanguisuga</i> , <i>S. suffreni</i> , <i>S. macrocephala</i>

have been transported to Tongatapu and Rarotonga on taro plants in recent times by man.

The majority (26 species out of 38) of the snails collected were nerites (Table 3). It has been suggested that the brackish and freshwater neritid genera, *Clithon*, *Neritina*, *Neritilia*, *Neritodryas* and *Septaria*, evolved at different times from the marine genus *Nerita*

probably in the Southeast Asia region (Govindan & Natarajan, 1972; Starmühlner, 1982). A few species have spread westward into the Indian Ocean, whereas many have spread eastward across the Pacific Ocean.

In this survey, many more species of nerites were found in the South Pacific (25 species) than in the North Pacific (11 spe-

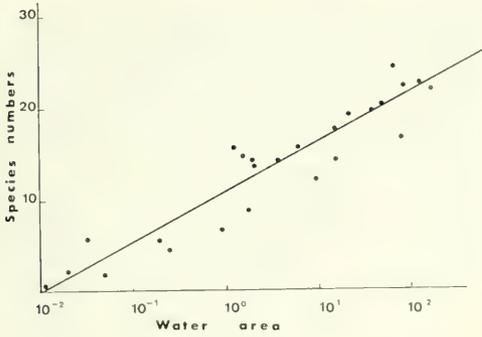


FIG. 2. Residual species numbers ($y - Y$) of freshwater gastropods plotted as deviations from the partial regression of species numbers against water area.

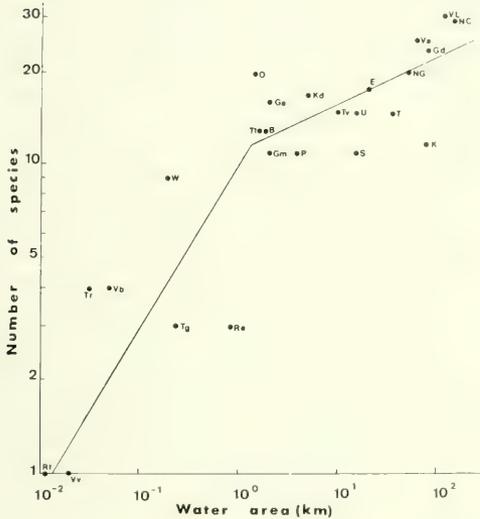


FIG. 3. The freshwater gastropod species numbers-water area curve for Pacific islands. B: Beqa, E: Efate, Ga: Gau, Gd: Guadalcanal, Gm: Guam, Kd: Kadavu, K: Kauai, O: Ovalau, NC: New Caledonia, NG: New Georgia, P: Ponepe, Ra: Rarotonga, Rt: Rotuma, S: Savai'i, T: Tahiti, Tv: Taveuni, Tg: Tongatapu, Tr: Truk, Tt: Tutuila, U: Upolu, Vb: Vanuabalavu, Va: Vanua Levu, Vv: Vava'u, VL: Viti Levu, W: Waya.

cies). All species found in the North Pacific were also present in the South Pacific (Table 3). It appears that more species have moved south through the New Guinea-Solomon Island region than have moved north into Micronesia. Such species as *Clithon nucleolus*, *Neritina asperulata* and *N. labiosa malanica*

do not appear to have dispersed further east than Solomon Islands and New Caledonia, whereas *Clithon pritchardi*, *Septaria macrocephala* and *S. suffreni* probably arose in the South Pacific as they are not found as far north as Vanuatu and Solomon Islands (Fig. 1).

Unlike land snails, which show considerable speciation on Pacific Islands, e.g. *Partula* on Samoa and zonitids in Fiji (Solem, 1959), comparatively few species of endemic freshwater gastropods have been found. Besides the two endemic species of Thiaridae, *Melanoides laxa* and *M. peregrina* collected from Upolu, other endemic species recorded on islands discussed in this paper are *Fiji-doma maculata* (Thiaridae), *Fluviopupa pupoidea* (Hydrobiidae) (Viti Levu); an opisthobranch, *Acochlidium* sp. (Vanua Levu); *Melanopsis frustulum*, *M. mariei* (Thiaridae), *Fluviopupa minor* and two other *Fluviopupa* spp., *Hemistomia caledonica* (Hydrobiidae), *Physastra petiti* (Planorbidae) (New Caledonia); *Fluviopupa brevior* (Efate) and the eight endemic species on Kauai mentioned above (Morrison, 1954; Starmühlner, 1970, 1976; Haynes, 1988b; Burch & Patter-son, 1971; Maciolek, 1978).

Although man has probably helped in the distribution of *Melanoides tuberculata* and *Physastra nasuta*, which live in taro patches, it is unlikely that man has been responsible for the spread of other species to Pacific islands. Most freshwater gastropods do not live on vegetation but are found on the mud or rocks of stream or river bottoms. They are not favored as food and therefore the chance of them being spread purposely by man is small. Some brackish-water neritid species may cling to wooden boats and be carried to nearby islands. Other neritid and thiarid species may be rafted out to sea on tree trunks during flooding and be washed ashore at a river or stream mouth. However, many species are probably distributed from island to island as veliger larvae. Most neritid and brackish-water thiarid gastropods hatch as veligers. These may be swept out to sea and settle in brackish water at the mouth of a stream on another island. Ford (1979) reported long lines of young *Neritina granosa* migrating upstream on Hawaiian Islands. He believed that the veligers, after being swept down to the sea, spent some weeks in salt water before settling at the mouth of a stream and starting their migration upstream. There is no evidence to suggest that this occurs in

all neritid species, but *Neritina*, *Clithon* and *Septaria* veligers kept in the laboratory can be acclimatized to sea water, and they have remained alive for 22 days without settling. This allows them time to be carried by currents to quite distant islands. However, they are more likely to reach and become established on islands that are near the source of the gastropod veligers.

Island Biogeography

According to the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), the greater the distance of an island from a source of colonization, the smaller the probability of colonization. However, if islands are the same distance from the source, immigration will be greater to the larger island. Isolated small populations on small islands will have a higher rate of extinction due to competition and population fluctuations. If further immigration occurs after all potential niches are filled, interspecific interactions will increase, and the extinction rate will increase and keep the species number in equilibrium.

On the 25 Pacific islands considered, the total area of water was the main factor influencing the number of freshwater gastropod species present (explaining 84% of the variation). Because island area and stream length are strongly correlated with water area, their influence on the number of species is incorporated in water area. Distance from the source contributes 8% to the variation in the number of species and unknown factors 7%. The contribution of height is also largely incorporated in water area ($r = 0.7312$) because an island with an altitude less than 300 m usually will be without streams, and in general the higher an island the greater its stream length, water area and habitat diversity.

The importance that distance contributes to species variation on small islands may be due to the strong possibility of the small area of water drying up and the consequent likelihood of extinction of some or all gastropods. The nearer such islands are to a source of gastropods the more likely immigration is to occur and the number of species to be restored. Ovalau (20 species) and Beqa (13 species), which are close to Viti Levu, have a relatively large number of species, whereas the more distant islands, such as Rarotonga (3 species), Truk (4 species) and Vanuabalavu (4 species), have few species (Tables 2, 3).

Freshwaters on Pacific islands can be di-

vided into six distinct habitats: (1) ponds, taro patches, ditches; (2) shaded brackish water; (3) open brackish water; (4) freshwater influenced by the tide; (5) fast flowing streams and rivers; and (6) cascades (Table 5). Some are inhabited by only a few gastropods, and others are suitable for colonization by a large number of gastropod species. Small islands and islands of low elevation do not have all these different habitats, but those they do have fall into one of these categories. The species inhabiting the habitats are not all the same for each island group.

The number of gastropod species on an island will partially depend on the number of each kind of habitat and their size. These are factors which account for some or all of the unknown 7% in variation of the number of gastropod species on islands.

The steeper slope for islands with a small area of water has been observed in species-area curves before (Fig. 3). Williams (1981) gives a similar plot for birds on the Solomon Islands, and Lassen (1975) drew another for freshwater snails in small eutrophic lakes in Denmark. This steeper slope for smaller ponds Lassen (1975) explained by lower immigration and an increased extinction rate with decreasing area. Birds carrying immigrant snails are less likely to visit small ponds, and small ponds are more likely to freeze.

Similarly, a steeper slope was obtained for Pacific islands with small water area, because the extinction rate increases due to ponds and lower courses drying up and because the survival rate of immigrants is low due to relatively few available habitats.

Most investigations into which factors determine the number of species on islands have involved plants or birds. Johnson & Raven (1970) found that island area, latitude and soil types were important in the species diversity of plants on the British Isles and on California islands. Harris (1973), using multivariate analysis, established that the variables that contributed to the variation of numbers of breeding land birds on the Galapagos Islands were total plants and altitude (87.7%) and distance (90.5%). Power (1972) found by multivariate analysis that the variation in the numbers of bird species on California islands was caused by the interaction of these variables: numbers of native plant species and distance from other islands and from the mainland. The variation in numbers of plant species was mainly explained by island area and latitude.

In this investigation, island area and height were important because they determine the diversity and size of the freshwater habitats available. The habitat diversity is best expressed as water area for purposes of multiple regression analysis. Distance from a possible source of new immigrants is also important in determining species numbers, probably because of the high rate of extinction caused by water drying up and sometimes by whole populations being washed away during tropical cyclones.

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ANALYSIS OF LYMNAEACEAN RELATIONSHIPS USING PHYLOGENETIC SYSTEMATICS

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ABSTRACT

Currently, evolutionary studies of lymnaeacean pulmonates are heavily dependent on a small number of classical morphological studies for family-level phylogenetic relationships. These classical studies are in general agreement on the relationships of the lymnaeacean families. Unfortunately, all of the previous studies infer relationships from *a priori* arguments for character evolution based on assumptions of the evolutionary or adaptive significance of the characters in question. Considering the widespread convergence in pulmonates, the assumptions may not be justified and the phylogenetic inferences derived from them are probably suspect.

The present study employs outgroup analysis and component analysis to test the phylogenetic implications of previously published character-state distributions. The purpose of this study is to determine whether the morphological descriptions reported in the literature support either the currently accepted phylogeny, or an alternative interpretation. The results of the outgroup analysis indicate that only a few of the characters described in the literature permit lymnaeaceans to be discriminated from all related pulmonates. The result of the component analysis indicate that the few informative characters provide weak support for accepting a revised lymnaeacean phylogeny, but strongly support rejection of the classical interpretation.

Key words: Lymnaeacea, phylogeny, component analysis, outgroup analysis.

INTRODUCTION

The pulmonate superfamily Lymnaeacea includes six families of freshwater snails: Chiliniidae, Latiidae, Acroloxidae, Physidae, Lymnaeidae and Planorbidae (Hubendick, 1978). (Although ICZN Recommendation 29A suggests superfamily names end in -oidea, -acea is conventional for this group and is the ending used in this paper.) The lymnaeaceans have a nearly global distribution (Hubendick, 1978) and occupy a wide variety of freshwater habitats (cf. Clarke, 1973). Associated with their large ecological range is tremendous morphological diversity, resulting in several hundred named species (cf., Clarke, 1973). This high level of diversity makes phylogenetic studies of the Lymnaeacea difficult.

Despite the difficulty of resolving relationships within the superfamily, interest in the problem persists. One motivation results from their ecological diversity; the Lymnaeacea are useful as indicators of ecological conditions, both in Recent (Aho, 1966; Clarke, 1979) and fossil (Ayyasamy et al., 1985; Good, 1987; La Rocque, 1966–1970) habitats. Phylogenetic studies may be useful in identifying traits or

taxonomic groups associated with particular environments. Another motivation results from the role of many species as intermediate hosts for trematode parasites (Gomez et al., 1986; Mandahl-Barth, 1957). Here, phylogenetic studies may be relevant to analyses of host-parasite co-evolution.

Interest in lymnaeacean phylogeny tends to focus on lower taxonomic levels: genera or species (e.g. Jelnes, 1986, *Bulinus*; Meier-Brook, 1983, *Gyraulus*). Studies at lower levels necessarily take the family-level phylogeny as given. The few previous family-level analyses (Hubendick, 1947, 1978; Starobogatov, 1967) support the phylogeny shown in Figure 1. The concordance of these studies would normally be taken as a sign of reliability and robustness, but these studies are based on similar material and share a common approach. The authors argue that the gonad (Hubendick, 1978; Starobogatov, 1967), prostate (Hubendick, 1947, 1978; Starobogatov, 1967) and male copulatory organs (Starobogatov, 1967) are more important than any other traits for phylogeny reconstruction because reproductive-tract characters are crucial to reproductive success.

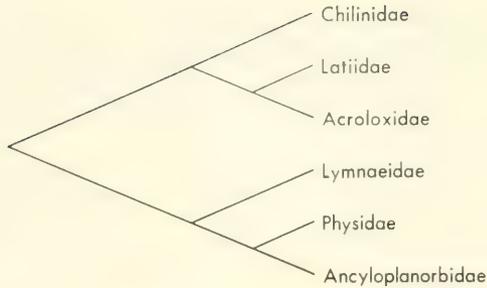


FIG. 1. Phylogenetic relationships supported by previously published analyses.

Therefore, a sequence of improvements in these structures should reflect phylogenetic history. However, reproductive success depends on many factors in addition to gamete production and mating ability. Survival and the opportunity to mate depend, in part, on respiratory and digestive abilities. Therefore, respiratory and digestive structures are also crucial to reproductive success, and should not be given less weight than reproductive structures in phylogenetic inference.

Harry (1964) uses Dollo parsimony to infer directions of character transformations from a phylogeny similar to Figure 1. Dollo parsimony assumes that acquisition of a new character state is rare, but that loss of a derived state, reverting to a more primitive state, is much more frequent. Harry's results indicate that reproductive traits, as well as digestive and respiratory traits, are convergent. In addition, Harry's results indicate that support for Figure 1 rests largely on shared primitive traits.

The criticisms of previous work should not be construed to mean that morphological traits used in previous studies of the Lymnaeacea provide no basis for phylogenetic inference. These criticisms are only intended to point out that inferred patterns of morphological change of all characters should be tested as hypotheses. Component analysis (Nelson & Platnick, 1981) is a cladistic approach to phylogeny reconstruction designed to test hypotheses of character evolution. Since a phylogenetic branching pattern can be represented as a series of nested sets of taxa, component analysis tests whether the sets of taxa implied by hypotheses of character evolution do nest. A character may have two states implying a transformation from a pre-existing, primitive state to a new, derived state. The state hypothesized to be derived is

expected to define a monophyletic group composed of all descendants of the species in which the character state transformation occurred. A component is the set of taxa that share the state hypothesized to be derived; it represents a hypothesis of monophyly. If two components nest, then both hypotheses of monophyly are consistent with the same phylogenetic pattern, and corroborate both hypotheses of character evolution (Le Quesne, 1969; Nelson & Platnick, 1981). In a special case, two derived states define identical, replicated components, providing the strongest possible corroboration of the two character transformation hypotheses (Nelson & Platnick, 1981). There are two cases in which components do not nest. In one case, the components are intersecting sets representing conflicting hypotheses of monophyly, and at least one of the character hypotheses must be rejected (Le Quesne, 1969). In the other case, the components are mutually exclusive, and the character hypotheses they represent need not be rejected (Le Quesne, 1969), but they are not corroborated either (Nelson & Platnick, 1981). The treatment of mutually exclusive components distinguishes clique or compatibility analysis from component analysis. In clique analysis, a clique is a set of components that do not conflict, and the largest clique is chosen as the best estimate of the phylogeny (Estabrook et al., 1977). In component analysis, only nested and replicated components are used, and the largest set of nested components, representing the largest set of mutually corroborated character hypotheses, is chosen as the best estimate of the phylogeny (Nelson & Platnick, 1981).

Component analysis, and all other cladistic methods, are critically dependent on the sources used to generate hypotheses of character transformation. Several sources have been used; three common ones are outgroup analysis, ontogenetic analysis and paleontological (stratigraphic) analysis (cf. Eldredge & Cracraft, 1980; Nelson & Platnick, 1981). For this study, I chose to use outgroup analysis because it is an extension of component analysis (Eldredge & Cracraft, 1980; Wiley, 1981). Outgroup analysis assumes that the study group (ingroup) is monophyletic and treats the ingroup as a component. Related taxa (outgroups) are members of larger components that include the ingroup. Outgroup analysis sorts character states into two sets: (1) those shared by both ingroup and outgroups, and (2) those restricted to the ingroup. Char-

acter states shared by the ingroup and any outgroup may be either primitive or convergent (Maddison et al., 1984; Wiley, 1981). In either case, these character states cannot be used for phylogeny reconstruction. Only derived states define components that are subsets of the ingroup; this is the essence of cladistic methodology (Estabrook et al., 1977; Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981). Outgroup analysis is a method that eliminates character transformation hypotheses inconsistent with the hypothesis of ingroup monophyly. When the consistent character hypotheses are used in component analysis, the resulting phylogeny would be based on the largest set of mutually corroborated character hypotheses consistent with the initial hypothesis of ingroup monophyly. The results could be refined iteratively by using the ingroup taxa found to be primitive as functional outgroups to order the states of characters not found in the original outgroups (Eldredge & Cracraft, 1980; Watrous & Wheeler, 1981).

The study presented here is a re-evaluation of the phylogenetic relationships of the six lymnaeacean families, using outgroup analysis and component analysis. Parsimony algorithms were not used because previous studies of the lymnaeaceans indicated considerably homoplasy; under these circumstances, parsimony algorithms become unreliable (Felsenstein, 1978). Because the purpose of this study is to test the phylogenetic conclusions of earlier studies, I have used published morphological descriptions. The principal sources of morphological descriptions of lymnaeaceans are the four previous studies of lymnaeacean phylogeny (Harry, 1964; Hubendick, 1947, 1978; Starobogatov, 1967). Additional studies of more limited taxonomic or morphological scope were examined if their data were prominently featured in the phylogenetic studies cited above (e.g. Demian, 1962, radula; Duncan, 1960a, 1069b, oviduct; Hubendick, 1964, ancylids). The superfamilies Amphibolacea and Ellobiacea were used as the outgroups, with descriptions provided primarily by Hubendick (1978).

I have provisionally accepted the family and superfamily taxonomy of Hubendick (1978), in which Lymnaeacea Rafinesque (1815) is equivalent to Hygrophila Ferussac (1821). Hubendick's (1978) six major subdivisions of the Lymnaeacea do not differ from the subdivisions of Hygrophila recognized by Harry (1964) or Starobogatov (1967). The differ-

ences among these three authors are primarily nomenclatural. Brief descriptions of the contents of the six lymnaeacean families are given in the Appendix.

OUTGROUP ANALYSIS

Outgroup analysis was performed by comparing the descriptions of the lymnaeaceans to the descriptions of the outgroups. Because of the large amount of convergence in the order Basommatophora, which includes the Lymnaeacea, the nearest relatives of the lymnaeaceans cannot be identified confidently (Duncan, 1960a; Hubendick, 1978; Tillier, 1984). While the inability to identify the nearest relative may be a problem for parsimony algorithms (Maddison et al., 1984), it need not be a problem for components analysis (Eldredge & Cracraft, 1980). The purpose of outgroup analysis is to identify the derived states of the ingroup. The nearest outgroup is likely to provide the best estimate (Wiley, 1981), but any outgroup will provide a partial estimate (Eldredge & Cracraft, 1980), and no single outgroup is likely to provide a completely accurate estimate (Maddison et al., 1984). Therefore, any non-lymnaeacean basommatophoran could be used as an outgroup. The outgroups used in this study were the Ellobiacea and Amphibolacea, which encompass most of the non-lymnaeacean basommatophorans. Any trait shared by lymnaeaceans with either of these other superfamilies was considered either primitive or convergent and rejected from the phylogenetic analysis. Only those traits unique to the Lymnaeacea were considered derived character states and subjected to further study.

As shown in Table 1, only five characters have derived states that are both unique to the Lymnaeacea and shared by at least two lymnaeacean families. These are the only character states that might reflect phylogenetic relationships (Nelson & Platnick, 1981). Each of the five characters in Table 1 are discussed below. For each character, the various states are briefly described, and the derived state is identified.

1—*Prostate morphology*. The prostates of the outgroups Ellobiacea and Amphibolacea are comprised of a smooth glandular epithelium along the male duct or groove. This type of prostate is present in most chliinids. Three, more complex morphologies are found in the lymnaeaceans: (1a) a patch of alveoli in some

TABLE 1. Character-state distributions across lymnaeacean families. Only characters with derived states shared by at least two families are listed. Derived states are italicized.

	Prostate morphology	Stomach muscles	Pneumostomal lappet	Ciliated pulmonary ridge	Radular row
Outgroups	smooth/pocket	cylinder/diverticula	single	present	horizontal
Chiliniidae	smooth/ <i>alveoli</i>	<i>bilobed</i>	single	present	<i>chevron</i>
Latiidae	smooth	cylinder	single	present	<i>chevron</i>
Acroloxidae	smooth	<i>absent</i>	single	present	<i>chevron</i>
Lymnaeidae	<i>folds</i>	<i>bilobed</i>	<i>siphon</i>	<i>absent</i>	horizontal
Physidae	<i>diverticula</i>	<i>reduced</i>	<i>siphon</i>	<i>absent</i>	<i>chevron</i>
Planorbidae	<i>diverticula</i>	<i>cylinder/bilobed</i>	single/ <i>siphon</i> /other	present/ <i>absent</i>	horizontal

chiliniids, (1b) series of elongate digitiform diverticula in Physidae and Planorbidae, (1c) a dilation of the vas deferens with invaginated folds in lymnaeids. The invaginated folds are unique to the Lymnaeidae and do not require further discussion in this paper. The comparison between alveoli and diverticula does merit further discussion. Starobogatov (1967) argues that all of the more complex morphologies arise in response to a need for more efficient packing of prostate tissue and that these morphologies increase secretory surface area relative to the total volume occupied by the prostate. He also argues that evagination and invagination are fundamentally distinct approaches to the packing problem. Following Starobogatov's argument, alveoli and diverticula are homologs, both are evaginations and the component defined by evagination includes Physidae, Planorbidae and some chiliniids. Alternatively, alveoli and diverticula are regarded as completely separate traits, so that diverticula define a component that includes only Physidae and Planorbidae. Because available literature does not provide sufficient information to resolve this issue, two components are listed in Table 2: 1', defined by evagination (some Chiliniidae, Physidae and Planorbidae); and 1'', defined by diverticula (Physidae and Planorbidae). Because there is no definitive evidence that diverticula are derived from alveoli, component 1'' cannot be considered a subset of 1'. Instead, 1' and 1'' are considered alternative interpretations of a single character, and their relationships to other components were examined independently.

2—*Stomach muscle arrangement.* Ellobiacea and Amphibolacea have well-developed stomach muscles in one of two arrangements: a cylindrical band around the stomach, or a muscular diverticulum. The muscular divertic-

ulum is found only in the outgroups; but the cylindrical band is found in some lymnaeaceans. Two new states are found in lymnaeaceans: (2a) reduction and loss of stomach muscle, and (2b), organization of muscles into two lobes. Reduction and loss are shared by Acroloxidae and Physidae. The bilobed arrangement is shared by Chiliniidae, Lymnaeidae and most Planorbidae. Because not all planorbids are included in component 2b, the family name is enclosed in brackets in Table 2.

3—*Pneumostomal lappet.* The pneumostomal lappet is a fold external to the pulmonary opening. In both outgroups, the lappet is a single lobe bisected by the rectum and may function as a gill. In Lymnaeidae, Physidae and most Planorbidae, the region anterior to the rectum is converted to a siphon, a tube which appears to function as a snorkel (Harry, 1964). In Lymnaeidae and Physidae, the region posterior to the rectum is absent. The posterior region is often reduced, but rarely absent, in planorbids with a siphon (Hubendick, 1955). Other variations of the pneumostomal lappet occur in those planorbids without a siphon (Hubendick, 1964).

4—*Ciliated pulmonary ridge.* This is an internal structure of the pulmonate lung that extends from the pulmonary opening to the apex of the lung on both dorsal and ventral surfaces. The ridge appears to facilitate gas exchange by regulating water flow through the lung (Pilkington et al., 1984; Sullivan & Cheng, 1974). The ridge is present in both outgroups and many lymnaeaceans, but is absent from Lymnaeidae, Physidae and several planorbids.

5—*Radular tooth arrangement.* The geometric arrangement of teeth in rows appears to be the only radular trait that is not highly variable and frequently convergent (Demian, 1962; Hubendick, 1978). Straight transverse

TABLE 2. Components defined by shared derived character states. Brackets indicate families in which not all species possess the derived state.

1'	[Chiliniidae], Physidae, Planorbidae
1''	Physidae, Planorbidae
2a	Acroloxidae, Physidae
2b	Chiliniidae, Lymnaeidae, [Planorbidae]
3	Lymnaeidae, Physidae, [Planorbidae]
4	Lymnaeidae, Physidae, [Planorbidae]
5	Chiliniidae, Latiidae, Acroloxidae, Physidae

tooth rows are present in all outgroups and some lymnaeaceans. Chevron-shaped rows distinguish four lymnaeacean families: Chiliniidae, Latiidae, Acroloxidae and Physidae.

COMPONENT ANALYSIS

All characters states unique to Lymnaeacea are hypothesized to be derived. Each character state defines a set of taxa that is hypothesized to represent a monophyletic group. Two states listed in Table 1 (folds in the lymnaeid prostate, alveoli in the chilinid prostate) define components that include only the members of individual families. Because these traits are not shared by two or more families, they cannot support inferences of relationships between families (Nelson & Platnick, 1981). These states are included in Table 1 for completeness in the lists of character-state distributions but are excluded from the component analysis. Other derived states unique to single families (e.g. preputial gland of Physidae; Te, 1975) were omitted from Table 1 and are not considered further. For each remaining derived state listed in Table 1, the component, the set of taxa sharing that state, is listed in Table 2.

Component analysis is performed by inspecting all possible pairs of components to determine whether there are pairs of nested sets. Nested pairs are consistent with a single phylogenetic branching pattern and therefore represent mutually corroborated hypotheses of monophyly. Next, all possible combinations of nested pairs are assembled. The largest combination, the largest number of mutually corroborated hypotheses of monophyly, is considered the best estimate of the actual phylogeny.

In a few cases, not all members of a family possess a particular derived state. Such components conflict with the hypothesis that the given family is a monophyletic group. Nor-

mally, the monophyly of a family would not be challenged by a study of family-level relationships, and the traits that conflict with the family definition would be rejected as homoplastic. However, several cases involve one family, the Planorbidae. Therefore, I examined the distribution of this set of traits across genera to determine whether they consistently divide the planorbids into two or more smaller groups.

Two traits co-occur in most planorbids: loss of the ciliated pulmonary ridge (character 3), and formation of a siphon (character 4). However, there are snails with a siphon that have not lost the ciliated ridge, and snails that have lost the ciliated ridge without acquiring a siphon (Hubendick, 1955, 1964, 1978). Thus, the presence of the siphon and the loss of the ridge do not coincide in all planorbids and do not support an argument for dividing the family. Furthermore, since these two traits have conflicting distributions, one or both must be homoplastic. Hubendick (1955) shows different patterns of partial ridge loss in the coiled planorbids: some losing the dorsal portion of the ridge, others losing the ventral portion of the ridge. This diversity in intermediate states may mean that the terminal state, complete ridge loss, can be reached by at least two different evolutionary routes. This is not proof that ridge loss is convergent, but it does support the argument of Hecht & Edwards (1976) that losses are more likely than new additions to be convergent.

The third trait dividing the Planorbidae is the organization of stomach muscles into two lobes (character state 2b). The published data on this trait are sparse but indicate that only the planorbid limpets lack the derived state (Hubendick, 1964, 1978). Thus, the trait represents a third way of dividing the Planorbidae. Only one, if any, can be right. The correct trait can be recognized only if it defines a component that nests with one of the components that include all of the Planorbidae.

Because the brackets do not represent identical or nested sets of genera, none of the components in Table 2 are identical: no two derived states independently support the same phylogenetic inference. Components 3 and 4 appear similar; both include Lymnaeidae, Physidae and some planorbids; but they divide the Planorbidae into different groups, representing conflicting hypotheses of relationship. In fact, most pairs of components represent conflicting hypotheses of relationships. One exception is composed of compo-

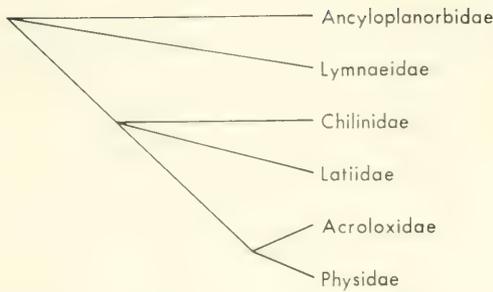


FIG. 2. Phylogenetic relationships supported by component analysis.

nents 2a (Acroloxidae and Physidae) and 2b (Chiliniidae, Lymnaeidae and Planorbidae). These two components are mutually exclusive, representing two independent hypotheses of character evolution in separate lineages. The components are not contradictory and could be used in clique analysis, but they do not corroborate each other. Consequently, the relationship between 2a and 2b does not contribute to the component analysis solution. The only nested components, representing mutually corroborated character transformation hypotheses, are 2a (Acroloxidae and Physidae) and 5 (Chiliniidae, Latiidae, Acroloxidae and Physidae). Therefore, the only phylogenetic relationships supported by component analysis are those shown in Figure 2.

The branching pattern in Figure 2 is not completely resolved: there are two trichotomies. Each trichotomy indicates that the relationship of three lineages remains unresolved. Each trichotomy has three possible solutions (Eldredge & Cracraft, 1980; Nelson & Platnick, 1981), so there are nine fully resolved trees consistent with Figure 2. However, Figure 2 does indicate that within Lymnaeacea there is a monophyletic group characterized by a unique, derived, chevron radular row (component 5). This group includes four families: Chiliniidae, Latiidae, Acroloxidae and Physidae. The relationships of Lymnaeidae and Planorbidae to each other and to the group remain unresolved. Within the group defined by component 5, the relationships of Chiliniidae and Latiidae are unclear, but Physidae and Acroloxidae (component 2a) appear to represent a distinct lineage characterized by reduced stomach muscles.

DISCUSSION

The relationships shown in Figure 2 are based on only two derived character states.

With so little support, this phylogeny could be rejected rather easily. Only one additional derived state defining a component that nests with any of the other components in Table 2 would produce an equally well-supported alternative phylogeny. Because phylogenies based on few traits are highly susceptible to revision, Figure 2 can only be regarded as a tentative hypothesis of lymnaeacean relationships.

Although outgroup analysis of the characters available in the lymnaeacean literature did not produce a strongly supported new phylogeny, the results indicate that the generally accepted phylogeny (Figure 1) should be rejected. Only one component of Figure 1 was confirmed by outgroup analysis: Physidae + Planorbidae, defined by the prostatic diverticula. None of the other monophyletic groups implied by Figure 1 is listed as a component in Table 2. Furthermore, half of the components in Table 2 conflict with the basal dichotomy shown in the conventional phylogeny. Components 3 and 4, defined by respiratory traits, are close to matching one branch of Figure 1, but they conflict over which planorbids belong to that lineage. Thus, the outgroup analysis provides an argument for rejecting the conventional lymnaeacean phylogeny, independent of the support it provides for a specific revision.

These results also cast doubt on the use of most reproductive tract characters for phylogeny reconstruction. This is significant because reproductive traits have been the principal characters considered in previous phylogenetic studies of the Lymnaeacea (separation of male and female ducts, Harry, 1964, Hubendick, 1947, 1978; prostate, Hubendick, 1947, 1978, Starobogatov, 1967; preputium, Harry, 1964, Hubendick, 1947). Based on outgroup analysis, most evolutionary changes in the lymnaeacean reproductive system are not unique to that superfamily. Only one reproductive character, prostate morphology, has a unique derived state listed in Table 1. Considering the number of separate, identifiable reproductive structures, the lack of unique derived states implies tremendous homoplasy. This large amount of homoplasy is not a surprise, however; because phylogenetic studies within lymnaeacean families frequently conflict when different reproductive traits are used (Hubendick, 1951, 1955; Meier-Brook, 1983; Te, 1975, 1978). In addition, the patterns of character evolution described for reproductive traits conflict with

the few patterns that have been described for respiratory and radular characters (Hubendick, 1955, 1978; Meier-Brook, 1983; Te, 1978). Evidently, evolutionary changes of the reproductive system do not unambiguously reflect lymnaeacean relationships.

While the results of the current study reject the use of reproductive characters for phylogeny reconstruction, this study does not reject the possible evolutionary significance of these traits. In fact, evolutionary significance may account for the lack of phylogenetic significance. A partial explanation of convergence is that the functional or adaptive importance of a trait ensures strong selective pressures favoring any changes that might improve function. This can be only a partial explanation of frequent convergence because the genetic and developmental sources of the necessary variation are not considered. Still, lymnaeacean reproductive characters may be examples of traits with great functional importance that are not unique innovations, but the results of frequent convergence.

Evolutionary significance and the causes of convergence are outside the scope of this paper. The focus of this study is that outgroup analysis of published data demonstrates that confidence in any interpretation of lymnaeacean relationships is misplaced. Failure to produce a well-corroborated phylogeny of the Lymnaeacea is due, in part, to the uncertainty concerning the outgroup phylogeny. If outgroup relationships were understood, it might be possible to determine which outgroup traits are most likely to be primitive and which traits are probably convergent (Maddison et al., 1984). Discriminating between primitive and convergent traits would help focus efforts aimed at identifying and discriminating among separate convergence events. Ultimately, recognition of the unique aspects of individual convergence events may enable the identification of separate monophyletic groups among convergent taxa (e.g. Lombard & Wake, 1986).

Resolving outgroups and reproductive convergence provides only a partial solution to the problem of lymnaeacean phylogeny. The results of this study show that the lymnaeacean phylogeny cannot be fully resolved using currently available, morphological data. New data should be generated both from descriptions of morphological traits in other organ systems and from analysis of molecular traits. Granted, new data may be as prone to convergence as the traits discussed in this

report, but there is no possibility of a solution until these other avenues are explored.

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APPENDIX

The superfamily Lymnaeacea (Pulmonata: Basommatophora) is composed of six families. These families share the following traits: a glandular oviduct divided into histologically and functionally distinct regions (Duncan, 1960a, 1960b), freshwater habitat, and loss of the operculum in both adult and embryo (Hubendick, 1978). None of these traits are unique to lymnaeaceans, but together these traits serve to distinguish the Lymnaeacea from other basommatophorans. Consequently, the Lymnaeacea is generally considered to be a monophyletic group. Brief descriptions of the six lymnaeacean families are given below:

Chiliniidae H. & A. Adams, 1855—This is a monogeneric family erected to accommodate *Chilina* Gray, 1828. Several species have been reported from the rivers and estuaries of Chile, Argentina and Paraguay (Ageitos de Castellano & Miquel, 1980; Brace, 1983). The variation reported for *Chilina* is limited to shell shape and pigmentation, and radular tooth shape.

Latiidae Hutton, 1882—This family includes only one species, *Latia neritoides* Gray, 1849, a freshwater limpet restricted to the streams of New Zealand (Burch & Patterson, 1964; Hubendick, 1962).

Acroloxiidae Thiele, 1931—This family of limpets is usually considered to comprise a single genus, *Acroloxus*, but the subgenus *Pseudancylostrum* is sometimes elevated to the generic level. The species *A. coloradensis* is found in Colorado, but the remaining species are found in Europe and northern Asia (Hubendick, 1978). The principle variations in this family are shell shape and radular tooth shape (Hubendick, 1962).

Physidae Fitzinger, 1833—Te (1978) presents a recent revision of this family, in which he recognizes 48 species in four genera. Te differentiated physids on the basis of shell shape, pigmentation patterns, mantle edge shape, kidney and gizzard shape, and the structures of the bursa copulatrix and the penial complex. This family is globally distributed.

Lymnaeidae Rafinesque, 1815—This family exhibits tremendous variation in shell morphology, supporting a large number of nominal genera. There also is considerable variation in anatomical traits, especially the male reproductive organs. Hubendick (1951) was unable to discern any clear pattern among anatomical traits or between anatomical and conchological traits. Therefore, he concluded that this family includes only two genera, the helicoid *Lymnaea* and the patelliform *Lanx*. The family is globally distributed.

Planorbidae Gray, 1840—This family represents the merging of three classical families: helicoid Buliniidae Hermansen, 1846; discoid Planorbidae Gray, 1840; and patelliform Ancyliidae Brown, 1844. In a series of papers, Hubendick (1947, 1948a, 1948b, 1955, 1964, 1978) demonstrated that these three groups are not clearly separable, but have complex interrelationships. Hubendick (1978) coined the name Ancyloplanorbidae to indicate the synthetic nature of the group. However, under Article 23 of the ICZN, Ancyloplanorbidae must be considered a junior synonym Planorbidae Gray, 1840; the oldest of three names from the merged families. The Planorbidae are globally distributed, and there is considerable variation in both shell morphology and internal anatomy.

LONGEVITY IN MOLLUSCS

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ABSTRACT

This paper compares longevity throughout an entire phylum, the Mollusca, in order to reveal common patterns underlying modes of reproduction. The comparison is based upon data gleaned from existing literature on the life durations of 547 species from marine, freshwater and terrestrial habitats.

Life-spans of molluscs range from two months to two hundred years. Molluscs living up to two years, or molluscs living more than two years but reproducing during only one season, are here defined as short-lived.

Many molluscs are long-lived, and bivalves are the most long-lived of molluscs. In the terrestrial and marine habitat, a short-lived mode of life is often correlated with: (1) Lack of an external shell. (2) Possession of an external shell that is semitransparent. (3) Dwelling in a microenvironment that is exposed to high solar radiation and to high temperatures. (In cold environments, on the other hand, the semelparous cycle of molluscs without external shells may be stretched, over two years or more.) (4) Dwelling in an environment that is predictable to such an extent that conditions favourable for reproduction occur (for an annual species) at least once a year. (5) Very minute size (in gastropods).

These generalizations apply almost fully to terrestrial and marine habitats and are partly valid in freshwater habitats.

The correlation between shell absence and longevity accounts for the greatest number of short-lived molluscs. This correlation may be explained in adaptive terms: shell absence may affect age-specific mortality via growth rates; or shell-less molluscs may utilise transient food resources. The difficulty in accepting any of these adaptive explanations stems from the ubiquity of the relation between shell-lessness and a short life span: almost every single shell-less mollusc, over a wide range of habitats in the sea and on the land, is short-lived.

The correlation may be also explained in non-adaptive terms: shell and longevity covary, so that an initial, adaptive change in the shell engenders a secondary, automatic change in the life-span. If this non-adaptive explanation is indeed valid, then the short life span of many molluscs may be a byproduct of selection on the shell rather than an independently selected trait. One major difficulty in accepting this non-adaptive explanation is that it lacks evidence at the genetic level.

Whatever the explanation for these correlations, they can be used to calculate the approximate number of short-lived gastropods. On a very broad and rough estimate, about one half of the land snail genera of western Europe may be short-lived.

Key words: longevity, molluscs, reproductive strategies, morphology, adaptation, non-adaptation, size, radiation.

INTRODUCTION

In this paper, I compare longevity throughout an entire phylum, the Mollusca. To the best of my knowledge this topic has previously been examined only twice, by Comfort (1957, 1964). On a more limited taxonomic range however, Zolotarev (1980) described the life spans of many bivalves from the Sea of Japan, and Powell & Cummins (1985) surveyed the longevities of some marine benthic prosobranchs and bivalves.

Records of the length of time a mollusc

lives are occasionally documented in ecological studies devoted to exploring the life histories of single species, or of several species within one genus. Frequently these data are presented in an incidental manner that does not relate to any larger evolutionary trends. Here, I collate data from existing literature to examine whether any general patterns of longevity can be traced throughout the entire mollusc phylum.

Methods of determining the age of molluscs include counting of growth checks in the shell (sometimes by shell-sectioning to reveal in-

ternal growth lines), population sampling, and the recapturing of marked animals. Infrequently the age is also determined by isotopic analysis of the shell (e.g. Turekian et al., 1975), and very infrequently by use of spectral analysis and flame photometry, or complex ionometric titration (Krasnov et al., 1975). The assembling of longevity data determined by any of these methods into comprehensive tables is a simple, straightforward process.

For the purposes of this study, I have aggregated all molluscs into two categories: short-lived (SL) and long-lived (LL). Short-lived molluscs are all those species that live up to two years, and also all those species that, regardless of how long they live, breed only over one season in their lifetimes. In contrast, long-lived molluscs are all those species that live for more than two years and breed over two seasons at least. These two categories can be compared to Kirkendall & Stenseth's (1985) classification of reproductive strategies. All their uniparous, uniseasonal and biseasonal molluscs fit into my short-lived category, whereas all their multi-seasonal iteroparous molluscs that live for more than two years are included in my long-lived category.

The present classification overcomes several entanglements arising from the fact that in some semelparous molluscs the life-span is variable, being annual in one habitat but stretching over several years in another because of a colder environment. When bearing in mind that life spans of molluscs range from several months to over two hundred years, the differences that this classification overlooks, in longevity amongst molluscs living up to two years, are minor. On the other hand, one of the disadvantages of this classification is that it lumps together, within the short-lived group, iteroparous molluscs that produce only a dozen progeny with semelparous species that produce many millions. I shall return to discuss this point later.

It is suggested that when analysing the data, the lowest group of long-lived molluscs, those with life-spans of 2–3 years, be separated as an intermediate category, to be excluded from later calculations. By doing so we avoid a situation whereby molluscs living three years but reproducing twice are classified as long-lived, whereas those living three years and reproducing once (such as certain cephalopods) are classified as short-lived. I do not think that this intermediate category

bears any biological uniqueness as compared to the short- or the long-lived categories.

With 60,000 Recent species, molluscs form the second-largest phylum within the animal kingdom. Longevity determines the number of seasons in which many of these species (the iteroparous ones) will reproduce. What are the life histories of molluscs? Which are the short-lived ones? Why is it that of two mollusc species living in the same environment and in very close proximity, feeding in a similar way and predated by similar enemies, one is short-lived and the other long-lived? These are the questions addressed in this paper.

METHODS

The available literature was searched, and each species classified as short- or long-lived.

Comfort (1957) reviewed the literature on the life duration of 135 molluscs. However, many of his records are of observations on captive specimens. This present paper therefore considers his data only to the extent that they refer to natural populations, to taxa traceable to the generic level (at least) in today's taxonomy, and to those for which no more recent records could be found. Some of the literature on freshwater gastropods (Calow, 1978; Browne & Russel-Hunter, 1978) bears conflicting evidence in that species listed as semelparous by one may be listed as iteroparous by the other. This reflects the fact that within a species, some populations may be semelparous, others iteroparous or "quasi-iteroparous" (a generally semelparous population that develops iteroparity under special circumstances). To overcome this difficulty, I have arbitrarily classified in this paper as short-lived any species that is enlisted as semelparous or quasi-iteroparous by at least one of these authors.

Tables 1–6, in the Appendix, present the maximum number of years a species lives, as recorded in the literature. Many authors describe various species as living "at least" a certain number of years. These minimum estimates of longevity are here presented as the life-span of the species, without further comment. The life-spans of short-living species are presented in these tables as SL, without further detail.

As there is a close relation between the age at maturity and longevity among limpets (Branch, 1981), opisthobranchs (Todd, 1981),

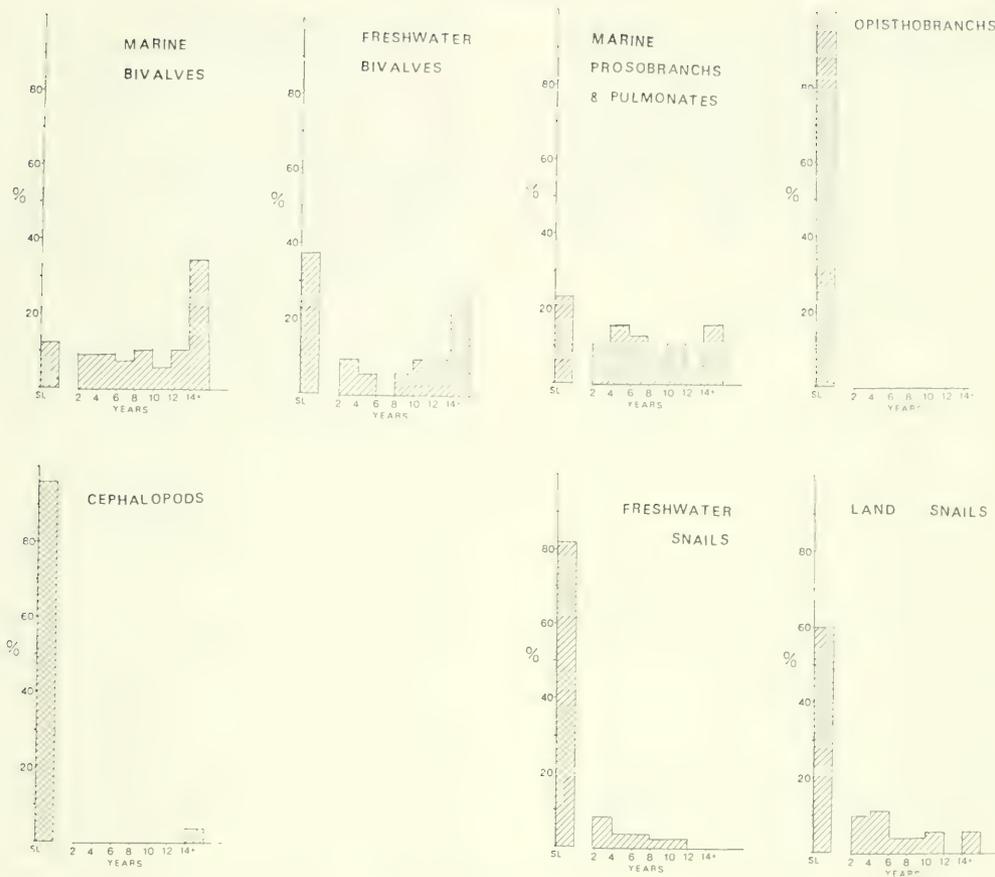


FIG. 1. Life-span frequencies in various mollusc groups. SL, short-lived category. In each histogram the highest (right-most) life-span category includes all species that live 14 years or more. Data from Tables 1-6.

land snails (Baur & Bengtsson, 1987) and, presumably, other mollusc groups, this trait is not presented in this paper.

LONGEVITY DATA

Fig. 1 illustrates the frequency of life spans in some various mollusc groups.

Chitons

Chitons are exclusively marine. Very few reliable data are available on their longevity, especially since Glynn (1970) severely criticised methods used by early workers in determining life spans. The only acceptable records I could find are of *Cryptochiton stelleri*, which lives for at least 25 years (MacGinitie & MacGinitie, 1968), and of *Chaetopleura*

apiculata, which lives up to 4 years (Grave, 1932).

Gastropods

Marine snails occur in two main groups, the prosobranchs and the opisthobranchs. Prosobranchs (20,000 species) are usually long-lived, whereas most opisthobranchs (about 2,000 species) are short-lived. They reproduce continuously once they reach sexual maturity, the frequency of their egg laying varying from several times per day to once every three weeks. They eventually die as a result of a senescent syndrome, typified by the shrinkage and breakdown of the digestive gland (Thompson 1976; Hadfield & Switzer-Dunlap, 1984). For nudibranchs (the largest group among the opisthobranchs), Todd (1981) distinguished three somewhat arbitrary

rary life-history patterns: (1) subannual species (life spans of a few weeks to a few months) are mostly small aeolids that feed on ephemeral prey, mainly hydrozoans; (2) annual species are larger (e.g. mostly dorids) and eat animals that persist in time, such as sponges, barnacles, bryozoans; and (3) biennial species are large animals (a few dendronotaceans and dorids) that feed on large, long-lived prey, such as alcyonarians. However, Hadfield & Switzer-Dunlap (1984) suggest that there is probably a continuum in the distribution of opisthobranch life spans, from species with life spans of a few weeks, through those with intermediate life spans of months, to others living one year or more. A few marine snails belong to the pulmonates, here represented by one family, the Siphonariidae, which are long-lived (Powell & Cummins, 1985).

Considering only the prosobranchs from among the marine gastropods, I found (Table 1) records for 105 species belonging to 52 genera and to 30 families. This amounts to about 2% of the 2,900 Recent genera (see Taylor & Sohl, 1962).

For the opisthobranchs, I found records of 63 species belonging to 37 genera and 25 families. This amounts to about 7% of the 500 Recent genera of opisthobranchs (see Taylor & Sohl, 1962). All are short-lived.

Of the marine pulmonates, I found records of three species, all belonging to one genus.

Freshwater snails belong to one of two major groups, the pulmonate basommatophorans and the prosobranchs. Most basommatophorans are short-lived. They are annual and semelparous, with complete replacement of generations after breeding in late spring or early summer. However, although this is the basic pattern, closer observation shows much variation. One such deviation from the basic pattern is the production of a second summer breeding generation without replacement of one generation by the other. Another deviation is production of two generations per year, with complete replacement. Sometimes there can also be three generations, again, with or without replacement. Lastly, a perennial, often biennial, pattern also occurs, with each generation capable of reproducing in two successive years. Such patterns of intraspecific variation in life histories are common amongst freshwater pulmonates and might be due either to ecological effects, genetic divergence, or to a combination of these factors (Russell-Hunter, 1978). In the freshwater pulmonate *Lymnaea*

elodes for example, intraspecific variation in life histories appears to be the result of phenotypic plasticity rather than of genetic differences (Brown, 1985). Freshwater prosobranchs tend to be more long-lived than freshwater pulmonates (Calow, 1978; Brown, 1983; Geraerts & Joosse, 1984). Freshwater prosobranchs also have smaller clutch sizes, lower growth rates, smaller shell sizes at maturity and larger shell sizes at death (Brown, 1983).

Both Calow (1978) and Geraerts & Joosse (1984) suggest that semelparity is a response to the harsh freshwater conditions that make it necessary to confine the whole embryonic development within the protecting egg mass. This procedure demands an increased reproductive effort but increases the chance of embryonic survival, and hence diminishes the need for a long adult phase as an insurance policy. Both studies suggest that this semelparous condition is associated with reproductive recklessness, in that the parents continue low reproductive activity under adverse conditions despite fatal effects, whereas in iteroparous species reproduction stops quickly and the available energy is saved for survival. Both also comment that freshwater snails with an iteroparous strategy are those that inhabit small, closed water bodies, where there is more competition, more density-dependent control, and hence a greater premium on the survival of a large, "experienced" adult.

I have found records of 60 species belonging to 29 genera and 11 families (Table 2). Both prosobranch and pulmonate freshwater snails have, on the whole, short life-spans as compared to marine snails (Table 1) and terrestrial ones (Table 3).

Land snails belong to one of two groups, the prosobranchs (mostly confined to the tropics) and the (mostly stylommatophoran) pulmonates, which are distributed world-wide. I could not find records concerning the longevities of terrestrial prosobranchs, but for the vague statement that *Pomatias elegans* is "said to live 4–5 years" (Fretter & Graham, 1978). The reproductive strategies of terrestrial pulmonates have been reviewed by Duncan (1975), who emphasized that maturation and growth of stylommatophorans are temperature-dependent, and suggested that small helicids mature more quickly and have a shorter life span than large species.

I found records of 75 species belonging to 57 genera and 30 families (Table 3). With an

overall estimate of 2,200 stylommatophoran genera (Taylor & Sohl, 1962), this is 3%.

Bivalves

Marine bivalves are represented by a very large array of groups. I found records of 150 species belonging to 90 genera and 37 families (Table 4). This amounts to about 6% of the 1,400 Recent genera (data from Vokes, 1967). Many of these records come from the study of Zolotarev (1980), who found that half of the species examined from the Sea of Japan have life spans of more than 20 years.

Most freshwater bivalves belong to two families, the unionids (in which the juveniles undergo a parasitic stage in fish) and the sphaeriids (in which the young are brooded in the mother's body, emerging as miniatures of the adult). I found records for 52 species belonging to 17 genera and to five families (Table 5). This amounts to about 4% of the 400 genera of Recent freshwater bivalves (data from Vokes, 1967).

Cephalopods

There are about 650 species of cephalopods, belonging to 140 genera (Voss 1977). I found (Table 6) records for 27 species belonging to 17 genera and to nine families. This amounts to about 12% of the 140 genera of Recent cephalopods. Except for one (*Nautilus*, which lives for well over 20 years; Saunders, 1984), all cephalopods are short-lived, reproducing through one season only, and death is the typical consequence of egg laying or mating (Arnold & Williams-Arnold, 1977; Wells & Wells, 1977; Calow, 1987).

According to Calow (1987), the failure of cephalopods to take advantage of the wide variety of reproductive tactics used by other mollusc groups is a consequence of selection for fast growth rates in the juveniles. He suggested that rapid growth would reduce the likelihood of juvenile mortality due to predation, because juveniles would be small and vulnerable for a shorter time. This, in turn, would make high adult investments in reproduction and semelparity less risky because the probability of offspring survival would be high. They seem to "live fast and die young." Theoretical predictions that the level of investment in reproduction by semelparous organisms should be high, that reduced levels of investment in reproduction should extend the lives of parents, and that the survival of juve-

niles should generally be good, are probably not valid in cephalopods (Calow, 1987). Moy-nihan & Rodaniche (1982) have suggested that semelparity, when it is followed by the death and disappearance of breeders, may be an effective discouragement to specialization by predators; it also leaves more resources for the offspring.

DATA ANALYSIS

Tables 1-6, with data on 547 species, clearly demonstrate the enormous variability in longevity of the molluscs: from several months to well over two hundred years.

These tables also demonstrate that short life spans are a very common strategy amongst molluscs. Our present state of knowledge is ripe to discuss the short-lived category, because it is usually based upon clear-cut, firm evidence that gives the species a definite life span, plus or minus one or two years (at the very most). Our knowledge on the long-lived group is still insufficient to enable analysis of variation within this category, because many of the data refer to information on minimum life spans rather than to actual longevity in nature. Our data are sufficient, however, to analyse and compare the short-lived group, as a whole, to the long-lived one, as a whole.

The intermediate category (consisting of species with life-spans of 2-3 years, as defined in the introduction, and amounting to 7% of the species listed) can now be excluded from calculations. The resulting picture is summarised in Table 7. At the level of both species and genus, almost half of the records are of short-lived molluscs.

As a rule, all species within one genus are either long- or short-lived. (Exceptions to this rule are the marine prosobranchs *Acmaea*, *Littorina* and *Cerithium* and the marine bivalve *Donax*.) This fact enables a stepping-up of the taxonomic level to that of genera. By doing so, we gain a firmer taxonomic ground. We also overcome the danger of distortion due to the fact that in certain genera very many species have been studied, and are thus over-represented in the literature.

Are there any morphological or environmental factors in which the short-lived genera differ from the long-lived ones? Should this high frequency of short-lived genera be considered as a representative picture of the mol-

TABLE 7. Number of short- and long-lived molluscs

	SHORT-LIVED		LONG-LIVED	
CHITONS	—	—	2 genera,	2 species
MARINE SNAILS				
Prosobranchs	16 genera,	25 species	36 genera,	73 species
Opisthobranchs	37 genera,	63 species	—	—
Pulmonates	—	—	1 genus,	2 species
FRESHWATER SNAILS	23 genera,	48 species	3 genera,	6 species
LAND SNAILS	30 genera,	44 species	22 genera,	26 species
MARINE BIVALVES	11 genera,	21 species	73 genera,	116 species
FRESHWATER BIVALVES	4 genera,	19 species	12 genera,	28 species
CEPHALOPODS	16 genera,	26 species	1 genus,	1 species
TOTAL:	137 genera,	246 species	150 genera,	254 species

Notes to Table 7:

1. "Long-lived" refers only to molluscs that live four years or more. "Short-lived" refers to molluscs that live up to two years, and also to those that reproduce throughout one season only, regardless of their life-span.
2. The data are from Tables 1–6, and from the text.
3. In the marine prosobranch category, the "mixed" genera *Acmaea*, *Notacmea*, *Littorina* and *Cerithium* are counted twice: as short- and as long-lived.

luschs in general? The following sections explore these questions.

Longevity and shell morphology

Could it be that the life-span of a mollusc is associated with the presence or absence of a well-calcified external shell?

To answer this question, each genus was classified into one of three shell categories: shell fully calcified and opaque; shell consisting mainly of conchiolin, with very little calcium in it and semi-transparent; shell reduced to such an extent that the snail cannot retract into it, or that it is internal or totally absent. Most terrestrial and marine molluscs fall easily into either of these three categories, but there is, of course, a continuum between the opaque and semitransparent shells, and the distinction between the two is, to a certain extent, arbitrary.

The results are given in Table 8, which presents the shell morphology in long-lived (excluding the intermediate category) and short-lived molluscs.

In marine prosobranchs, only two genera, *Enteroxenos* and *Thyonicola*, lack an external shell, and only *Lacuna* and *Patina* have a semitransparent one. All other marine prosobranchs have opaque, well-calcified shells. It is unfortunate that no data are available on the Lamellariidae and the Heteropoda, two other groups of shell-less prosobranchs.

The majority of opisthobranchs listed in Table 1 are shell-less. Genera with semi-transparent shells are *Limacina*, *Cavolina*, *Clio*,

Creseis, *Cuvierina* and *Diarca*. The only genus with an opaque, external calcified shell is *Pupa*.

Land snails belonging to the shell-less category include *Arion*, *Bielzia*, *Catinella*, *Dero-ceras*, *Eucobresia*, *Limax*, *Milax*, *Omalonyx*, *Parmacella*, *Semilimac*, *Testacella*, *Vaginulus* and *Vitrina*. Those belonging to the intermediate category, with semitransparent shells, include *Aegopinella*, *Carychium*, *Elona*, *Monacha* and *Oxychilus*. All other genera have opaque, external shells. Comfort (1957) mentions *Geomalacus* as living seven years, based upon animals studied in captivity. If this observation does indeed reflect longevities in natural populations and if, on the other hand, the weak evidence for a short life span in *Veronicella* is valid, then for shell-less snails the ratio between short-lived and long-lived genera would be 15:2 (as compared to genera with opaque shells, where the ratio is 12:21). *Cochlicopa* and *Euconulus* are not included in Table 2 because our present knowledge of their longevities places them within the intermediate group. If they do indeed live more than three years, then for semitransparent snails the ratio between short-lived and long-lived genera would be 4:2, an intermediate position between the shell-less and the opaque-shelled landsnails.

Most marine bivalves are well-calcified. The only totally naked marine bivalve is *Chlamydoconcha* (Chlamydoconchidae), in which the shell is completely enclosed by the mantle. No data on its longevity were found. Shipworms (Teredinidae) are virtually shell-

TABLE 8. Relation between shell and life span in mollusc genera

		LIFE-SPAN	
		short-lived	long-lived
A. MARINE SNAILS (PROSOBRANCHS)			
SHELL	opaque	12	36
	semitransparent	2	—
	no external shell	2	—
B. MARINE SNAILS (OPISTHOBRANCHS)			
SHELL	opaque	1	—
	semitransparent	6	—
	no external shell	30	—
C. LAND SNAILS			
SHELL	opaque	12	21
	semitransparent	4	—
	no external shell	12	1
D. MARINE BIVALVES			
SHELL	opaque	9	74
	semitransparent	—	1
	no external shell	2	—
E. CEPHALOPODS			
SHELL	opaque	—	1
	semitransparent	—	—
	no external shell	16	—

less, with a body that resembles a worm: The shell is greatly reduced, has lost its protective function and become an effective drilling tool for boring into wood. Soft-shelled clams (*Mya* and *Panopea*) have large siphons that are permanently extended, being much too large to be accommodated within the shell. However, their valves are large, opaque and calcified to such an extent that I have placed them in the opaque category. The major semitransparent family is the Pinnidae (fan mussels), in which the valves consist largely of flexible organic conchiolin. Although *Pinna atropurpurea* (= *P. bicolor*) may perhaps be annual in Hong Kong (Wu, 1985), in Australia it lives substantially more than three years, and may well reach 12 years of age (Butler & Brewster, 1979).

There are about 150 genera of cephalopods (Voss, 1977). Except for one (*Nautilus*, which has an external, calcified shell), the shell of all cephalopods is internal and reduced (squids), or absent (octopuses).

The statistical analysis of the data was carried out twice, and Fischer's exact test for independence in 2×2 contingency tables (Sokal & Rohlf, 1981) was applied in both cases. First, for simplicity, the three shell categories were lumped into two: shell present

(categories 1 and 2) and shell absent (category 3). The frequency of the shell-less genera among the short-lived molluscs was significantly higher than their frequency among long-lived ones, among marine gastropods (prosobranchs alone, or prosobranchs and opisthobranchs combined), land snails and cephalopods. The frequency of shell-less genera that are short-lived is significantly higher than those that are long-lived ($P = 5.1 \times 10^{-21}$, Fisher's exact test).

Next, categories 1 and 2 were separated and the Fisher's exact test again applied. The frequency of genera that have semitransparent shells among the short-lived molluscs is significantly higher than among the long-lived ones, in marine gastropods ($P = 0.0405$) and land snails ($P = 0.0380$) separately, and for marine and land snails combined ($P = 0.0013$). Amongst marine bivalves, there are no significant differences.

To sum up Table 8, out of 49 mollusc genera without an external shell, 99% are short-lived; of 13 mollusc genera with a shell that is external but poorly calcified, 92% are short-lived; and of 165 genera with an external, well-calcified shell, only 21% are short-lived.

The only freshwater shell-less molluscs I know of are the acochliacean genera *Aco-*

TABLE 9. Relation between shell morphology and habitat type

	HABITAT	
	fully-exposed	not fully-exposed
LONG-LIVED LAND SNAILS		
shell solid	1	20
shell transparent or absent	0	1
SHORT-LIVED LAND SNAILS		
shell solid	7	5
shell transparent or absent	1	16

chlidium and *Tantulum*, found on a few islands in the Pacific and on one island in the Caribbean (Rankin, 1979). I found no data on their longevity. Shipworms, though normally requiring marine conditions for successful spawning, are occasionally recorded from inland waters (Nair & Saraswathy, 1971). Freshwater molluscs are not represented in this calculation since their classification into calcified versus semitransparent genera runs into difficulties. Apparently some individuals within a genus may be opaque and others semitransparent. Whereas in Israel many genera are semi-transparent (*Valvata*, *Bithynia*, *Hydrobia*, *Semisalsa*, *Pseudamnicola*, *Galba*, *Stagnicola*, *Radix*, *Ancylus*, *Ferrissia*, *Bulinus*, *Planorbis*, *Segmentina*, *Gyraulus*, *Biomphalaria*, *Helisoma*, *Physella*, *Pisidium*), in Europe or North America these same genera may be opaque. It is unfortunate that much of the taxonomic literature does not refer to this trait in sufficient detail. A very welcome exception is the study of Fretter & Graham (1978), who describe the following freshwater prosobranchs as semitransparent: *Potamopyrgus*, *Pseudamnicola*, *Bithynia*. As for *Viviparus*, *V. contectus* is described as semitransparent and *V. viviparus* as opaque. As for *Viviparus ater*, snails from Lake Maggiore have partially dissolved shells whereas those of Lake Zurich do not (Ribi & Gebhardt, 1986). Since I am not confident that the classification of genera or even species into opaque and semitransparent categories is consistent amongst freshwater molluscs, they (and the amphibious genus *Succinea*) are omitted from the present analysis. Omitting the snails is not very significant because most of them (88% of the species) live less than 4 years anyway, regardless of whether they belong to the first shell category or the second. As concerning bivalves, however, this is rather unfortunate, because their longevities in freshwater range from less than one year to

well over a century. It should at least be noted that all long-lived genera of freshwater bivalves are unionids, and are well-calcified—what one would indeed expect from the longevity pattern in the marine and terrestrial environments.

Land snails: Life span and habitat

Whereas amongst marine molluscs the majority of short-lived genera are shell-less or with semitransparent shells, amongst terrestrial molluscs over 35% of the short-lived genera have well-calcified shells. Further information concerning these genera is gained when their habitat is considered. To examine whether the life-span of a terrestrial snail is associated with the environment in which it lives, and whether short-lived genera occupy a different micro-habitat than that of the long-lived ones, each genus was classified into one of two habitat categories (as described in literature): (1) Genera frequently exposed to heavy solar radiation. This includes molluscs that sit out on the tips of the vegetation, where they are fully exposed to the sun even when aestivating. (2) Genera not exposed to solar radiation, or found in habitats with intermediate exposure to the sun. This includes all genera that are crevice-dwellers, litter-dwellers, or that sit in the more concealed, shady parts of vegetation or on shady parts of trees.

The results are given in Table 9.

Long-lived land snail genera that sit out on the vegetation include *Cerion*. Intermediate genera (not presented in Table 8) include *Trochoidea*. Short-lived genera include *Brephulopsis*, *Bulimulus*, *Catinella*, *Cernuella*, *Helicella*, *Monacha*, *Theba* and *Xeropicta*.

Statistical analysis of the data given in Table 9 reveal that the frequency of the species that are both exposed and calcified among the short-lived land snails is significantly higher than the frequency of the species that

are both exposed and calcified among the long-lived ones ($P = 0.0672$, by Fisher's exact test).

Life span and shell size

Ten of the gastropods with opaque shells surveyed in this study are very minute (i.e. the reproducing adult is less than 4 mm). Amongst the land snails, *Carychium* is less than 2 mm, *Vertigo* less than 3 mm, and *Punctum* less than 2 mm. Amongst marine prosobranchs, *Rissoa parva* is 3–4 mm, *Skeneopsis* reaches 2 mm, *Omalogyra* 1 mm, *Rissoella* 2 mm, *Barleeia* 3 mm, *Littorina neglecta* reaches 2–3 mm, and *Littorina acutispira* usually up to 2 mm. All are short-lived.

DISCUSSION

The data presented so far allow for statements about several patterns of longevity among molluscs.

One general pattern concerns the association between the loss of a mollusc's calcified shell on the one hand and its short life-span on the other. Molluscs in which the shell has become internal or lost, and frequently also in those in which the shell is external but has lost its calcification or becomes rudimentary, are short-lived. This relationship holds true whether the mollusc is a gastropod (prosobranch, opisthobranch or pulmonate) or a cephalopod; whether it lives in the sea or on the land; whether its mode of reproduction involves gonochorism or hermaphroditism, planktonic larvae or hatchlings that resemble adults; whether it moves by crawling, jet-propulsion or is sedentary; and whether it feeds as a herbivore, carnivore or omnivore.

Describing correlations is one thing, explaining them is another matter. Correlations can be explained in many ways, and the approach may be adaptive or non-adaptive, each with its drawbacks.

The relation between shell absence and longevity may be explained in adaptive terms, in that shell absence affects age-specific mortality directly. It enables high growth rates and juveniles of shell-less molluscs grow to adult size quicker than shelled ones, speeding through the vulnerable juvenile phase. Once they reach adult size their survival chances are similar to those of their parents, and since semelparity is favoured whenever the survival

chances of the parents and offspring are similar (Calow, 1981), semelparity will eventually indeed develop.

Differences in growth rates between shelled and shellless molluscs do exist. Among terrestrial molluscs for example, a slug such as *Deroceras reticulatus* matures within the first year, breeds in the second and then dies (Runham & Hunter, 1970), whereas a shelled landsnail such as *Arianta arbustorum* matures within two years, breeds and may then live on for another ten (Baur & Raboud, 1988). Similarly among cephalopods, a 120 mm-long squid can mature at the age of six months (Moynihan & Rodaniche, 1982), whereas *Nautilus* matures within several years. From these aspects, the consistently faster growth rates of the shell-less molluscs may indeed be an advantageous trait.

Whether these rapid growth rates should always and consistently lead to semelparity is another question. Such an argument would imply ubiquity in the ecology of entire groups of shell-less molluscs, which is difficult to accept. It is not reasonable to assume that all 2,500 molluscan species—which have had different taxonomic origins ever since the Palaeozoic, which live in environments as different as a whole spectrum of habitats in the sea and on land, which practice a wide scope of reproductive strategies ranging from planktonic veligers to direct development (with or without parental caring of eggs), which are either hermaphroditic or gonochoristic—should always and consistently practice a semelparous reproductive strategy only because, since they enjoy a faster growth rate, their survival chances come to resemble those of their parents at an earlier age. The advantages to be gained from semelparity must surely be overwhelming if such a general correlation, cutting through an entire animal phylum, should be explained on its selective basis.

Another, somewhat similar adaptive approach to the relation between shell absence and longevity could be that when extrinsic mortality risks (such as starvation, accident, disease or predation) are higher for parents than for offspring, it pays the parent to increase its investment in the reproduction of many offspring. This increase would eventually lead to a semelparous reproductive strategy (Calow, 1981, 1984). As applied to molluscs, this means that shell absence directly affects age-specific mortality: If the shell-less mollusc (slug, octopus or opisthobranch)

were to live on after reproduction, then its survival chances would be very low as compared to its progeny, due to such environmental factors.

This age-specific-mortality argument can definitely be applied to many opisthobranchs, in which the parent feeds upon food that is transient, whereas the juveniles feed upon another source. Thus in *Aplysiomorpha* and *Sacoglossa*, the adult feeds upon seasonally abundant green seaweed, whereas the juvenile is a planktonic veliger that feeds upon unicellular algae (Kandel, 1979; Carefoot, 1987). Among the bivalves, shipworms offer another excellent example of a mollusc utilizing a transient habitat. They have rapid growth rates, reach an early maturity within 3–6 weeks and have very high reproductive rates (Nair & Saraswathy, 1971; Turner, 1973).

Again however, whether shell-less molluscs always and consistently feed upon transitional prey is another question. Opisthobranchs feed upon a wide variety of prey (hydrozoans, sponges, polychaetes, gastropods, bivalves, ascidians, sessile barnacles—see Thompson, 1976), and many of these food resources are rather stable and not of a transient nature. Octopuses and cuttlefish are opportunistic carnivores that feed upon shrimps, prawns, crabs, polychaetes, bivalves, gastropods and fishes (Boucaud-Camou & Boucher-Rodoni, 1983), food resources that are stable rather than transient. Slugs eat dead leaves, stems, bulbs, tubers, fungi, lichens and algae (Runham & Hunter, 1970), a diet similar to that of shelled land-snails. It is questionable whether all of these food resources are indeed transient, but even if they are, this does not explain the question but merely rephrases it into "why are the shell-less molluscs, whether herbivores, omnivores or carnivores, capable of feeding only upon transient, rather than stable resources?" This is back almost to the starting point.

Extrinsic mortality risks include also predation, and it could perhaps be argued that groups in which the extent of predation increases with adulthood are likely to be short-lived. To make such a claim acceptable, some sort of evidence must be presented that shows that in nature, predation pressures on adult shell-less molluscs are indeed greater than those on their progeny, thereby lowering their survival chances. Together with such data, additional evidence must also be pre-

sented that adult shelled molluscs do not face such severe predation risks. At present, I do not know of such evidence.

To conclude, it should be re-emphasized that the question emerging from the data analysis is not whether some molluscs are short-lived, but why all shell-less molluscs are short-lived. The disadvantage of the adaptive approach is that it does not cope with the ubiquity of the relation between shell and longevity, and when the whole spectrum of shell-less molluscs is considered, it loses much of its attractiveness.

The ubiquity of the relation may be explained in non-adaptive terms: A short life span may be a byproduct of selection on the shell, rather than an independently selected trait. Shell and longevity may covary so that an adaptive change in the shell engenders an automatic switch in longevity, the latter being irrelevant to adaptation and not under immediate control of the environment.

Loss of the shell occurred independently in several molluscan lineages, as a result of a wide variety of selective forces that, at least as considered today, have very little to do with life cycles. In marine prosobranchs, predatory pressure by crabs and fish has resulted in the survival of heavy, ridged or spiny shells (Vermeij, 1978). Pressure on marine cephalopods to form a very light, buoyant animal capable of swimming actively in the water body (rather than passively drifting with the currents in a flying-balloon, *Nautilus*-style) has led to the persistence of those with an internal shell, or with no shell at all. Opisthobranchs' initial exploitation of the infaunal (burrowing) environment by the primitive order *Bullomorpha*, combined with their development of chemical defence supplied by the integument to replace the mechanic defense supplied by the shell, led to the reduction of the shell and its eventual loss (Thompson, 1976). In such planktonic opisthobranchs as the Euthecosomata, a (transparent) shell is retained, however, and functions as a retreat into which the animal withdraws, so as to sink and thereby rapidly avoid predators (Be & Gilmer, 1977). In terrestrial molluscs, the ability for deeper penetration into the ground and, in addition, the invasion of calcium-deficient, moisture-rich environments has been the outcome of developing a shell-less slug form in several unrelated taxonomic families (Solem, 1978). Alternatively, the slug form may have developed through the habit of climbing up trees (Cain, pers. comm.). Once the shell is lost, in

any of these mollusc lineages and for any of these selective reasons, a mollusc will automatically become short-lived.

Within the severe limits of a short life span, life history strategies vary in evolutionary response to different environmental conditions. For example, some of the species of British nudibranchs have fully annual life cycles with one breeding period, whereas others pass through numerous generations a year. The purely annual species feed on organisms that are abundant and stable throughout all seasons of the year, whereas those passing through a number of generations a year are species that feed upon seasonal, transitory prey (Thompson, 1976). Seasonal food shortage may thus determine the relatively short life span of the one, as compared to a stable food supply that determines the slightly longer life span of the other. However, both have an overall short life span that does not exceed one year, two at the most. When we consider them together, as one single category, in comparison to the long-lived (and shell-possessing) prosobranchs, these differences between them seem trivial. This non-adaptive approach may suggest that shell absence is the overriding factor in determining whether a mollusc will be short- or long-lived. Once this major factor is set and the mollusc becomes short-lived, then environmental factors determine the fine tuning.

The non-adaptive approach may suggest (in a very schematic and over-simplified manner) that many molluscs, short-lived because they lost their shells, invaded the "transient food niche" where there is less competition from the long-lived (shelled) molluscs. However, a transient food niche is not a prerequisite of shelllessness, and many short-lived (shell-less) molluscs may enjoy a stable food niche, their short life-spans bearing no direct relevance to their food resources (and vice-versa).

The advantage of this non-adaptive approach is that it copes well with the ubiquity of the relationship between shell absence and short longevity.

One severe weakness of the non-adaptive approach is that it requires a nearly single-gene linkage between shell-lessness and longevity. There is, as yet, no direct evidence for any such link.

A further weakness is that it cannot explain exceptional records, of shell-less molluscs that are not short-lived. This includes the terrestrial slug *Testacella*, if we restrict ourselves to longevity records based upon evidence

from natural populations. If also records of molluscs reared in captivity are accepted, then this also includes the landsnail *Geomalacus* (Comfort, 1957). Data on the longevity of slugs from additional pulmonate families, such as the Helicariionidae, Charopidae, Athoracophoridae and Endontidae, could also help, since long life spans in these families would weaken the non-adaptive approach considerably, at least as a phenomenon that sweeps through the entire phylum.

It should be emphasized that whereas for gastropods we have data on 45 shell-less genera, for bivalves we have data for only two. Both are short-lived, but this is obviously not nearly enough to enable generalisations about the entire class. A reminder as to why (in this respect) the bivalves should be approached cautiously comes from *Nausitora fusticula*, a large oviparous terebratulid of tropical mangroves. Collected as a fully grown adult (age unknown), a specimen of this species lived for two and a half years in an aquarium at Harvard University (R. Turner, pers. comm.).

To conclude, the disadvantages of the non-adaptive approach is that it lacks, as yet, genetic support and that it relies very heavily upon the ubiquity of the association, so that it cannot explain exceptions.

A second pattern to emerge from the data in this study is that the life history of well-calcified molluscs is influenced by the temperature of their environment. A short life-span may occur in well-calcified molluscs that live in very hot environmental conditions. The rate of gamete development is directly dependent on temperature, and high temperatures increase the rate of gonad maturation. The scallop *Argopecten irradians*, for example, matures within 12 months in its natural habitat, but maturing can be accelerated by laboratory exposure to higher temperatures, and it then reaches reproductive stage within six months (Sastry, 1979). A warm environment will also enable the rapid growth of juvenile gastropods (see Runham & Hunter, 1970, for slugs; Geraerts & Joosse, 1984, for freshwater gastropods). In the marine environment, the term hot applies to geographically widespread species, where populations from tropical waters complete their life-span in a much shorter time (Cerrato, 1980; Hadfield & Switzer-Dunlap, 1984). In the freshwater environment, it applies to snails and bivalves that live in relatively warm waters (Geraerts & Joosse, 1984; Mackie, 1984). In the terrestrial environment, my study suggests that it refers to

those micro-habitats in which the land snails sit out on the vegetation, where they are fully exposed to solar radiation. Low temperature, on the other hand, can stretch a semelparous cycle that is annual in the warmer parts of a species' range, into a biennial one in the colder parts. (*Theba pisana* from Israel as compared to that of England is one such case; see Heller, 1982, and Cowie, 1984. *Arianta arbustorum* of the lower Alps as compared to that of higher altitudes is another example; Baur & Raboud, 1988.) The short life-span of molluscs of hot micro-habitats may be a phenotypic response to the environment, or it may be a genetically controlled trait, subject to selection.

In land snails, the relation between longevity and exposure may be explained in adaptive terms, in that ionizing radiation increases the rate of ageing and reduces the average life-span of animals. Experimental evidence reviewed by Comfort (1978) showed that large doses of hard radiation (gamma and fast neutrons) shorten life considerably. These conclusions should be approached with caution, however, since the experiments made use of extremely heavy doses that exceed natural quantities reaching the earth by several orders of magnitude. The effects of ultraviolet radiation on molluscs are as yet unknown, but upon entering a reptile's body ultraviolet radiation can cause a breakdown of molecules and thereby alter vital biochemical processes (Porter, 1967). A short life span could thus be enforced in landsnails dwelling on the tips of vegetation, where they are subject to heavier ultraviolet radiation than snails dwelling underneath stones. Even visual daylight radiation may be an important environmental factor that influences the gonad of land snails. Continuous illumination of the slug *Deroceras reticulatum* for five weeks increases the thickness of the germinal epithelium, rate of meiosis and also the numbers of sertoli cells, male gametes, multinucleated spermatids, and it upsets in cytokinesis (Pari-var, 1978, and references therein).

An exception to this generalisation that land snails of warm, strongly radiated environments are short-lived concerns snails that inhabit environments that, in addition to being hot, are also extremely unpredictable, such as the shadeless vegetation of deserts. In such hot surroundings, where conditions for growth and reproduction are both very infrequent and unpredictable, semelparous annual populations would quickly become ex-

inct. Molluscs of these habitats may be expected to be more long-lived than their close relatives from more favourable conditions. Short-lived molluscs are restricted, accordingly, to environments in which there is a predictable weather.

A third pattern to emerge from the data in this study is that among the shell-possessing gastropods, longevity is related to size. Though the linear relationship between body size and life-span found in mammals (Kohn, 1971) definitely does not occur in molluscs, short life spans appear to occur more frequently among very minute gastropods than among larger ones. Every single one of the very minute gastropods found in this study are short-lived. (This does not apply to the bivalves, in which minute genera, such as *Myssella*, may live for six years.) Furthermore, to the extent that the short-lived group can be divided into semelparous animals on the one hand and iteroparous animals on the other, most of these small snails belong to the latter group: They mature within several weeks early in the season, lay several eggs (up to about 30) throughout the remainder of the season, and gradually die off by the end of the season (Fretter, 1948; Morton, 1954; Southgate, 1982; Hughes, 1986; Baur, 1987; Pokryszko, pers. comm). *Littorina acutispira* (see Underwood & McFadyen, 1983) and *Rissoa* reproduce by planktonic veligers, and consequently have more juveniles than the rest of this group. Marine gastropods that are both well-calcified, short-lived and produce a very large number of offspring (such as *Cerithium scabridum*; see Ayal, 1978) are infrequent.

A fourth pattern to emerge is that bivalves are more long-lived than other groups. Though they form only 40% of the species listed in the longevity tables, they constitute 88% of the species that live over 25 years, 92% of the species that live over 50 years, and they are the only molluscs that live over a century. Short life-spans are not a very common strategy amongst bivalves, and only 15% of the bivalve genera are short-lived (as compared to short life spans in 63% of the gastropods). A sedentary mode of life apparently bears the potential for a long life-span.

CONCLUSIONS

This paper paints the longevity pattern of molluscs in very broad strokes. To conclude, we can to a certain extent generalize about

the relationship between a mollusc's longevity, its morphology and its environment.

Bivalves are the most long-lived of molluscs.

Amongst bivalves, prosobranchs and pulmonates, short life-spans are more common in the freshwater than in the marine or terrestrial environment.

In the terrestrial and marine habitat, a short-lived mode of life is often correlated with:

1. Lack of an external shell.
2. Possession of an external shell that is semitransparent.
3. Dwelling in a micro-environment that is exposed to high solar radiation and to high temperatures. (In cold environments, on the other hand, the semelparous cycle of molluscs without external shells may be stretched, over two years or more.)
4. Dwelling in an environment that is predictable to such an extent that conditions favourable for reproduction occur (for an annual species) at least once a year.
5. Very minute size (in gastropods).

Of these generalizations, the correlation between shell absence and longevity accounts for the greatest number of short-lived molluscs.

When combined together, these correlations, of shell-morphology exposure and minute size, account for 84% of the short-lived marine snails, and 93% of the land snails mentioned in this study. Confining ourselves to the gastropods, we can now apply these correlations to predict, very approximately, the number of short-lived genera. In the terrestrial habitat, present information concerns mainly Europe. If we combine, from Kerney & Cameron (1979), all the genera that are shell-less, have semitransparent shells, dwell in exposed habitats where they sit out on the vegetation, or are very minute (less than 4 mm) and assume that all these snails are short-lived, then as a very rough and broad estimate, half of the genera of Britain and northwestern Europe may be short-lived. Similar calculations reveal that about half of the 45 genera of the Mediterranean region of Israel may be short-lived, whereas in the Negev Desert, where slugs and snails with semitransparent shells cannot survive because of the dangers of desiccation, only one of the

nine genera is short-lived and another one is intermediate.

The empiric rules proposed in this paper are based upon evidence from 547 mollusc species. Future research will probably modify them considerably.

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APPENDIX

TABLE 1. Life spans in marine snails

Species	Lifespan	Authority
PROSOBRANCHIA.		
Haliotidae		
<i>Haliotis cracherodii</i>	51	Powell & Cummins, 1985
<i>Haliotis iris</i>	10	Powell & Stanton, 1985
<i>Haliotis laevigata</i>	10	Shepherd et al., 1982
<i>Haliotis ruber</i>	10	Shepherd et al., 1982
<i>Haliotis rufescens</i>	13	Shepherd et al., 1982
<i>Haliotis tuberculata</i>	6	Hayashi, 1980a, b
Fissurellidae		
<i>Fissurella barbadensis</i>	3	Hughes & Roberts, 1980a, b
<i>Fissurella crassa</i>	10	Bretos, 1980
<i>Montfortula rugosa</i>	3	Powell & Cummins, 1985
Patellidae		
<i>Cellana grata</i>	15	Comfort, 1957
<i>Cellana radiata</i>	4	Powell & Cummins, 1985
<i>Cellana tramoserica</i>	5	Fletcher, 1984
<i>Nacella concinna</i>	21	Picken, 1980
<i>Nacella delesserti</i>	10	Blankley & Branch, 1985
<i>Patella aspersa</i>	12	Powell & Stanton, 1985
<i>Patella cochlear</i>	25	Powell & Cummins, 1985
<i>Patella granatina</i>	6	Powell & Cummins, 1985
<i>Patella granularis</i>	8	Powell & Cummins, 1985
<i>Patella longicosta</i>	16	Grahame & Branch, 1985
<i>Patella oculus</i>	3	Powell & Cummins, 1985
<i>Patella vulgata</i>	15	Comfort, 1957
<i>Patina pellucida</i>	SL	Vahl, 1971

(continued)

TABLE 1. (continued)

Species	Lifespan	Authority
Acmaeidae		
<i>Acmaea antillarum</i>	SL	Kenny, 1977
<i>Acmaea digitalis</i>	5	Choat & Black, 1979
<i>Acmaea dorsuosa</i>	15	Comfort, 1957
<i>Acmaea insessa</i>	SL	Choat & Black, 1979
<i>Acmaea paradigitalis</i>	20	Powell & Cummins, 1985
<i>Acmaea pelta</i>	4	Powell & Cummins, 1985
<i>Acmaea scabra</i>	12	Sutherland, 1970
<i>Acmaea testudinalis</i>	7	Zaika, 1973
<i>Notacmea petterdi</i>	10	Powell & Cummins, 1985
<i>Notacmea scutum</i>	SL	Phillips, 1981
<i>Patelloida alticostata</i>	6	Powell & Cummins, 1985
<i>Patelloida latistrigata</i>	4	Powell & Cummins, 1985
Trochidae		
<i>Falsimargarita iris</i>	3	Egorova, 1978
<i>Gibbula umbilicalis</i>	5	Williamson & Kendall, 1981
<i>Margarites helycinus</i>	SL	Zaika, 1973
<i>Monodonta lineata</i>	15	Williamson & Kendall, 1981
<i>Tegula funebris</i>	30	Williamson & Kendall, 1981
<i>Trochus niloticus</i>	15	Smith, 1987
Turbidae		
<i>Turbo setosus</i>	3	Sire & Bonnet, 1984
Neritidae		
<i>Nerita albicilla</i>	12	Frank, 1969
<i>Nerita atramentosa</i>	6	Powell & Cummins, 1985
<i>Nerita fulgurans</i>	6	Powell & Cummins, 1985
<i>Nerita japonica</i>	3	Comfort, 1957
<i>Nerita polita</i>	4	Powell & Cummins, 1985
<i>Nerita tessellata</i>	6	Hughes & Roberts, 1980a, b
<i>Nerita versicolor</i>	8	Hughes & Roberts, 1980a
Littorinidae		
<i>Littorina acutispira</i>	SL	Underwood & McFadyen, 1983
<i>Littorina coccinea</i>	4	Comfort, 1957
<i>Littorina littorea</i>	9	Hughes & Roberts, 1980b
<i>Littorina neglecta</i>	SL	Hughes, 1986
<i>Littorina neritoides</i>	15	Hughes & Roberts, 1980b
<i>Littorina nigrolineata</i>	9	Hughes & Roberts, 1980b
<i>Littorina obtusata</i>	3	Goodwin, 1978
<i>Littorina rudis</i>	11	Hughes & Roberts, 1980b
<i>Littorina scabra</i>	5	Comfort, 1957
<i>Littorina sitkana</i>	SL	Powell & Cummins, 1985
Lacunidae		
<i>Lacuna pallidula</i>	SL	Grahame, 1977
<i>Lacuna vincta</i>	SL	Grahame, 1977
Skeneopsidae		
<i>Skeneopsis planorbis</i>	SL	Fretter, 1948
Omalgyridae		
<i>Omalgyra atomus</i>	SL	Fretter, 1948
Rissoellidae		
<i>Rissoella diaphana</i>	SL	Fretter, 1948
<i>Rissoella opalina</i>	SL	Fretter, 1948
Rissoidae		
<i>Barleeia unifasciata</i>	SL	Southgate, 1982
<i>Rissoa parva</i>	SL	Powell & Stanton, 1985
<i>Rissoa splendida</i>	SL	Zaika, 1973

TABLE 1. (continued)

Species	Lifespan	Authority
Entoconchidae		
<i>Enteroxenos bonnievie</i>	SL	Lutzen, 1979
<i>Thyonicola americana</i>	SL	Bryne, 1985
Modulidae		
<i>Modulus modulus</i>	SL	Houbrick, 1980
Cerithiidae		
<i>Cerithium coeruleum</i>	10	Ayal, 1978
<i>Cerithium eburneum</i>	SL	Houbrick, 1974
<i>Cerithium lutosum</i>	SL	Houbrick, 1974
<i>Cerithium muscarum</i>	SL	Houbrick, 1974
<i>Cerithium rupestre</i>	5	Ayal, 1978
<i>Cerithium scabridum</i>	SL	Ayal, 1978
Diastomidae		
<i>Diastoma varium</i>	SL	Powell & Stanton, 1985
Potamididae		
<i>Batillaria attramentaria</i>	7	Powell & Cummins, 1985
<i>Cerithidea decollata</i>	9	Powell & Stanton, 1985
Calyptraeidae		
<i>Calyptraea chinensis</i>	5	Comfort, 1964
Trichotropidae		
<i>Trichotropis cancellatum</i>	3	Comfort, 1964
Strombidae		
<i>Strombus costatus</i>	5	Wefer & Killingley, 1982
<i>Strombus gigas</i>	7	Wefer & Killingley, 1982
<i>Strombus luhuanus</i>	6	Frank, 1969
Naticidae		
<i>Conuber sordida</i>	5	Powell & Cummins, 1985
<i>Polinices duplicatus</i>	4	Edwards & Huebner, 1977
Thaididae		
<i>Dicathias orbita</i>	5	Phillips & Campbell, 1974
<i>Morula musiva</i>	9	Tong, 1986
<i>Nucella lamellosa</i>	6	Hughes, 1986
<i>Ocenebra poulsoni</i>	15	Fotheringham, 1971; Phillips & Campbell, 1974
<i>Shaskyus festivus</i>	20	Fotheringham, 1971, Phillips & Campbell, 1974
<i>Thais clavigera</i>	7	Tong, 1986
<i>Thais lapillus</i>	10	Hughes & Roberts, 1980a,b
<i>Urosalpinx cinerea</i>	4	Powell & Stanton, 1985
Buccinidae		
<i>Neptunea antiqua</i>	10	Powell & Stanton, 1985
Nassariidae		
<i>Bullia rhodostoma</i>	20	Brown, 1982
<i>Nassarius obsoleta</i>	3	Comfort, 1957
<i>Nassarius reticulatus</i>	15	Powell & Stanton, 1985
Mitridae		
<i>Thala floridana</i>	6	Maes & Raeihle, 1975
Fasciolaridae		
<i>Latrolagena smaragdula</i>	12	Frank, 1969
Vasidae		
<i>Vasum turbinellus</i>	10	Frank, 1969
Conidae		
<i>Conus arenatus</i>	19	Powell & Cummins, 1985
<i>Conus pennaceus</i>	10	Perron, 1982

(continued)

TABLE 1. (continued)

Species	Lifespan	Authority
Terebridae		
<i>Terebra gouldi</i>	10	Powell & Cummins, 1985
OPISTHOBRANCHIA		
Acteonidae		
<i>Pupa kirki</i>	SL	Rudman, 1972
Retusidae		
<i>Retusa obtusa</i>	SL	Thompson, 1976
Limacinidae		
<i>Limacina bulimoides</i>	SL	Wells, 1976
<i>Limacina inflata</i>	SL	Wells, 1976
<i>Limacina trochiformis</i>	SL	Wells, 1976
Cavoliniidae		
<i>Cavolinia gibbosa</i>	SL	Wells, 1976
<i>Clio pyramidata</i>	SL	Wells, 1976
<i>Creseis virgula</i>	SL	Wells, 1976
<i>Cuvierina columella</i>	SL	Wells, 1976
<i>Diacria trispinosa</i>	SL	Wells, 1976
Aplysiidae		
<i>Aplysia californica</i>	SL	Gev et al., 1984
<i>Aplysia depilans</i>	SL	Gev et al., 1984
<i>Aplysia fasciata</i>	SL	Gev et al., 1984
<i>Aplysia juliana</i>	SL	Gev et al., 1984
<i>Aplysia kurodai</i>	SL	Gev et al., 1984
<i>Aplysia punctata</i>	SL	Comfort, 1957
<i>Dolabella auricularia</i>	SL	Pauly & Calumpong, 1984
<i>Phyllaplysia taylori</i>	SL	Pauly & Calumpong, 1984
Limapontiidae		
<i>Limapontia capitata</i>	SL	Miller, 1962
<i>Limapontia depressa</i>	SL	Comfort, 1957
<i>Limapontia senestra</i>	SL	Miller, 1962
Elysiidae		
<i>Elysia viridis</i>	SL	Miller, 1962
Tritoniidae		
<i>Tritonia hombergi</i>	SL	Miller, 1962
Dendronotidae		
<i>Dendronotus frondosus</i>	SL	Miller, 1962; Nybakken 1974
<i>Dendronotus subramosus</i>	SL	Nybakken, 1974
Hancockiidae		
<i>Hancockia californica</i>	SL	Nybakken, 1974
Dotoidae		
<i>Doto amyra</i>	SL	Nybakken, 1974
<i>Doto coronata</i>	SL	Miller, 1962
<i>Doto fragilis</i>	SL	Miller, 1962
<i>Doto kya</i>	SL	Nybakken, 1974
Tethyidae		
<i>Melibe leonia</i>	SL	Comfort, 1957
Goniodorididae		
<i>Ancula cristata</i>	SL	Todd, 1981
<i>Goniodoris nodosa</i>	SL	Miller, 1962; Thompson, 1976
Onchidorididae		
<i>Adalaria proxima</i>	SL	Thompson, 1976
<i>Acanthodoris pilosa</i>	SL	Miller, 1962; Todd, 1981
<i>Onchidoris bilamellata</i>	SL	Thompson, 1976
<i>Onchidoris depressa</i>	SL	Todd, 1981

TABLE 1. (continued)

Species	Lifespan	Authority
<i>Onchidoris muricata</i>	SL	Miller, 1962; Thompson, 1976
<i>Onchidoris pusilla</i>	SL	Miller, 1962; Todd, 1981
Triophidae		
<i>Triopha maculata</i>	SL	Nybakken, 1978
Polyceridae		
<i>Limacia clavigera</i>	SL	Miller, 1962
<i>Polycera quadrilineata</i>	SL	Miller, 1962
Chromodorididae		
<i>Chromodoris nodosus</i>	SL	Comfort, 1957
<i>Chromodoris zebra</i>	SL	Comfort, 1957
Archidorididae		
<i>Archidoris pseudoargus</i>	SL	Thompson, 1976
Kentrodorididae		
<i>Jorunna tomentosa</i>	SL	Miller, 1962
Heroidae		
<i>Hero formosa</i>	SL	Miller, 1962
Coryphellidae		
<i>Coryphella lineata</i>	SL	Miller, 1962
<i>Coryphella triilineata</i>	SL	Nybakken, 1974
Facelinidae		
<i>Facelina coronata</i>	SL	Todd, 1981
Aeolidiidae		
<i>Aeolidia papillosa</i>	SL	Miller, 1962
Eubranchidae		
<i>Eubranchius exiguus</i>	SL	Miller, 1962
<i>Eubranchius olivaceus</i>	SL	Nybakken, 1974
<i>Eubranchius pallidus</i>	SL	Miller, 1962; Todd, 1981
<i>Eubranchius rustyus</i>	SL	Nybakken, 1974
Cuthonidae		
<i>Catronia alpha</i>	SL	Nybakken, 1974
<i>Tergipes despectus</i>	SL	Miller, 1962
<i>Trinchesia abronia</i>	SL	Nybakken, 1974
<i>Trinchesia albocrusta</i>	SL	Nybakken, 1974
<i>Trinchesia amoena</i>	SL	Miller, 1962
<i>Trinchesia flavovulta</i>	SL	Nybakken, 1974
<i>Trinchesia foliata</i>	SL	Todd, 1981
<i>Trinchesia lagunae</i>	SL	Nybakken, 1974
PULMONATA		
Siphonariidae		
<i>Siphonaria denticulata</i>	6	Powell & Cummins, 1985
<i>Siphonaria lessoni</i>	5	Powell & Cummins, 1985
<i>Siphonaria virgulata</i>	3	Powell & Cummins, 1985

Notes to Table 1:

Acmaea insessa lives on the kelp *Egregia laevigata* and must mature and reproduce within a year, before death of the alga (Choat & Black 1979).

Margarites helicinus is a small topshell of Arctic oceans.

The rissosocean genera *Skeneopsis*, *Omalogyra* and *Rissoella* are minute (about 2 mm) herbivorous gastropods of rocky tide pools. They are hermaphrodites, and *Omalogyra* may practice self-fertilization (Fretter, 1948). *Barleeia* dwells amongst filamentous red algae, where it grazes upon diatoms.

Enteroxenos is a genus of greatly modified, shellless prosobranchs that live as endoparasites in aspidochirote holothurians. The population breeds throughout the year, but each female produces only one egg batch, after which she dies (Lutzen, 1979).

Thyonicola americana is an endoparasite of holothurians. Evisceration in these holothurians is a seasonal (autumn) event which sheds the parasites, that then die. Minimal life span of the parasite is 6 months (Bryne, 1985).

M. modulus lives upon angiosperm sea-grasses (Houbrick, 1980).

Retusa obtusa feeds upon the marsh-dwelling prosobranch *Hydrobia ulvae* (Thompson, 1976).

Limacinids and cavoliniids are euthecosomatous pteropods, a small group of planktonic gastropods occurring mainly in tropical oceans (Wells, 1976).

Onchidoris bilamellata feeds upon barnacles (Thompson, 1976).

Comfort (1957) in stating that the opisthobranch *Haminea hydatis* lives four years, quotes Berrill (1931). I could not find evidence for this in Berrill's paper.

Comfort (1957) mentions *Philine aperta* as living 3–4 years, an exceptionally long life-span for an opisthobranch. As I could not reach the original reference and as I do not know whether this species is iteroparous or semelparous, *P. aperta* is not included in this present list.

TABLE 2. Life spans in freshwater snails

Species	Lifespan	Authority
PROSOBRANCHIA		
Neritidae		
<i>Neritina granosa</i>	7	Ford, 1987
<i>Theodoxus fluviatilis</i>	2	Fretter & Graham, 1978
Viviparidae		
<i>Campeloma rufum</i>	3	Van Cleave & Altringer, 1937
<i>Viviparus ater</i>	8	Ribi & Gebhardt, 1986
<i>Viviparus contectoides</i>	1–3	Van Cleave & Lederer, 1932
<i>Viviparus georgianus</i>	3–4	Buckley, 1986
<i>Viviparus malleatus</i>	5	Stanzkowska et al., 1971
<i>Viviparus viviparus</i>	11	Spoel, 1958
Hydrobiidae		
<i>Amnicola limosa</i>	SL	Pinel-Alloul & Magnin, 1973
<i>Falsihydrobia streletzkiensis</i>	SL	Chukhchin, 1978
<i>Hydrobia acuta</i>	SL	Chukhchin, 1978
<i>Hydrobia pusilla</i>	SL	Chukhchin, 1978
<i>Hydrobia ulvae</i>	SL	Kondratenkov, 1978
<i>Hydrobia ventrosa</i>	SL	Chukhchin, 1978
<i>Potamopyrgus antipodarum</i>	SL	Winterbourn, 1970
<i>Potamopyrgus jenkinsi</i>	SL	Winterbourn, 1970
Bithyniidae		
<i>Bithynia leachi</i>	SL	Fretter & Graham, 1978
<i>Bithynia tentaculata</i>	2–3	Lilly, 1953
Valvatidae		
<i>Valvata cristata</i>	SL	Fretter & Graham, 1978
<i>Valvata humeralis</i>	SL	Calow, 1978
<i>Valvata piscinalis</i>	SL	Calow, 1978
<i>Valvata pulchella</i>	SL	Zaika, 1973
Pleuroceridae		
<i>Leptoxis carinata</i>	SL	Aldridge, 1982
Thiaridae		
<i>Brotia hainanensis</i>	3	Dudgeon, 1982
<i>Melanoides tuberculata</i>	SL	Dudgeon, 1986
<i>Melanopsis costata</i>	6	Ra'anana, 1986
PULMONATA:		
Lymnaeidae		
<i>Acella haldemani</i>	SL	Calow, 1978
<i>Austropelma vinosa</i>	SL	Blair & Finlayson, 1981
<i>Lymnaea elodes</i>	SL	Calow, 1978
<i>Lymnaea humilis</i>	SL	Calow, 1978
<i>Lymnaea natalensis</i>	SL	Fashuyi, 1981

TABLE 2. Life spans in freshwater snails

Species	Lifespan	Authority
<i>Lymnaea palustris</i>	SL	Browne & Russell-Hunter, 1978
<i>Lymnaea peregra</i>	SL	Calow, 1978
<i>Lymnaea trunculata</i>	SL	Calow, 1978
<i>Lymnaea stagnalis</i>	SL	Berrie, 1965
Physidae		
<i>Aplexa hypnorum</i>	SL	Calow, 1978
<i>Physa acuta</i>	SL	Calow, 1978
<i>Physa fontinalis</i>	SL	Calow, 1978
<i>Physa gyrina</i>	SL	Calow, 1978
<i>Physa integra</i>	SL	Calow, 1978
<i>Physa virgata</i>	SL	Calow, 1978
Planorbidae		
<i>Anisus vortex</i>	SL	Zaika, 1973
<i>Armiger cristata</i>	SL	Richardot & Alfaro, 1985
<i>Biomphalaria glabrata</i>	SL	Appleton, 1978
<i>Biomphalaria pfeifferi</i>	SL	Appleton, 1978
<i>Bulinus forskalii</i>	SL	Fashuyi, 1981
<i>Bulinus globosus</i>	SL	Fashuyi, 1981
<i>Bulinus nasutus</i>	SL	Brown, 1980
<i>Helisoma trivolis</i>	SL	Eversole, 1978
<i>Planorbis albus</i>	SL	Calow, 1978
<i>Planorbis carinatus</i>	SL	Calow, 1978
<i>Planorbis contortus</i>	SL	Calow, 1978
<i>Planorbis corneus</i>	SL	Calow, 1978
<i>Planorbis planorbis</i>	SL	Calow, 1978
<i>Planorbis vortex</i>	SL	Calow, 1978
Ancyliidae		
<i>Ancylus fluviatilis</i>	SL	Durrant, 1980
<i>Ancylus lacustris</i>	SL	Calow, 1978
<i>Ferrissia rivularis</i>	SL	Calow, 1978
<i>Hebetancylus excentricus</i>	SL	Calow, 1978
<i>Laevapex fuscus</i>	SL	Calow, 1978

Notes to Table 2:

Netina granosa is a rheophilic gastropod endemic to Hawaiian freshwater streams. The species is diadromous. The female reproduces thousands of planktivorous veligers, that accumulate at stream mouths (Ford, 1987).

Campeloma is a freshwater snail of North America that breeds parthenogenetically (Van Cleave & Altringer, 1937).

In *Viviparus contectoides* the males live slightly longer than one year, but the females live about three years (Van Cleave & Lederer, 1932).

In *Viviparus georgianus* males live for three years, females for four (Buckley, 1986).

Bithynia tentaculata lives only up to 2 years in the Bielorussian lakes (Zaika, 1973).

Falsihydrobia streletzkiensis is similar to *Hydrobia* in various aspects of its morphology, but differs in its genitalia. Its taxonomic assignment at the family level is still unclear (Chukhchin, 1978).

Leptoxis carinata, a freshwater cerithiacean of North America, is a semelparous biennial (Aldridge, 1982).

Melanoides tuberculata is an ovoviviparous, usually parthenogenetic snail. In Hong Kong, studies at the population level suggest that the life span is at least one year and at the most two, with a single peak in juvenile recruitment coinciding with the warmer months (Dudgeon, 1986). However, although release of hatchlings is strictly seasonal, fully developed larvae are found in the brood pouches throughout the year. In Malaysia (Berry & Kadri, 1974) snails reach a life-span of 3 1 2 years, as extrapolated from laboratory growth rates.

Melanopsis is the most common freshwater snail in Israel. Isolated pairs of *M. costata* were kept by Ra'anana (1986) in captivity for six years.

TABLE 3. Life spans in landsnails.

Species	Lifespan	Authority
Veronicellidae		
<i>Vaginulus borellianus</i>	SL	Runham & Hunter, 1970
<i>Veronicella ameghini</i>	SL	Dundee, 1977
Ellobiidae		
<i>Carychium tridentatum</i>	SL	Morton, 1954
<i>Melampus</i> sp.	4	Apley, 1970
<i>Ovatella myosotis</i>	4	Meyer, 1955
Achatinellidae		
<i>Achatinella mustelina</i>	9	Hadfield & Mountain, 1980
Cochlicopidae		
<i>Cochlicopa lubrica</i>	3	Uminski & Focht, 1979
Vertiginidae		
<i>Vertigo pusilla</i>	SL	Pokryszko, 1986.
Chondrinidae		
<i>Solatopupa similis</i>	8	Boato & Rasotto, 1987
Enidae		
<i>Brephulopsis bidens</i>	SL	Livshitz & Shileyko, 1978; Livshitz, 1985.
Clausiliidae		
<i>Cochlodina laminata</i>	2	Cameron, 1982
<i>Vestia elata</i>	7	Piechocki, 1982
Cerionidae		
<i>Cerion</i> spp.	10	Woodruff, 1978
Achatinidae		
<i>Achatina achatina</i>	5	Hodasai, 1979
<i>Achatina fulica</i>	8	Mead, 1961
<i>Archachatina marginata</i>	11	Plummer, 1982
Endodontidae		
<i>Discus rotundatus</i>	SL	Cameron, 1982
<i>Punctum pygmaeum</i>	SL	Baur, pers. comm.
Arionidae		
<i>Arion ater</i>	SL	Runham & Laryea, 1968
<i>Arion circumscriptus</i>	SL	Godan, 1983
<i>Arion hortensis</i>	SL	Bett, 1960; Hunter, 1968
<i>Arion intermedius</i>	SL	Godan, 1983
<i>Arion subfuscus</i>	SL	Bett, 1960
Succineidae		
<i>Catinella arenaria</i>	SL	Baker, 1965
<i>Omalonyx felina</i>	SL	Shrader, 1974
<i>Succinea ovalis</i>	SL	Strandine, 1941
Vitrinidae		
<i>Eucobresia nivalis</i>	SL	Uminski, 1979
<i>Semilimax kotulai</i>	SL	Uminski, 1975
<i>Vitriina alaskana</i>	SL	Boag & Wishart, 1982
<i>Vitriina pellucida</i>	SL	Taylor, 1907; Uminski & Focht, 1979
Zonitidae		
<i>Aegopinella nitidula</i>	SL	Mordan, 1978
<i>Aegopinella nitens</i>	SL	Mordan, 1978
<i>Oxychilus cellarius</i>	SL	Mordan, 1978
<i>Oxychilus helveticus</i>	SL	Cameron, 1982

TABLE 3. (continued)

Species	Lifespan	Authority
Euconulidae		
<i>Euconulus fulvus</i>	2	Uminski & Focht, 1979
Milacidae		
<i>Milax budapestensis</i>	SL	Hunter, 1968
<i>Milax sowerbii</i>	SL	Bett, 1960
<i>Milax gagates</i>	SL	Focardi & Quattrini, 1972
Limacidae		
<i>Bielzia coerulans</i>	SL	Smolenska, 1936
<i>Deroceras caucasicum</i>	SL	Uvalieva, 1978
<i>Deroceras reticulatum</i>	SL	Godan, 1983
<i>Deroceras sturanyi</i>	SL	Kosinska, 1980
<i>Limax flavus</i>	SL	N. Runham, pers. comm.
<i>Limax maximus</i>	SL	N. Runham, pers. comm.
Parmacellidae		
<i>Parmacella rutellum</i>	SL	Uvalieva, 1978
Bulimulidae		
<i>Bulimulus dealbatus</i>	SL	Randolph, 1973
<i>Liguus fasciatus</i>	6	Voss, 1976; Tuskes, 1981
Elonidae		
<i>Elona quimperiana</i>	SL	Daguzan, 1982
Testacellidae		
<i>Testacella</i> sp.	6	Taylor, 1907
Polygyridae		
<i>Allogona profunda</i>	4	Blinn, 1963
<i>Mesodon roemeri</i>	3	Randolph, 1973
<i>Polygyra thyroideus</i>	4	Van Cleave & Foster, 1937
Oleacinidae		
<i>Euglandina rosea</i>	SL	Chiu & Chou, 1962
Pleurodontidae		
<i>Caracolus caracolus</i>	10	Heatwole & Heatwole, 1978
Camaenidae		
<i>Amplirhagada napierana</i>	8	Solem & Christensen, 1984
Sphincterochilidae		
<i>Sphincterochila prophetarum</i>	15	Steinberger, pers. comm.
<i>Sphincterochila zonata</i>	15	Steinberger, pers. comm.
Helminthoglyptidae		
<i>Helminthoglypta arrosa</i>	10	Laan, 1971; Pilsbry, 1939
Bradybaenidae		
<i>Bradybaena fruticum</i>	6	Comfort, 1957
Helicidae		
<i>Arianta arbustorum</i>	17	Raboud, 1986
<i>Cepaea nemoralis</i>	9	Cook & Cain, 1980
<i>Cernuella virgata</i>	SL	Lazaridou, 1981
<i>Eobania vermiculata</i>	5	Lazaridou, pers. com.
<i>Helicella caperata</i>	SL	Baker, 1968
<i>Helix aspersa</i>	5	Lazaridou, pers. com.
<i>Helix lucorum</i>	5	Staikou & Lazaridou, 1986
<i>Helix pomatia</i>	15	Falkner, 1984
<i>Levantina hierosolyma</i>	7	pers. observations
<i>Monacha cartusiana</i>	SL	Chatfield, 1968
<i>Monacha haifaensis</i>	SL	pers. observations
<i>Theba pisana</i>	SL	Heller, 1982; Cowie, 1984

(continued)

TABLE 3. (continued)

Species	Lifespan	Authority
<i>Trichia hispida</i>	SL	Cameron, 1982
<i>Trochoidea simulata</i>	3	Yom-Tov, 1971
<i>Xeropicta arenosa</i>	SL	Lazaridou, 1981
<i>Xeropicta vestalis</i>	SL	Heller & Volokita, 1981

Notes to Table 3:

Vaginulus borellianus is an Argentinian slug that lives for about a year to 18 months. Eggs are laid in a mucus envelope on the soil surface (Lanza & Quattrini, 1964; in Runham & Hunter, 1970).

Veronicella ameghini is an introduced species in the southern USA. The suggestion that its longevity is "likely around two years" (Dundee, 1977: 114) is a free estimate that is not based upon concrete facts.

Achatinella mustelina is a tree-dwelling snail of Hawaii.

Ovatella and *Melampus* dwell in salt marshes along sea coasts. They live above sea level, like land snails, but reproduce by veligers, as marine snails do. I arbitrarily classify them as terrestrial. *Ovatella myosotis* first develops the masculine system and functions as a male, then also the female system and continues to function as both male and female (Meyer, 1955).

Carychium tridentatum is a primitive pulmonate that lives in a saturated atmosphere under fallen leaves and logs. The snails change sex throughout their lifetime: a period of 12 months is required for the completion of a single sperm-producing phase, followed by a single egg-producing one. Morton suggests that the snails appear to have a "double-phase" semelparous reproductive strategy. I accept Morton's semelparous interpretation, but with heavy doubts, as his fig. 2 suggests that at any time of the year there are not nearly enough juveniles in the population to replace the much larger adult group. His data may well suggest that *Carychium* is an iteroparous, long-lived species with a few juvenile snails joining the population and a few adults dying off each year.

Omalonyx felina is a tropical succineid of Venezuela.

Punctum pygmaeum is a minute (1.5 mm) snail that has a Holarctic distribution. Its biology in Sweden is currently being studied by B. Baur.

Euconulus fulvus and *Discus cronkhitei* in Canada have, on their shell, "one or more varices which suggests that they survive one or more winters" (Boag & Wishart, 1982: 2636).

Aegopinella nitidula has a biennial life cycle with delayed maturity and overlapping generations, and Mordan (1978) suggests that this may be advantageous in unstable environmental conditions.

Limax flavus and *L. maximus* are generally annual species and hence short-lived (N. Runham, personal communication). Comfort (1957) mentions them as living 5 years (based upon animals studied in captivity), and Godan (1983) suggests that they live three years. Since N. Runham has been personally involved in studying them, I prefer his evidence.

Elona quimperiana matures within two years, and lives for another year and a half (Daguzan, 1982). Its classification as a short-lived species stretches the definition of "short-lived" to its limit.

Liguus fasciatus is a tree snail of Antillean origin that is found in tropical hardwood trees and exhibits great variability in shell coloration. Voss (1976) suggests that reproduction occurs at the end of the fourth year, after which many snails die, and it should therefore be classified as exhibiting a semelparous strategy. However, the size distributions in his fig. 1-2 suggest an iteroparous cycle, with a few juveniles joining the adult population every year. In addition, his table 1 shows an increase in size of the yearly classes, and this can only be explained by the slow accumulation of individuals into the various size classes over several years, namely an iteroparous strategy, with a very long life-span. Also Tuskes (1981), when studying *Liguus fasciatus*, reached conclusions differing considerably from those of Voss.

Euglandina rosea is a carnivorous snail that feeds mainly upon other land snails. *Sphincterochila zonata* and *S. prophetarum* are found in the Negev Desert, where they were studied by Yom-Yov (1971), who suggested that *S. zonata* lives more than 8 years, and Y. Steinberger (unpublished data), who informs me that they live 15 years at least.

Levantina hierosolyma is found in Mediterranean to arid habitats of the Middle East, where it dwells in rock-crevices and beneath stones.

Cerņuella virgata, a European species, maintains a short life span with an annual life cycle also in populations introduced into Australia (Pomeroy, 1969).

Eobania vermiculata in Greece is found at the lower parts of the vegetation. Sexual maturity is reached in two years, and it may then live for another three years (Lazaridou, pers. com.).

TABLE 4. Life spans in marine bivalves

Species	Lifespan	Authority
Nuculidae		
<i>Acila insignis</i>	9	Zolotarev, 1980
<i>Nucula annulata</i>	8	Cerrato, 1980
<i>Nucula nucleus</i>	12	Comfort, 1964
<i>Nucula sulcata</i>	17	Comfort, 1964
<i>Nucula turgida</i>	10	Comfort, 1957
Nuculanidae		
<i>Nuculana minuta</i>	7	Ansell & Parulekar, 1978
<i>Nuculana pernula</i>	9	Zolotarev, 1980
<i>Yoldia limatula</i>	4	Powell & Cummins, 1985
Mallettiidae		
<i>Tindaria callistiformis</i>	100	Turekian et al., 1975
Arcidae		
<i>Arca boucardi</i>	20	Zolotarev, 1980
<i>Anadara broughtoni</i>	46	Zolotarev, 1980
<i>Senilia senilis</i>	9	Powell & Stanton, 1985
Glycymeridae		
<i>Glycymeris yessoensis</i>	64	Zolotarev, 1980
Mytilidae		
<i>Bathymodiolous thermophila</i>	19	Rhoads et al., 1981
<i>Brachiodontes variabilis</i>	3	Powell & Cummins, 1985
<i>Crenomytilus grayanus</i>	150	Jones, 1983
<i>Geukensia demissa</i>	23	Lutz & Castagna, 1980
<i>Modiolus demissus</i>	8	Zaika, 1973
<i>Modiolus modiolus</i>	61	Zolotarev, 1980
<i>Mytilaster lineatus</i>	3	Zaika, 1973
<i>Mytilus californiensis</i>	5	Cerrato, 1980
<i>Mytilus coruscus</i>	39	Zolotarev, 1980
<i>Mytilus edulis</i>	15	Zolotarev, 1980
<i>Mytilus galloprovincialis</i>	12	Powell & Stanton, 1985
<i>Mytilus variabilis</i>	5	Comfort, 1957
<i>Perna viridis</i>	3	Lee, 1985
<i>Septifer keenae</i>	15	Zolotarev, 1980
Dreisseneidae?		
<i>Mytilopsis sallei</i>	SL	Morton, 1981
Pinnidae		
<i>Pinna atropurpura</i>	12	Butler & Brewster, 1979
Pteriidae		
<i>Pinctada martensii</i>	8	Powell & Cummins, 1985
<i>Pinctada vulgaris</i>	7	Comfort, 1957
Pectinidae		
<i>Adamusium colbecki</i>	10	Ralph & Maxwell, 1977
<i>Amusium balloti</i>	4	Powell & Cummins, 1985
<i>Amusium japonicum</i>	4	Williams & Dredge, 1981
<i>Argopecten gibbus</i>	SL	Williams & Dredge, 1981
<i>Argopecten irradians</i>	SL	Sastry, 1979
<i>Argopecten japonicum</i>	SL	Powell & Cummins, 1985
<i>Chlamys albidus</i>	8	Zolotarev, 1980
<i>Chlamys islandica</i>	23	Powell & Cummins, 1985
<i>Chlamys opercularis</i>	6	Williams & Dredge, 1981
<i>Chlamys varia</i>	7	Powell & Cummins, 1985
<i>Notovola meridionalis</i>	11	Williams & Dredge, 1981
<i>Patinopecten caurinus</i>	15	Powell & Cummins, 1985
<i>Patinopecten yessoensis</i>	12	Ventilla, 1982
<i>Pecten maximus</i>	12	Cerrato, 1980

(continued)

TABLE 4. (continued)

Species	Lifespan	Authority
<i>Placopecten magellanicus</i>	12	Williams & Dredge, 1981
<i>Swiftopecten swifti</i>	15	Zolotarev, 1980
Ostreidae		
<i>Crassostrea madrasensis</i>	4	Powell & Cummins, 1985
<i>Crassostrea virginica</i>	6	Comfort, 1957
<i>Ostrea edulis</i>	20	Christensen & Dance, 1980
Lucinidae		
<i>Cavatidens omissa</i>	SL	Powell & Cummins, 1985
Thyasiridae		
<i>Thyasira flexuosa</i>	SL	Lopez-Jamar et al., 1987
Ungulinidae		
<i>Felaniella usta</i>	9	Zolotarev, 1980
Galeommatidae		
<i>Lasaea rubra</i>	4	McGrath & O'Foighil, 1986
Montacutidae		
<i>Mysella bidentata</i>	7	Ockelmann & Muus, 1978
<i>Mysella cuneata</i>	6	Gage, 1968
<i>Mysella planulata</i>	4	Franz, 1972
Carditidae		
<i>Venericardia crebricostata</i>	58	Zolotarev, 1980
Cardiidae		
<i>Cardium ciliatum</i>	25	Petersen, 1978
<i>Cardium corbis</i>	16	Powell & Cummins, 1985
<i>Cardium edule</i>	7	Cerrato, 1980
<i>Cardium corbis</i>	10	Cerrato, 1980
<i>Cerastoderma glaucum</i>	7	Powell & Stanton, 1985
<i>Clinocardium nuttallii</i>	14	Zolotarev, 1980
<i>Keenocardium californiense</i>	11	Zolotarev, 1980
<i>Serripes groenlandicus</i>	22	Petersen, 1978
Macluridae		
<i>Mactra sulcataria</i>	12	Zolotarev, 1980
<i>Mulinia lateralis</i>	3	Cerrato, 1980
<i>Rangia cuneata</i>	10	Powell & Cummins, 1985
<i>Spisula sachalinensis</i>	55	Zolotarev, 1980
<i>Spisula solidissima</i>	31	Jones et al., 1978
<i>Spisula voyi</i>	52	Zolotarev, 1980
<i>Tresus capax</i>	16	Powell & Cummins, 1985
Mesodesmatidae		
<i>Mesodesma ventricosum</i>	9	Comfort, 1957; Powell & Cummins, 1985
Solenidae		
<i>Solen corneus</i>	5	Powell & Cummins, 1985
<i>Solen krustensterni</i>	12	Zolotarev, 1980
Cultellidae		
<i>Ensis siliqua</i>	12	Comfort, 1964
<i>Siliqua alta</i>	24	Zolotarev, 1980
<i>Siliqua patula</i>	17	Cerrato, 1980
Tellinidae		
<i>Cadella lubrica</i>	17	Zolotarev, 1980
<i>Gastrana contabulata</i>	15	Zolotarev, 1980
<i>Macoma balthica</i>	18	Zolotarev, 1980
<i>Macoma calcarea</i>	17	Petersen, 1978
<i>Macoma litoralis</i>	6	Powell & Cummins, 1985
<i>Macoma middendorffi</i>	24	Zolotarev, 1980
<i>Peronidia venulosa</i>	31	Zolotarev, 1980

TABLE 4. (continued)

Species	Lifespan	Authority
<i>Peronidia zyanoensis</i>	61	Zolotarev, 1980
<i>Tellina alternata</i>	3	Powell & Cummins, 1985
<i>Tellina deltoidalis</i>	4	Powell & Cummins, 1985
<i>Tellina tenuis</i>	5	Comfort, 1957
Donacidae		
<i>Donax denticulatus</i>	SL	Powell & Cummins, 1985
<i>Donax gouldii</i>	3	Powell & Cummins, 1985
<i>Donax incarnatus</i>	3	Powell & Cummins, 1985
<i>Donax hanleyanus</i>	3	Ansell, 1983
<i>Donax semistriatus</i>	SL	Ansell, 1983
<i>Donax serra</i>	SL	Ansell, 1983
<i>Donax sordidus</i>	SL	Powell & Cummins, 1985
<i>Donax spiculum</i>	SL	Powell & Cummins, 1985
<i>Donax trunculus</i>	3	Ansell, 1983
<i>Donax tumida</i>	SL	Powell & Cummins, 1985
<i>Donax variabilis</i>	SL	Ansell, 1983
<i>Donax venustus</i>	SL	Ansell, 1983
<i>Donax vittatus</i>	7	Ansell, 1983
Psammobidae		
<i>Gari kazunensis</i>	14	Zolotarev, 1980
<i>Nuttallia ezonis</i>	40	Zolotarev, 1980
<i>Nuttallia olivacea</i>	20	Zolotarev, 1980
Scrobiculariidae		
<i>Scrobicularia plana</i>	18	Comfort, 1957
Semelidae		
<i>Abra ovata</i>	4	Zaika, 1973
<i>Cumingia tellinoides</i>	4	Comfort, 1957
<i>Theora fragilis</i>	SL	Powell & Cummins, 1985
Solecurtidae		
<i>Tagelus divisus</i>	3	Powell & Stanton, 1985
Arcticidae		
<i>Arctica islandica</i>	220	Jones, 1983
Vesicomylidae		
<i>Calyptogena magnifica</i>	11	Jones, 1983
Veneridae		
<i>Anomalocardia squamosa</i>	3	Powell & Stanton, 1985
<i>Callista brevisiphonata</i>	76	Zolotarev, 1980
<i>Callista chione</i>	40	Powell & Cummins, 1985
<i>Callithaca adamsi</i>	29	Zolotarev, 1980
<i>Dosinia angulosa</i>	26	Zolotarev, 1980
<i>Dosinia elegans</i>	3	Powell & Cummins, 1985
<i>Dosinia exoleta</i>	7	Comfort, 1964
<i>Dosinia hepatica</i>	6	Powell & Cummins, 1985
<i>Dosinia japonica</i>	27	Zolotarev, 1980
<i>Gemma gemma</i>	SL	Sellmer, 1967
<i>Katelysia opima</i>	3	Powell & Cummins, 1985
<i>Mercenaria mercenaria</i>	9	Kennish, 1980
<i>Mercenaria stimpsoni</i>	40	Zolotarev, 1980
<i>Protothaca euglypta</i>	14	Zolotarev, 1980
<i>Protothaca jedoensis</i>	15	Zolotarev, 1980
<i>Protothaca staminea</i>	13	Powell & Cummins, 1985
<i>Tapes philippinarum</i>	SL	Powell & Cummins, 1985
<i>Tivela stultorum</i>	14	Cerrato, 1980
<i>Venerupis japonica</i>	25	Zolotarev, 1980
<i>Venerupis pullastra</i>	9	Cerrato, 1980

(continued)

TABLE 4. Life spans in marine bivalves

Species	Lifespan	Authority
<i>Venus gallina</i>	8	Cerrato, 1980
<i>Venus mercenaria</i>	15	Cerrato, 1980
<i>Venus striatula</i>	10	Guillou & Sauriau, 1985
Myidae		
<i>Mya arenaria</i>	28	Jones, 1983
<i>Mya japonica</i>	42	Zolotarev, 1980
<i>Mya priapus</i>	15	Zolotarev, 1980
<i>Mya truncata</i>	18	Petersen, 1978
Corbulidae		
<i>Anisorbula venusta</i>	8	Zolotarev, 1980
<i>Corbula trigona</i>	SL	Maslin & Bouvet, 1986
<i>Corbula vicaria</i>	4	Powell & Cummins, 1985
<i>Potamocorbula amurensis</i>	5	Zolotarev, 1980
Hiatellidae		
<i>Hiatella byssifera</i>	15	Petersen, 1978
<i>Panope generosa</i>	120	Jones, 1983
Teredinidae		
<i>Bankia gouldi</i>	SL	Hoagland, 1986
<i>Teredo bartschi</i>	SL	Hoagland, 1986
<i>Teredo navalis</i>	SL	Hoagland, 1986
Pandoridae		
<i>Pandora pulchella</i>	11	Zolotarev, 1980
Laternulidae		
<i>Laternula elliptica</i>	13	Ralph & Maxwell, 1977

Notes to Table 4:

Tindaria callistiformis is a minute (8.6 mm) nuculanacean that lives on the sea bottom, at a depth of 3,800 m (Turekian et al., 1975).

Comely 1978 suggests that *M. modiolus* lives only 35 years.

Data for *Perna viridis* concern a polluted habitat where the mussels suffer precocious mortality due to unnaturally stressful conditions (Lee, 1985).

Mysella bidentata lives in association with the ophiuroid *Amphiura*. In the second year of its life it functions as a male; from three years onwards it is a hermaphrodite. (Ockelmann & Muus, 1978).

Mysella cuneata, a bivalve of minute size (up to 3 mm) is a commensal of a sipunculid which occupies discarded shells (Gage, 1968).

Mysella planulata, of minute size (4 mm), lives in muddy sands. It is a simultaneous hermaphrodite (Franz, 1972).

Lasaea rubra is an intertidal bivalve of minute size (3.2 mm). It is ovoviviparous (McGrath & O'Foighil, 1986).

Calyptogena magnifica and *Bathymodiolous thermica* belong to the hydro-thermal vent fauna of Galapagos. The biology of these species is described by Childress et al., 1987.

Donax vittatus has a life-span of 3 years at the southern end of its geographical range, but longevity increases at higher latitudes and may reach 7 years in northern populations (Ansell, 1983).

Corbula trigona dwells in coastal lagoons in western Africa (Maslin & Bouvet, 1986).

Teredo is a highly specialised bivalve adapted for boring into wood. Its average life-span in Miami is about 10 weeks (Nair & Saraswathy, 1971).

TABLE 5. Lifespans of freshwater bivalves

Species	Lifespan	Authority
Mytilidae		
<i>Limnoperna fortunei</i>	SL	Morton, 1977
Unionidae		
<i>Amblema plicata</i>	16	Comfort, 1957
<i>Anodonta anatina</i>	10	Neguus, 1966
<i>Anodonta californiensis</i>	5	Heard, 1975
<i>Anodonta corpulenta</i>	8	Heard, 1975
<i>Anodonta gibbosa</i>	16	Heard, 1975
<i>Anodonta imbecilis</i>	12	Heard, 1975
<i>Anodonta minima</i>	10	Neguus, 1966
<i>Anodonta peggyae</i>	15	Heard, 1975
<i>Anodonta piscinalis</i>	15	Comfort, 1957
<i>Anodonta woodiana</i>	12	Morton, 1986
<i>Anatontoides subcylindraceus</i>	9	Comfort, 1957
<i>Elliptio complanata</i>	12	Matteson, 1948
<i>Elliptio dilatata</i>	12	Comfort, 1957
<i>Lampsilis anodontoides</i>	8	Comfort, 1957
<i>Lampsilis ovata</i>	19	Comfort, 1957
<i>Lampsilis recta</i>	18	Comfort, 1957
<i>Lampsilis siliquoidea</i>	19	Comfort, 1957
<i>Margaritifera margaritifera</i>	116	Hendelberg, 1960; Smith, 1976; Bauer, 1987
<i>Pleurobema coccineum</i>	12	Comfort, 1957
<i>Pleurobema cordatum</i>	30	Yokley, 1972
<i>Quadrula</i> sp.	50	Comfort, 1957
<i>Trifogonia verrucosa</i>	11	Comfort, 1957
<i>Unio crassus</i>	15	Comfort, 1957
<i>Unio pictorum</i>	15	Neguus, 1966
<i>Unio tumidus</i>	11	Neguus, 1966
Dreissenidae		
<i>Dreissena polymorpha</i>	5	Morton, 1969
Corbiculidae		
<i>Corbicula fluminea</i>	4	Morton, 1986
<i>Corbicula</i> cf. <i>fluminalis</i>	10	Morton, 1986
Sphaeriidae		
<i>Byssanodonta cubensis</i>	3	Mackie & Huggins, 1976
<i>Pisidium amnicum</i>	SL	Baas, 1979
<i>Pisidium annandalei</i>	SL	Morton, 1986
<i>Pisidium casertanum</i>	SL	Mackie, 1984
<i>Pisidium clarkeanum</i>	SL	Morton, 1986
<i>Pisidium compressum</i>	3	Meier-Brook, 1970
<i>Pisidium hibernicum</i>	3	Meier-Brook, 1970
<i>Pisidium lilljeborgi</i>	3	Meier-Brook, 1970
<i>Pisidium variabile</i>	SL	Mackie, 1979
<i>Sphaerium corneum</i>	SL	Dussart, 1979
<i>Sphaerium fabalis</i>	SL	Mackie, 1979
<i>Sphaerium occidentale</i>	SL	Heard, 1977
<i>Sphaerium rivicola</i>	SL	Heard, 1977
<i>Sphaerium simile</i>	3	Avolizi, 1976
<i>Sphaerium solidum</i>	SL	Heard, 1977
<i>Sphaerium striatinum</i>	SL	Mackie, 1984
<i>Sphaerium transversum</i>	SL	Gale, 1977
<i>Sphaerium partumeium</i>	SL	Gale, 1977
<i>Musculium japonicum</i>	SL	Heard, 1977
<i>Musculium lacustre</i>	SL	Morton, 1986
<i>Musculium partumeium</i>	SL	Mackie, 1984
<i>Musculium securis</i>	SL	Mackie, 1979
<i>Musculium transversum</i>	SL	Mackie, 1984

(continued)

Notes to Table 5:

Limnoperna fortunei is an inhabitant of freshwater rivers and streams in China and southeast Asia (Morton, 1977).

Margaritifera margaritifera is a slow-growing mussel that takes about 20 years to reach sexual maturity.

Within the Sphaeriidae, Heard (1977) suggests that most *Pisidium* and *Sphaerium* inhabit permanent lentic and lotic waters, in contrast to most *Musculium* that are found in ephemeral habitats.

Pisidium clarkeanum is generally iteroparous, but may also be semelparous. It lives for 4–8 months (Morton, 1986).

Sphaerium corneum lives for about 4–8 months in Canada, one year in Germany and Russia, but may live 3–4 years in Sweden (Heard, 1977).

Sphaerium simile in New York may live up to 4–5 years (Heard, 1977).

Sphaerium transversum may reach densities of 10,000/m². It can complete its life history in less than a month (Gale, 1977).

TABLE 6. Lifespans in cephalopods

Species	Lifespan	Authority
NAUTILOIDEA		
Nautilidae		
<i>Nautilus pompilus</i>	20	Saunders, 1984
COLEOIDEA.		
Spirulidae		
<i>Spirula spirula</i>	SL	Comfort, 1957
Sepiidae		
<i>Sepia officinalis</i>	SL	Boletzky, 1983a
Sepiolidae		
<i>Euprymna scolopes</i>	SL	Singley, 1983
<i>Rossia pacifica</i>	SL	Anderson, 1987
<i>Sepietta oweniana</i>	SL	Bergstrom & Summers, 1983
<i>Sepiola robusta</i>	SL	Boletzky, 1983b
Loliginidae		
<i>Loligo forbesi</i>	SL	Holme, 1974
<i>Loligo opalescens</i>	SL	Hixon, 1983
<i>Loligo pealei</i>	SL	Summers, 1983
<i>Loligo vulgaris</i>	SL	Worms, 1983
<i>Sepioteuthis sepiola</i>	SL	Moynihan & Rodaniche, 1983
Gonatidae		
<i>Gonatus fabricii</i>	SL	Kristensen, 1983
Ommastrephidae		
<i>Dosidicus gigas</i>	SL	Nesis, 1983
<i>Illex illecebrosus</i>	SL	O'Dor, 1983
<i>Tadarodes pacificus</i>	SL	Okutani, 1983
Cranchiidae		
<i>Teuthowenia megalops</i>	SL	Nixon, 1983
Octopodidae		
<i>Bathypolypus arcticus</i>	SL	O'Dor & Macalaster, 1983
<i>Eledone cirrhosa</i>	SL	Boyle, 1983
<i>Eledone moschata</i>	SL	Mangold, 1983b
<i>Octopus briareus</i>	SL	Hanlon, 1983a
<i>Octopus cyanea</i>	SL	Van Heukelem, 1983a
<i>Octopus dofleini</i>	SL	Hartwick, 1983a
<i>Octopus joubini</i>	SL	Hanlon, 1983b
<i>Octopus maya</i>	SL	Van Heukelem, 1983b
<i>Octopus tetricus</i>	SL	Joll, 1983
<i>Octopus vulgaris</i>	SL	Mangold, 1983

Notes to Table 6:

Octopus dofleini is one of the largest octopod species, with an arm span of up to 9.6 m and a weight of 272 kg (Hochberg & Fields, 1980, as cited in Boyle, 1987, table 16.1). It takes 2–3 years to reach maximum size. Both males and females stop eating and die after the reproductive period, but males may perhaps live 1 or 2 years longer if they don't reproduce (Hartwick, 1983).

Bathypolypus arcticus is a deep sea octopus that lives at depths of 1000 m, in temperatures that rarely range above 6°C. It requires nearly 4 years to complete its life cycle: one year of embryonic development, one of growth, one of gametogenesis and one of brooding (O'Dor & Macalaster, 1983).

COMPARATIVE MORPHOLOGY OF LIVING *NAUTILUS* (CEPHALOPODA) FROM THE PHILIPPINES, FIJI AND PALAU

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ABSTRACT

Morphological features of *Nautilus* from the Philippines, Fiji and Palau are compared from a taxonomic viewpoint on the basis of live-caught animals. In spite of their widely separated distributions, animals from the three populations share quite similar overall shell morphology, ontogenetic shell variation, and radular and jaw structures. Shell coloration and sculpture, and the shape of radular teeth, all of which have been used in previous taxonomic studies, are also markedly variable even in specimens of individual populations, and their ranges of variation overlap among the three samples. The three samples can be distinguished mainly by adult features, such as the dimensions of the shells and total number of septa, which are probably attributed to the difference in their pre-reproductive ages. Judging from these observations and available genetic data, it is suggested that the Palau population, previously distinguished as *N. belauensis* and the other two populations belong to the same, wide ranging species, *N. pompilius*, or otherwise they are closely related sibling species, *N. belauensis* and *N. pompilius* respectively.

Key words: *Nautilus pompilius*, *Nautilus belauensis*, southwest Pacific, morphology, taxonomy.

INTRODUCTION

The superfamily Nautilaceae (Cephalopoda, Nautiloidea) first appeared in the Triassic, and flourished mainly during the Mesozoic and Middle Tertiary. They suddenly declined after the Miocene, and at the present time only a few species of the genus *Nautilus* survive, in the relatively deep waters of the tropical southwestern Pacific.

Although 11 species and seven variants of *Nautilus* have hitherto been proposed (see Saunders, 1987, table 1), their taxonomic validity has long been obscured because of the seemingly morphological conservatism of the genus, extreme splitting of phenotypes based on small collections, and the lack of knowledge of the morphological and genetic variation within individual populations. Recently, Saunders (1987) revised these "species" and variants into five or possibly six recognized species (*Nautilus pompilius* Linnaeus, 1758; *N. macromphalus* Sowerby, 1849; *N. scrobiculatus* [Lightfoot, 1786]; *N. stenomphalus* Sowerby, 1849; *N. belauensis* Saunders, 1981; and possibly *N. repertus* Iredale, 1944), but some malacologists (e.g. Habe, 1980; Ab-

bott & Dance, 1983) regard the latter three species as geographic variants of *N. pompilius*.

The species-level taxonomy of *Nautilus* should, therefore, be re-examined in view of recent biometric and electrophoretic analyses of large live-caught collections (Ward et al., 1977; Tanabe et al., 1983, 1985; Saunders & Davis, 1985; Tanabe & Tsukahara, 1987; Masuda & Shinomiya, 1983; Woodruff et al., 1983, 1987; Swan & Saunders, 1987), for these works detected marked morphological and genetic variation even within individual populations.

This paper considers the taxonomic relationships of two closely allied morphospecies, *N. belauensis* and *N. pompilius*, on the basis of the comparative morphologic examination of large collections from several populations.

MATERIAL AND METHODS

Material

The following three samples of *Nautilus* populations from widely separated areas were used in this study: (1) 34 specimens (10

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males and 24 females) of *N. pompilius* captured with baited traps from off Bindoy Village (depth of 120–310 m), Tañon Strait, the Philippines, in September 1981 (specimens B1–B32, B41 and B52 among 52 animals listed in Hayasaka et al., 1982, table 10); (2) A total of 280 specimens (245 males, 34 females and one unsexed juvenile) of *N. pompilius* captured alive from off Suva (Kandavu Passage; depth of 290–450 m), Viti Lebu, Fiji, on two occasions (August–September 1983 and 1986; see Tanabe, 1985, fig. 5, tables 1–3, and Tanabe, 1988, fig. 3, tables 1–4, for their locations and biological data), and (3) 94 specimens (57 males, 36 females and one unsexed juvenile) of *N. belauensis* captured live from eastern Mutremdu Bay (= Mutremdu Point of Saunders, 1981a, figure 1); depth of 190–400 m, off Augulpelu Reef, Palau, in August–September 1988 and in January 1989. In addition to the above three live-caught samples, two specimens caught from off Siquijor Island, Bohol Strait, the Philippines (provided by the courtesy of native fishermen; sp. nos. SQ 1–2 in Hayasaka et al., 1982) were used for comparison of ontogenetic septal growth and mature shell size.

The specimens illustrated are kept at the University Museum, University of Tokyo (UMUT), and the remaining ones used for measurements are deposited at the Geology and Biology Institutes, Kagoshima University. Of three (Habe, 1980) or possibly six (Saunders, 1987) currently recognized *Nautilus* species, *N. pompilius* has the widest geographic range, extending from the Philippines in the northwest to American Samoa in the southeast (Saunders, 1987). The two samples from the Philippines (Tañon Strait) and Fiji thus represent the western and eastern marginal populations of this species. The two specimens from Bohol Strait (Philippines) are compared with the morphotype distinguished as *N. pompilius suluensis* by Habe & Okutani (1988, figs. 1–4). *N. belauensis* is known only from Palauan waters, about 800 km from the range of *N. pompilius*.

Methods

Following the methods described in Tanabe & Tsukahara (1987), all animals captured were weighed, sexed, and measured (see Hayasaka et al., 1982, table 10, and the revised version in Tanabe et al., 1983, table 1; Tanabe, 1988, table 3; Tanabe & Tsukahara, 1989, table 2). Some were tagged and re-

leased near the sampling locations for long-term growth analysis, and most of the remaining animals were dissected, and their fresh soft tissues and gonads were weighed by means of a dial scale (accuracy ± 10 mg) for biometry. In addition, the buccal mass was removed from the body of selected specimens. It was soaked in a 20% KOH solution for 20 minutes, and thereafter the mandible and radular ribbon were carefully removed. The radular and jaw morphologies of each specimen were observed under the optical and scanning electron microscopes.

We further analyzed the ontogenetic shell growth patterns in several specimens selected from each sample. For this purpose, radius vector (R), breadth (B), height (H) and flank length (F) of a whorl, and half length of umbilicus (C), disregarding secondary umbilical deposits (callus), which were measured in each dorso-ventrally sectioned shell at intervals of 180° using a profile projector (NIKON, V16), attached to a digital micrometer (accuracy $\pm 1 \mu\text{m}$) (magnification $\times 20$; see Tanabe & Tsukahara, 1987, figure 1, for measurements). Based on these measurements, four geometric parameters; i.e. whorl expansion rate $[(R_n/R_{n-1})^2; n > 1\pi]$, flank position (F/D), whorl inflation (B/H) and involution (C/R) at different growth stages were calculated for each specimen.

SHELL MORPHOLOGY

Gross Morphology and Coloration

The shells of the Palau, Philippine (Tañon) and Fiji *Nautilus* essentially resemble one another in overall morphology and shell coloration. Their whorls are tightly coiled with a narrow umbilicus, mostly filled with a callus in the middle-late growth stages. The shell coloration consists of two elements, i.e. irregular reddish brown to brown serrate radial stripes extending from the inner flank to venter and branching across the mid-flank, and a longitudinal stripe of the same color around the umbilical area (Fig. 1). In mature and almost mature shells, the former element tends to disappear toward the aperture, retaining only its trace on the inner flank. The mode of distribution, strength and hue of the shell coloration is fairly variable even in the specimens from the same area, but the Fiji sample consists mostly of the phenotype with relatively short and broad radial stripes (Fig. 1).

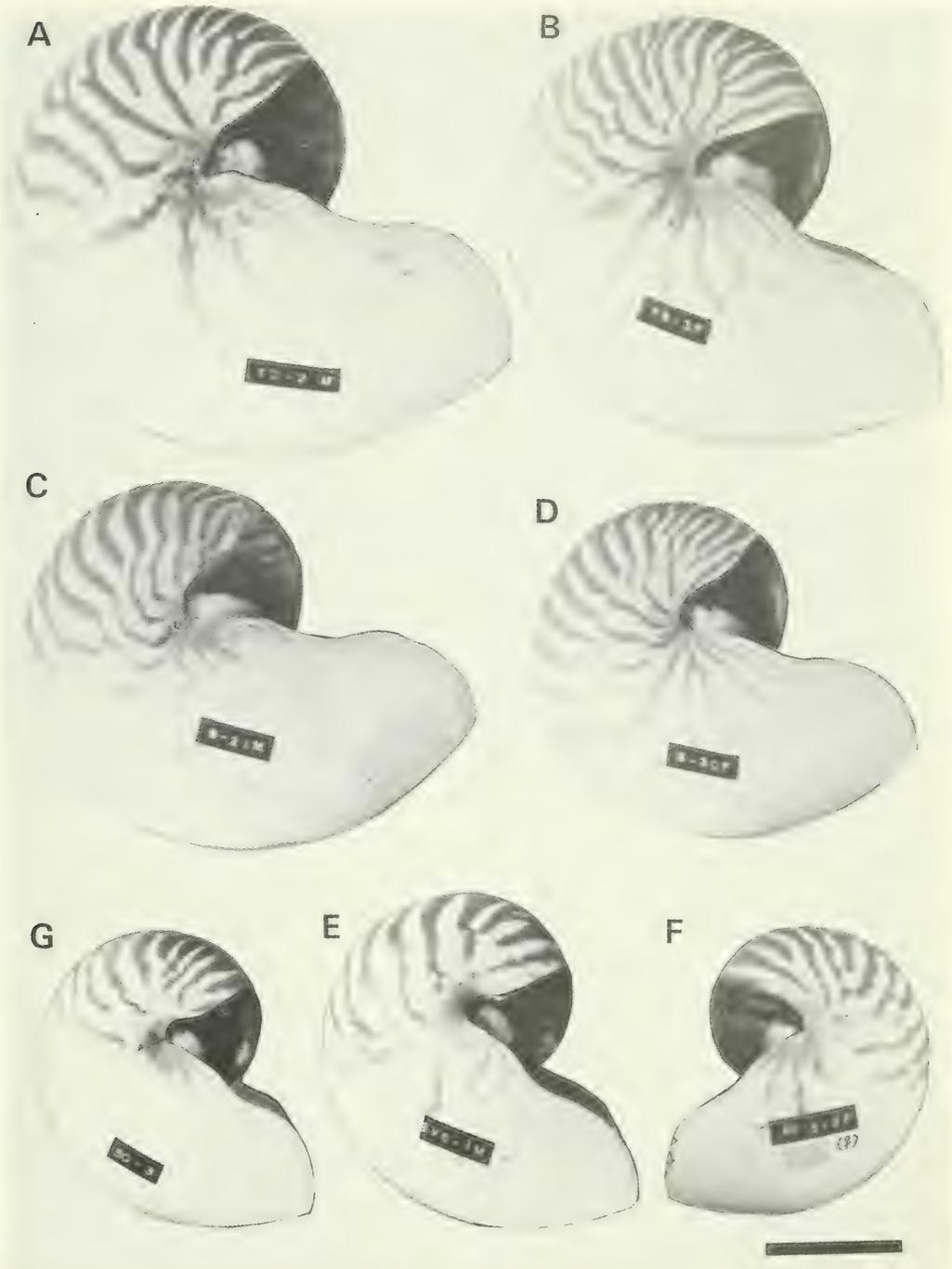


FIG. 1. Mature shells of *Nautilus belauensis* (A–B) and *Nautilus pompilius* (C–G), showing the similarity in overall morphology and coloration. A–B. Male (A: T3-2; UMUT RM 18708-3) and female (B: T9-3; UMUT RM 18708-9) from Palau. C–D. Male (C: B21; UMUT RM 18705-3) and female (B30; UMUT RM 18705-7) from Tañon Strait, the Philippines. E–F. Male (E: SV6-1; UMUT RM 18707-2) and female (F: SV5-3; UMUT RM 18707-1) from off Suva, Viti Lebu Island, Fiji. G. Sex-unknown specimen (SQ3; UMUT RM 18706-2) from Bohol Strait near Siquijor Island, the Philippines. Scale bar represents 5 cm.

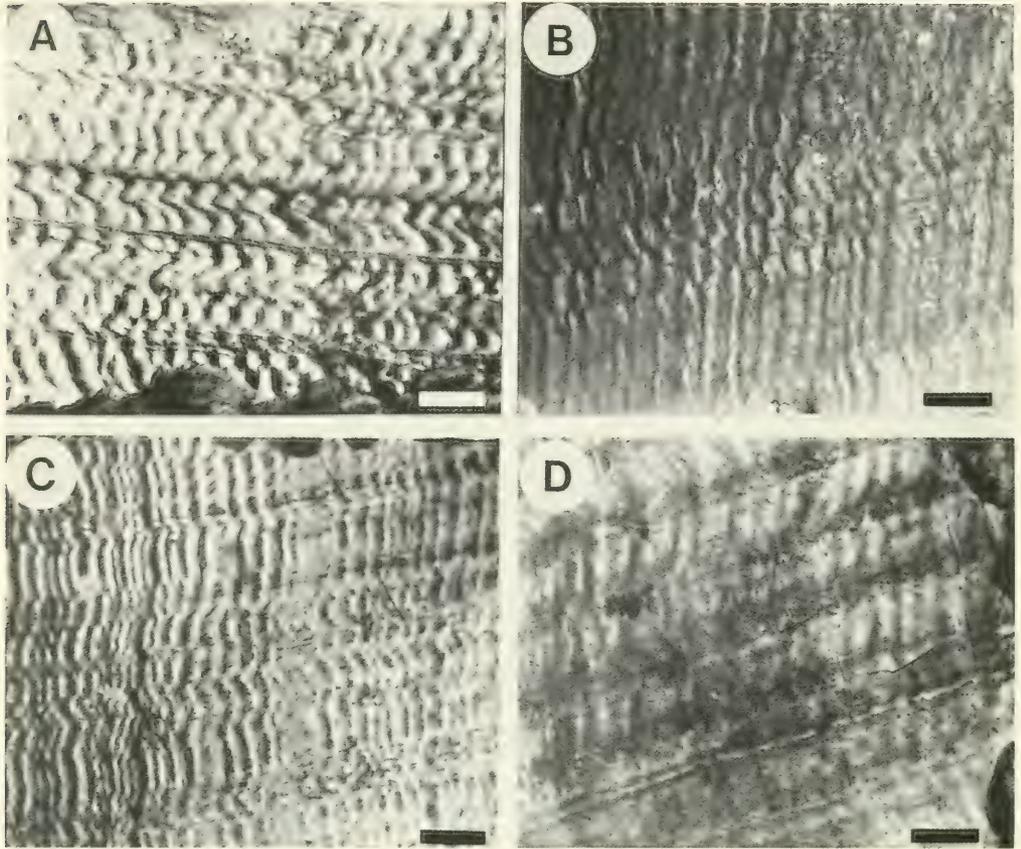


FIG. 2. Optical micrographs of the ventral shell surface of *Nautilus belauensis* (A) and *Nautilus pompilius* (B–D), showing longitudinally crenulated sculpture. A. UMUT RM 18708-2 (T2-4; female) from Palau. B. UMUT RM 18707-7 (SV13-8; female) from Fiji. C. UMUT RM 18707-8 (SV13-13; male) from Fiji. D. UMUT RM 18705-8 (B31; female) from the Philippines (Tañon Strait). Scale bars indicate 500 μm .

The whorls of every specimen exhibit dense sinuous growth lines. In addition, well-marked, longitudinally crenulated ridges showing a reticulate pattern are developed in every specimen from Palau. This sculpture was assigned by Saunders (1981a) as one of the diagnoses for distinguishing the Palauan *N. belauensis* from *N. pompilius*. However, it also occurs on the ventral side of many specimens of *N. pompilius* from Fiji and the Philippines, although it is especially conspicuous in the Palau specimens (Fig. 2).

Ontogenetic Shell Variation

Biometric analysis of selected specimens in dorso-ventral section reveals that the three samples exhibit similar ontogenetic patterns

of shell geometric parameters, as represented by the gradual decrease of whorl inflation (B/H) with increase of whorl number, sudden decline of flank position (F/D) near the end of the first whorl, and abrupt increase and subsequent decline of distance of the whorls to the coiling axis (C/R) in the second-third whorls (Fig. 3). In every sample, the ranges of variation of geometric parameters are larger in the early stage than in the later stage. The observed ranges of each parameter at a given whorl stage in Fiji and Palau specimens mostly overlap each other, except for the larger C/R ratio in the later stage of the Palau specimens. The umbilicus of every specimen is initially free from a callus. The callus begins to appear during the development of the second whorl, increasing its thick-

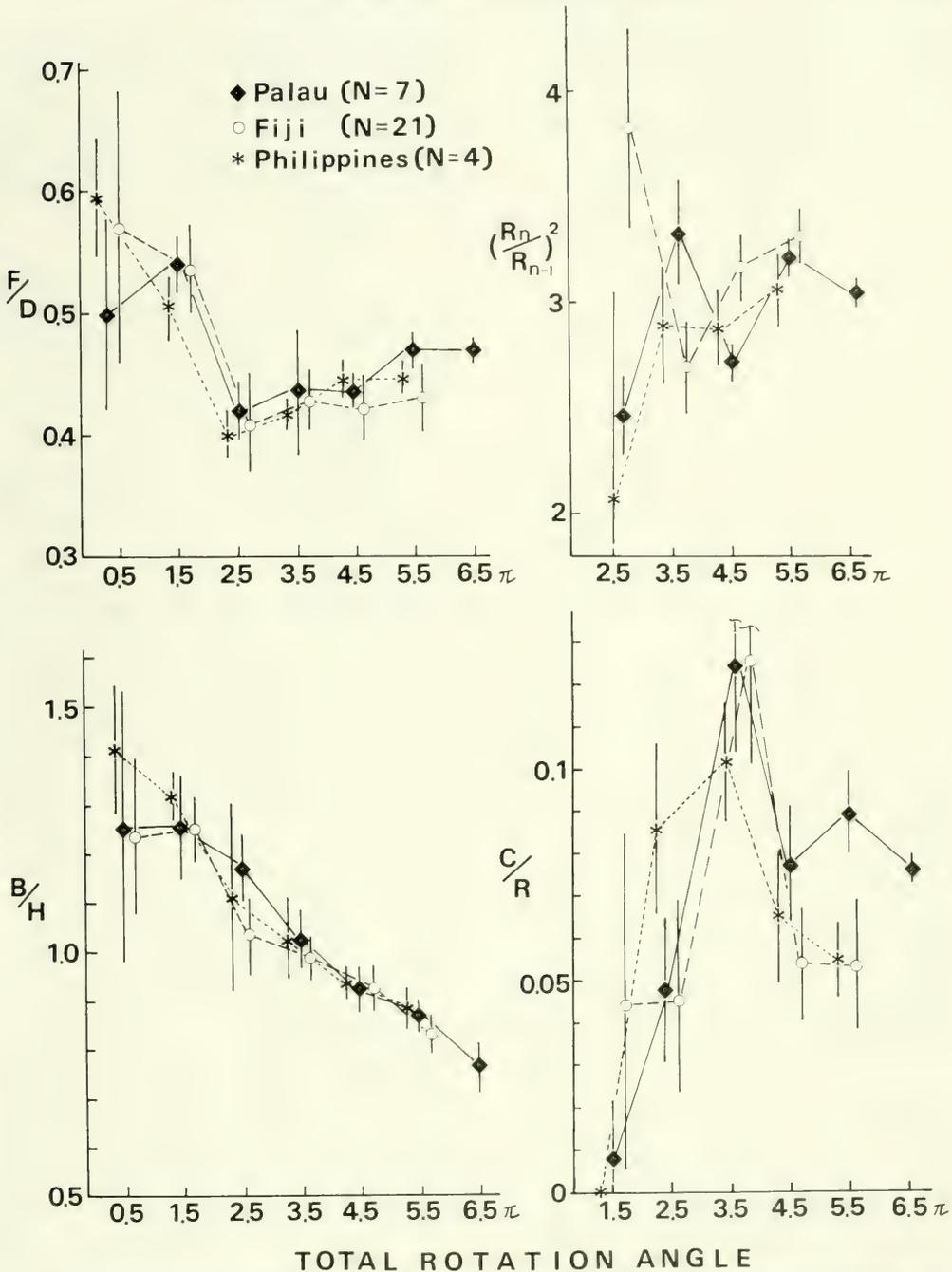


FIG. 3. Ontogenetic changes of whorl expansion rate $[(R_n/R_{n-1})^2]$, frank position (F/D), whorl inflation rate (B/H), and whorl involution rate (C/R) versus total rotation angle of spiral for specimens of *Nautilus belauensis* from Palau and *Nautilus pompilius* from the Philippines (Tañon Strait) and Fiji. Vertical bars indicate the range of one standard deviation.

ness as the shell grows (Fig. 4). A complete seal of the umbilicus by the callus occurs dur-

ing the formation of the second whorl for the Fiji and Philippine specimens, while it is de-

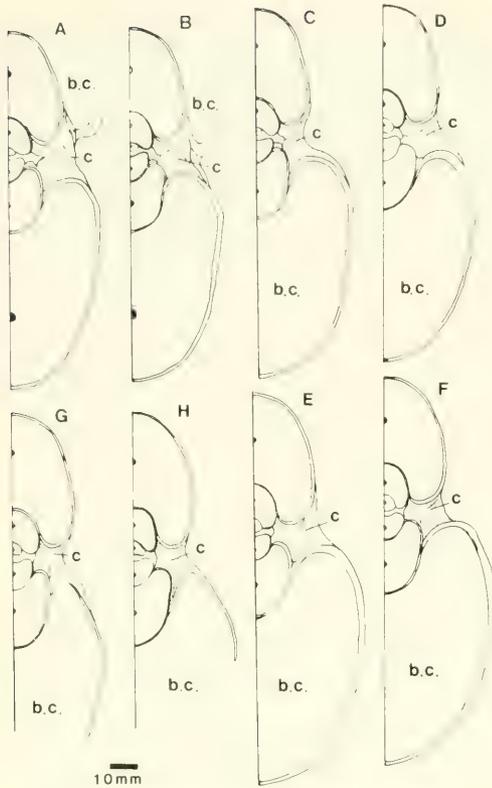


FIG. 4. Drawings of cross-sectioned specimens of *Nautilus belauensis* from Palau (A–C) and *Nautilus pompilius* from the Philippines (Tañon Strait) (D–F) and Fiji (G–H). A. UMUT RM 18708-7 (T9-1, mature male), B. UMUT RM 18708-8 (T9-2, mature male), C. UMUT RM 18708-2 (T2-4, mature female), D. UMUT RM 18705-5 (B27, mature male), E. UMUT RM 18705-6 (B29, mature male), F. UMUT RM 18705-4 (B22, submature female), G. UMUT RM 18707-3 (SV12-1, submature female), H. UMUT RM 18707-5 (SV13-1, submature male). b.c.: body chamber, c: callus.

layed after the formation of the second whorl for the Palau specimens. This observation correlates well with the description of Saunders (1987, pp. 43–44).

The scatter plot of B/H ratios of all captured animals exhibits wide ranging intra- and inter-population variation of this parameter at least for premature and mature specimens (Fig. 5). At the same shell size ($D = 150\text{--}160$ mm) most Fiji specimens have a more compressed shell than the Philippine specimens. The Palau specimens display remarkably wide variation in B/H ratio both in the immature and mature stages, and the values of

immature and submature specimens partly overlap those of mature specimens from Fiji and the Philippines.

The ontogenetic pattern of chamber length (= distance between contiguous septa) in the early to middle stages is fairly alike among specimens of the three samples and the one Siquijor specimen (Fig. 6).

Variation of Mature Shells

As demonstrated by previous authors (Haven, 1977; Ward et al., 1977; Saunders & Spinosa, 1978; Ward & Martin, 1980; Hayasaka et al., 1982, 1987; Tanabe et al., 1983; Tanabe & Tsukahara, 1987), species of living *Nautilus* show distinct sexual dimorphism in the size and weight of animals and shell proportions at maturity. Namely, mature males are generally larger and possess broader shells than mature females.

By examining the gonad development in live-caught animals, Tanabe & Tsukahara (1987) discussed the sexual dimorphism in *N. pompilius* from the Philippines (Tañon Strait) and Fiji. The difference in shell size at maturity among the Palau, Fiji and Philippine (Tañon) populations is made clear by summarizing the gonad and tissue weight data on live-caught animals (Tsukahara, 1985; Tanabe & Tsukahara, 1987) (Fig. 7). In each sample, abrupt increase of gonad weight initiates at the same shell size for both sexes. Full development of the gonad is well marked in the male specimens from Palau and Fiji, and this causes the relatively larger shell size in males than in females at the same gonad index [= gonad weight/tissue weight (%)] (Fig. 7).

Figure 7 also shows the difference in shell diameter at maturity among the three samples. The average diameters of male and female specimens in the Palau sample (ca. 210 mm and 190 mm respectively) are much larger than those in the Fiji sample (ca. 150 mm and 140 mm, respectively). Those in the Philippine (Tañon) sample (ca. 170 mm and 160 mm; see also Tanabe et al., 1983, table 3) are intermediate between the Fiji and Palau samples. Thus, the above differences in mature shell size among the three samples are much larger than that between sexes within the same sample.

Recognition of maturity is also shown by such characteristic shell features as approximation of the final two or three septa, a thickened last septum, and blackened and thickened aperture (e.g. Stenzel, 1964; Collins &

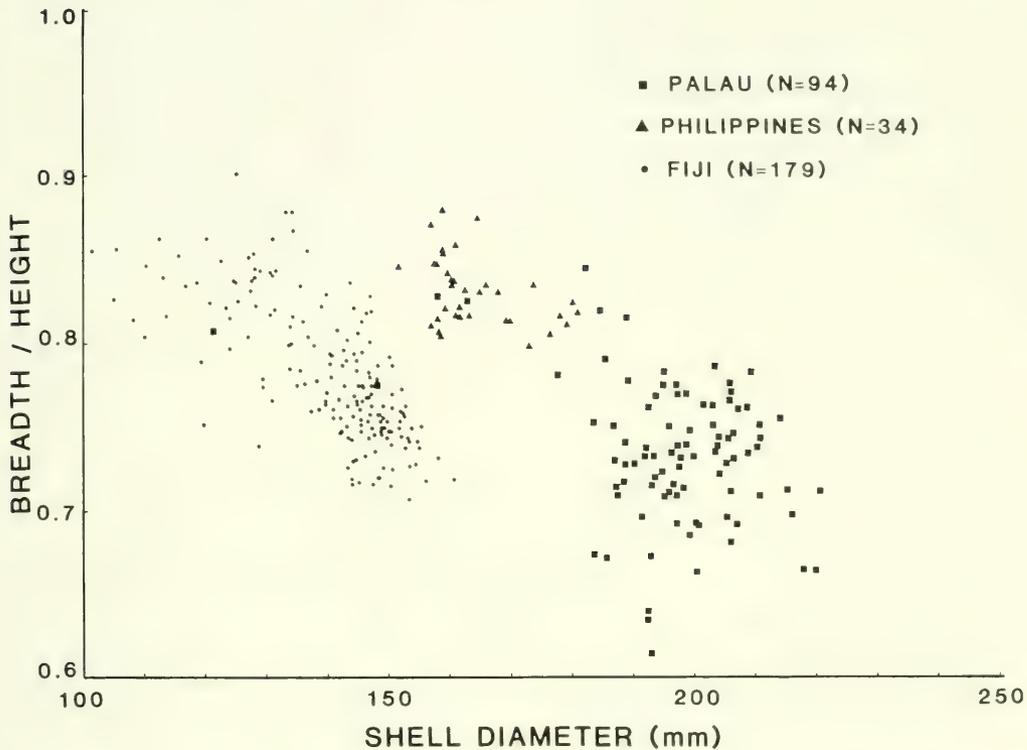


FIG. 5. Scatter plot of shell breadth/height ratio (B/H) versus shell diameter for specimens of *Nautilus belauensis* from Palau and *Nautilus pompilius* from the Philippines (Tañon Strait) and Fiji. Measurements of 179 animals captured in 1986 (Tanabe, 1987, table 3) are used for the Fiji sample.

Ward, 1987), because these features commonly occur in specimens with a large gonad index. In accordance with these criteria, the two specimens from Bohol Strait near Siquijor Island (the Philippines) are regarded as mature or submature shells. They are much smaller in shell diameter (ca. 130 mm; Fig. 1G) than the mature specimens from Tañon Strait. Total number of septa at maturity appears to be different among the three samples (33–39, 32–35, and 28–32 septa in the Palau, Philippine (Tañon) and Fiji samples respectively) (Fig. 8).

RADULAR AND JAW MORPHOLOGIES

Radula

The radula of *Nautilus* is secreted by columnar epithelial cells, named odontoblasts, in the posterior part of the radular sac, and is

generated anteriorly in a series of rows (Tanabe & Fukuda, 1987). Each row consists of nine primary teeth (one central rachidian, and two pairs of laterals and marginals on each side) and two pairs of marginal support plates (Thiele, 1893; Vayssièrè, 1896; Griffin, 1900; Naef, 1923; Solem & Richardson, 1975; Lehmann, 1976; Mikami et al., 1980; Saunders, 1981a, 1987; Tanabe & Fukuda, 1987). This arrangement is clearly distinguished from that in modern coleoids, which in general have seven primary teeth and a pair of marginal plates (Solem & Richardson, 1975).

Morphological features of each radular element are essentially identical among the Philippine (Tañon), Fiji and Palau *Nautilus* (Figs. 9–10). Namely, the central rachidian tooth is triangular in shape, being more than two or three times as high as the two laterals (Fig. 9). The two marginal teeth are much longer than the central and laterals; they are gently

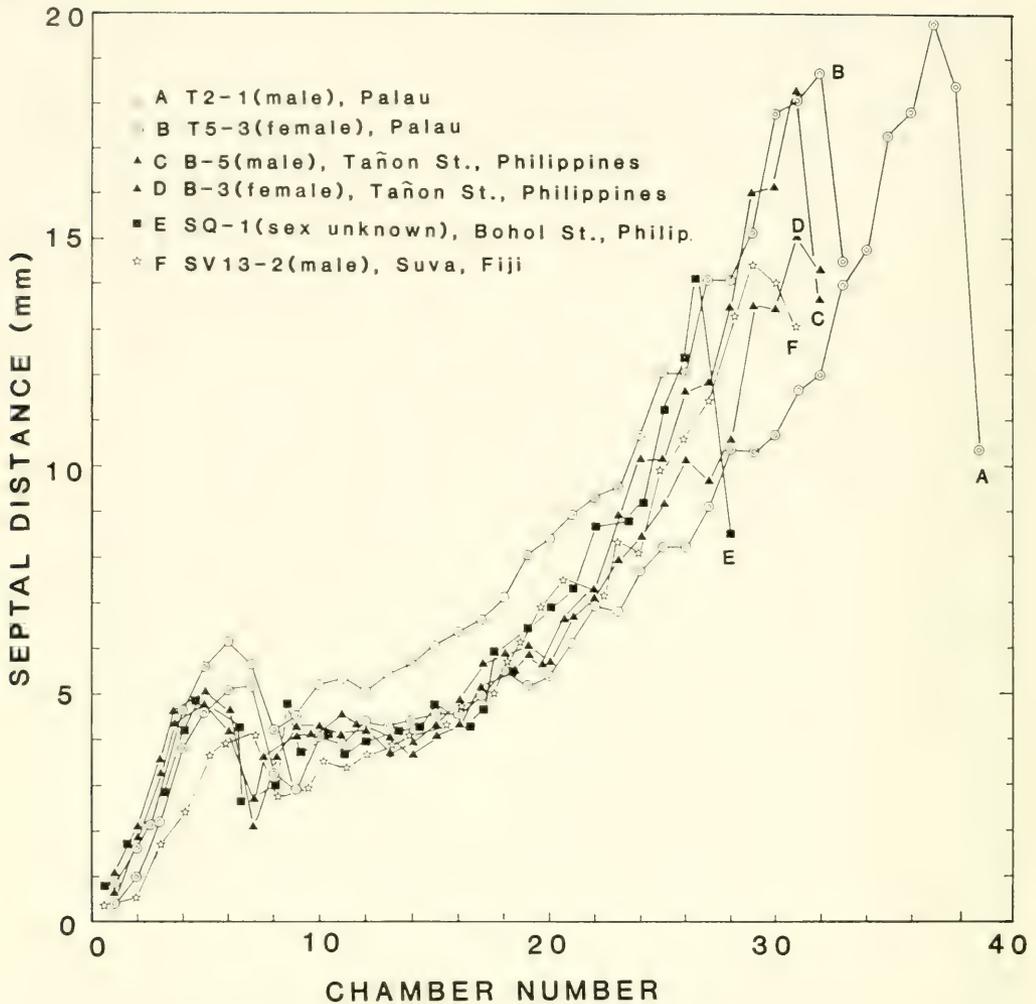


FIG. 6. Ontogenetic change of chamber length (= sepal interval) for selected mature specimens of *Nautilus belauensis* from Palau and *Nautilus pompilius* from the Philippines (Tañon and Bohol Straits) and Fiji. A. UMUT RM 18708-1, B. UMUT RM 18708-5, C. UMUT RM 18705-2, D. UMUT RM 18705-1, E. UMUT RM 18706-1, F. UMUT RM 18707-6.

curved and acutely projected anteriorly, with two strong grooves along their longitudinal axis (Fig. 10). In the anterior portion, the teeth are subcircular in cross section with a round tip, but they become rapidly broaden and compressed toward the base. A characteristic spatula-like anterior expansion is present at the base of the marginal teeth of every specimen from Palau and Fiji (Fig. 10A-C & E), but this feature is not so prominent in many specimens from the Philippines (Fig. 10D; see also Saunders, 1981a, figure 2). The marginal support plates are rectangular in outline; the inner one is larger than the outer.

A marked depression is developed in the anterior portion of the outer plate.

The shape of each radular element is markedly variable even in the specimens from the same area, and the range of variation of the height/width ratio of the central tooth in the Palau sample apparently overlaps those in the Fiji and the Philippine samples (Fig. 11).

Jaws

The jaw apparatus of *Nautilus* differs from those of modern coleoids by the presence of conspicuous anterior calcareous coverings

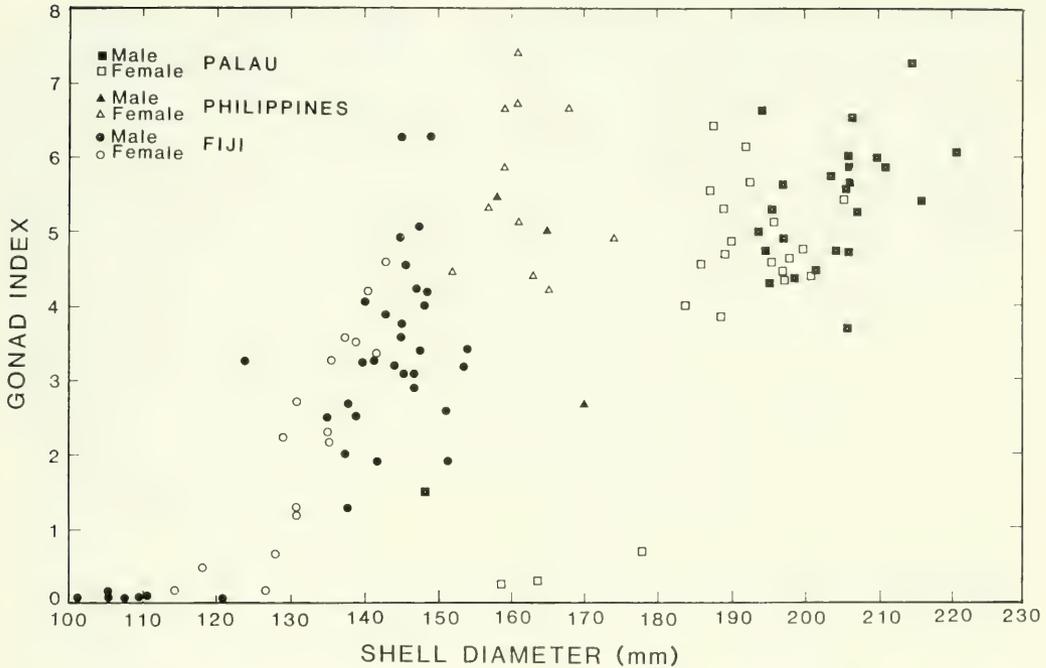


FIG. 7. Scatter plot of gonad index [gonad weight/tissue weight (%)] versus shell diameter for specimens of *Nautilus belauensis* from Palau and *Nautilus pompilius* from the Philippines (Tañon Strait) and Fiji.

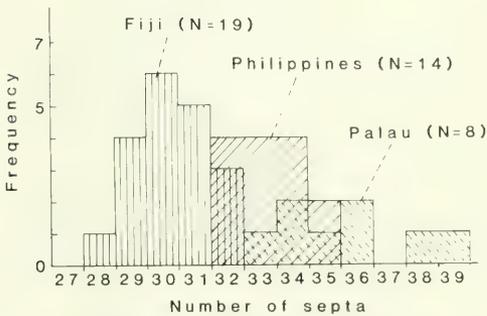


FIG. 8. Variation in the total number of septa at maturity for *Nautilus belauensis* from Palau and *Nautilus pompilius* from the Philippines (Tañon Strait) and Fiji.

on the chitinous plates of the upper and lower jaws and by the shorter inner lamellae of the lower jaw (Okutani & Mikami, 1977; Saunders et al., 1978; Tanabe & Fukuda, 1987). Its overall morphology, composition and structural relationship with the jaw muscles are the same among the species of *Nautilus*, and are well designed for a cutting and shearing func-

tion (Saunders et al., 1978; Tanabe & Fukuda, 1987).

The lower jaws of the Fiji and Palau specimens are both characterized by a distinct anterior depression in the antero-dorsal margin of the outer lamella, followed by a rather straight shoulder (Fig. 12A-B & E-F). In contrast, the lower jaws of the Philippine (Tañon) specimens mostly lack such a depression, and their outer lamella has gently concave antero-dorsal margin and roundly convex shoulder (Fig. 12C-D).

DISCUSSION

Taxonomic Relationships

The present study shows that the Philippine (Tañon Strait), Fiji and Palau *Nautilus* populations have strong affinities in overall shell morphology and radular and jaw structures. Furthermore, the large collections from the populations display similar ontogenetic patterns for the shell shape parameters and chamber length, and they can be distin-

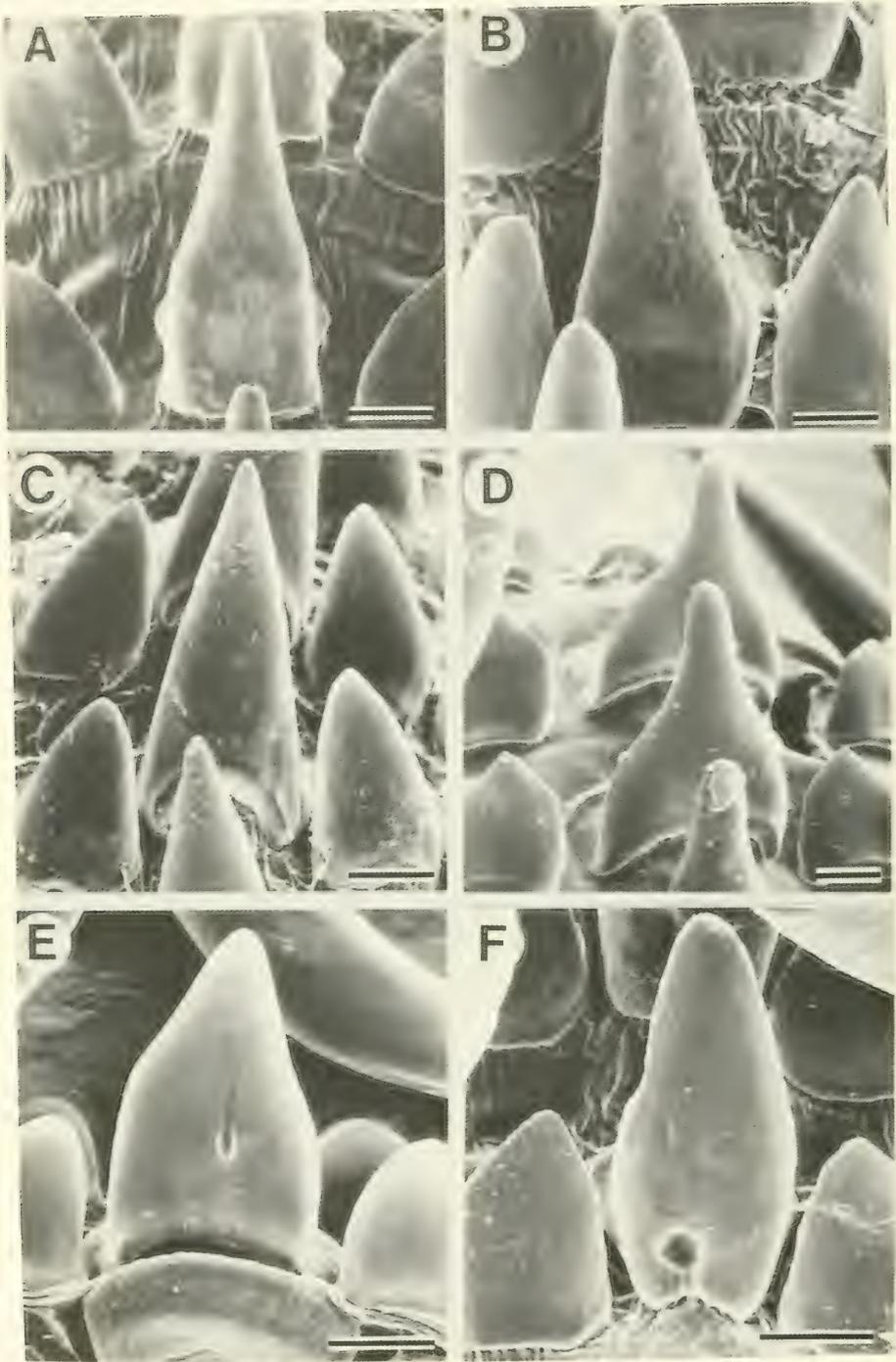


FIG. 9. Scanning electron micrographs of central rachidian and lateral (in part) radular teeth in *Nautilus belauensis* from Palau (A–B) and *Nautilus pompilius* from the Philippines (Tañon Strait) (C–D) and Fiji (E–F). A. UMUT RM 18708-6 (T5-4, mature female), B. UMUT RM 18708-8 (T9-2, mature male), C. UMUT RM 18705-7 (B30; mature female), D. UMUT RM 18705-5 (B27; mature male), E. UMUT RM 18707-4 (SV12-3; immature female), F. UMUT RM 18707-9 (SV13-14; immature female). Scale bars indicate 200 μm .

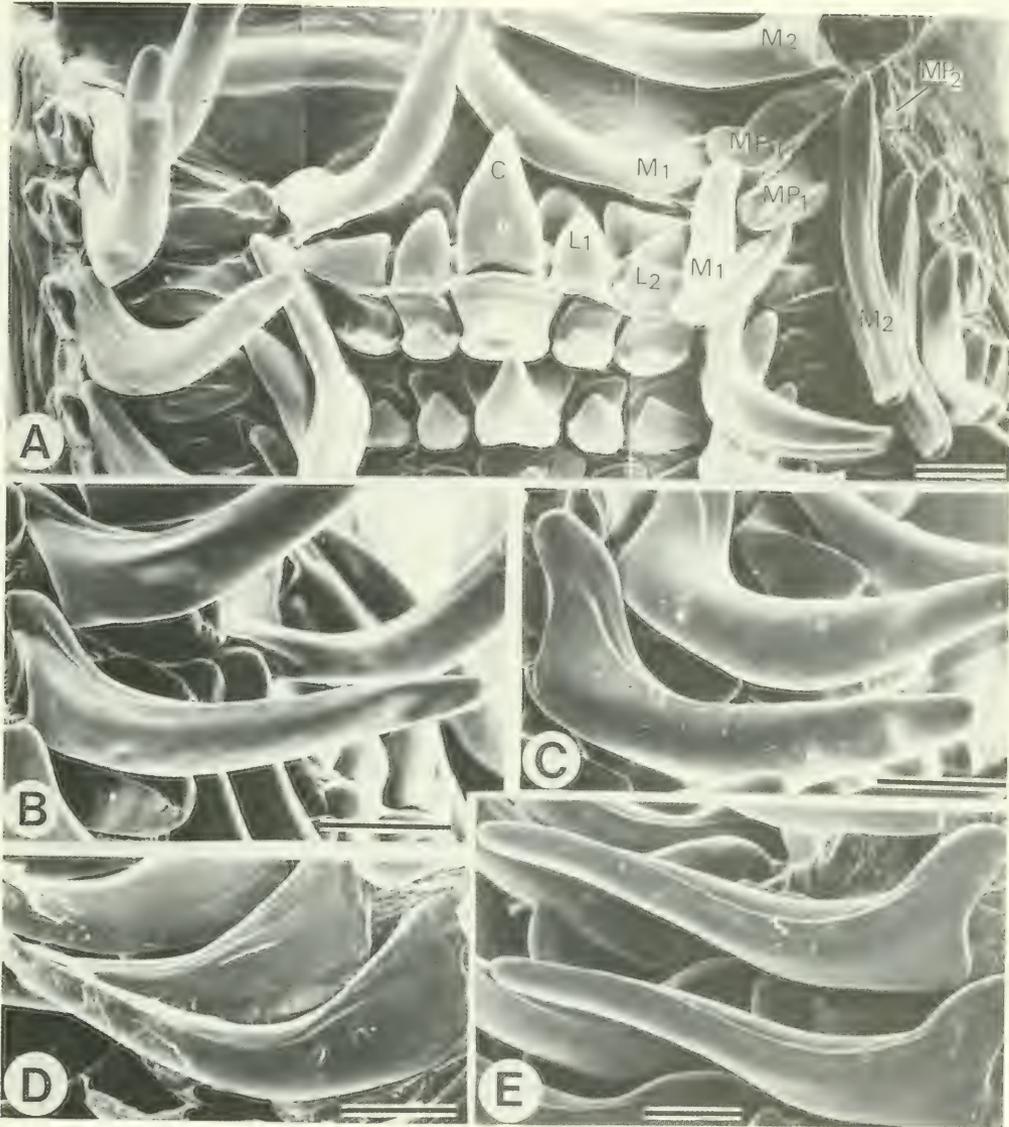


FIG. 10. Scanning electron micrographs of overall radula (A) and its marginal element (B–E) for specimens of *Nautilus pompilius* from Fiji (A–B) and the Philippines (Tañon Strait) (C–D), and *Nautilus belauensis* from Palau (E). A–B. UMUT RM 18707-4 (SV12-3). C. UMUT RM 18705-5 (B27). D. UMUT RM 18705-7 (B30). E. UMUT RM 18708-6 (T5-4). Scale bars indicate 500 μ m. Anatomy: c: central rachidian tooth, L₁ and L₂: inner and outer lateral tooth, M₁ and M₂: inner and outer marginal tooth, MP₁ and MP₂: inner and outer marginal support plates.

guished mainly by the dimensions of adult animals, such as the total live weight, shell size, and total number of septa. These observations may offer serious problems in recognizing the Palauan population as a separate species.

The Palauan *Nautilus* was identified by

Dugdale & Faulkner (1976) as *Nautilus* sp. It was subsequently identified as *N. pompilius* (Faulkner, 1976; Saunders & Ward, 1979; Carlson, 1979) or *N. cf. pompilius* (Saunders et al., 1978; Saunders & Spinosa, 1978, 1979). Later, Saunders (1981a) proposed a new species, *N. belauensis*, on the basis of

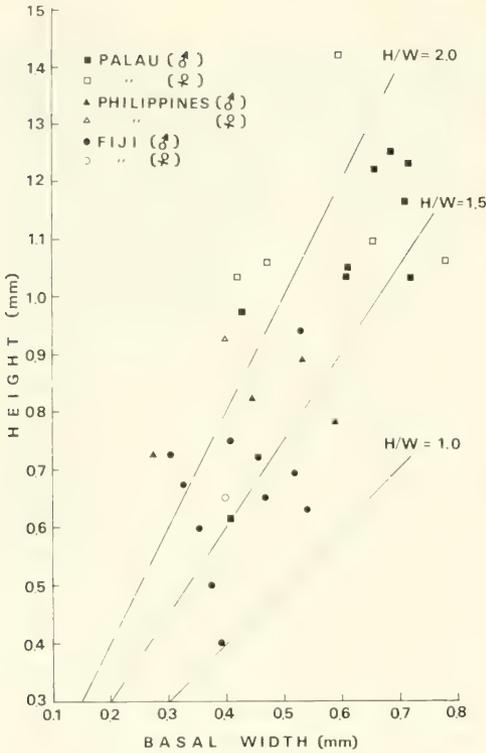


FIG. 11. Scatter plot of central rachidian tooth height (H) and basal width (W) for specimens of *Nautilus belauensis* from Palau and *Nautilus pompilius* from the Philippines (Tañon Strait) and Fiji.

examination of more than 1,000 live caught animals. According to Saunders (1981a, b, 1987), *N. belauensis* is distinguished from *N. pompilius* by its larger mature size and wider central rachidian radular tooth, and by the presence of longitudinally crenulated growth lines on the shell. The present work, however, confirms the presence of crenulated shell ornamentation in many specimens of *N. pompilius* from Fiji and the Philippines. Furthermore, the width/height ratios of radular elements are highly variable even in the specimens from the same area, suggesting that the shape of radular teeth appears to be of little significance at least for the species-level systematics of living *Nautilus*. The remaining diagnosis of the Palau population, unusually large mature shell size, should not be relied on for distinguishing species for the following reasons. Indeed, the widespread species, *N. pompilius* displays well-marked morphological differentiation regarding overall weight and size at maturity, proportion and coloration

of shells, and the trends of the allometric relationships of several characters of the shells and soft tissues, not only among the geographically separated populations (Ward et al., 1977; Hayasaka et al., 1982, 1987; Tanabe & Tsukahara, 1987; Saunders, 1987; K. Tanabe's observations on specimens from various localities housed in the U.S. National Museum of Natural History), but also among neighboring populations (Hayasaka et al., 1982; Saunders, 1987; Swan & Saunders, 1987; Habe & Okutani, 1988). The minor difference in the lower jaw morphology between the Philippine and Fiji specimens can probably be attributed to conspecific variation.

In addition to the above results at morphological level, recent examinations of large collections using electrophoretic techniques provided interesting data relevant to taxonomic relationships of *Nautilus* populations from a genetic viewpoint (Masuda & Shinomiya, 1983; Woodruff et al., 1983, 1987). These works have made clear that *Nautilus* exhibits normal or slightly high levels of genetic variation and that the isolated populations are well differentiated genetically. Relying upon Nei's (1978) genetic distance coefficients, Woodruff et al. (1987) suggested that the Palau population (*N. belauensis*) and possibly the Fiji population (*N. pompilius*) are closely related to, but well differentiated at a species level from the populations of *N. pompilius* in the waters around New Guinea and Queensland. The genetic distance coefficients between the samples of *N. belauensis* from Palau and *N. pompilius* from eight localities in the southwestern Pacific excluding the Philippines (< 0.2) are, however, much smaller than those between paired samples of *N. scrobiculatus*, *N. macromphalus* and *N. pompilius* (> 0.5) (see Woodruff et al., 1987, table IV & fig. 2). As Woodruff et al. (1987) documented, there is no simple basis to translate a genetic distance into a taxonomic decision, because the processes of speciation are not closely coupled to the changes of structural genes. To sum up the above-mentioned morphological and genetic data, two different interpretations can be considered for the taxonomic relationship among the three populations. The one is that the populations in the Philippine, Fiji and Palauan waters are summarized into the amphimictically outbreeding species, *N. pompilius*, with high levels of genetic and morphological differentiation, and the other is that *N. belauensis* is a distinct species reproductively isolated from

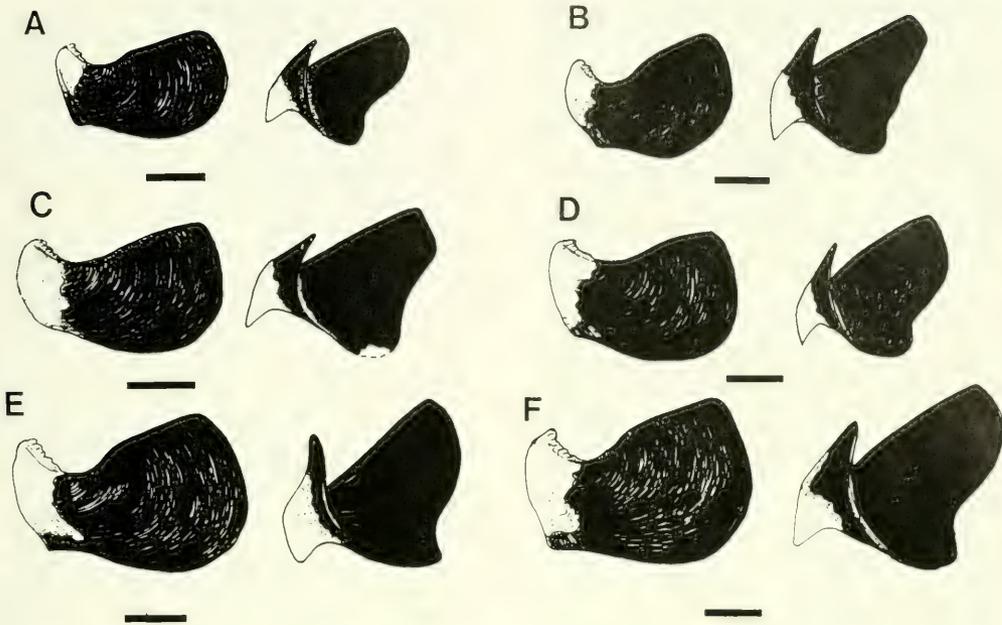


FIG. 12. Drawings of upper (right side) and lower (left side) jaws for specimens of *Nautilus pompilius* from Fiji (A–B) and the Philippines (Tañon Strait) (C–D), and *Nautilus belauensis* from Palau (E–F) (lateral views). A. UMUT RM 18707-9 (SV13-14; mature female), B. UMUT RM 18707-10 (SV28-4-2; mature male), C. UMUT RM 18705-7 (B30; mature female), D. UMUT RM 18705-2 (B5, mature male), E. UMUT RM 18708-5 (T5-3; mature female), F. UMUT RM 18708-4 (T5-1; mature male). Scale bars indicate 1 cm.

the populations of *N. pompilius*. In this paper, we refrain from choosing between the two because of the insufficient data for the genetic variation of *N. pompilius* throughout its wide geographic range, especially of the populations in the Philippine waters.

Interpretation on Mature Shell Size Variation

In his discussion of *Nautilus* systematics, Saunders (1987) suggested that the difference in mature shell size between *N. belauensis* and *N. pompilius* does not result from the difference in the period of growth, on the basis of counting of septal number and the stage of the umbilical callus appearance. Although the absolute growth and longevity of *Nautilus* in their natural habitats are not fully understood, previous direct and indirect growth rate measurements by release-recapture experiments of tagged specimens, radiographic observation of aquarium specimens, and radiometric dating of septa have shown that the period of chamber (septal) formation increases exponentially with increasing chamber number (Cochran et al., 1981; Saunders, 1983, 1984;

Ward, 1985; Cochran & Landman, 1984; see compilation in Landman & Cochran, 1987, figure 4, table V). The marked difference in the total number of septa among the mature specimens from Fiji, the Philippines and Palau can be, therefore, interpreted as reflecting the difference in the pre-reproductive age among them. This interpretation is in accord with Landman & Cochran's (1987) age estimate from septal growth equations (10.9 y and 5.9 y for *N. belauensis* and *N. pompilius* respectively). The Palau population may attain sexual maturity at slower rates than the Fiji and Philippine populations, although its rate of septal formation in earlier stages may not differ greatly from those in the Philippine and Fiji populations. The rate of shell growth and the time required to attain sexual maturity may be controlled by both ecology (food supply, temperature, water depth etc.) and genetic factors, and the degrees of dependence of these factors on growth apparently differ among individual populations. Based on the data from genetic analysis, Woodruff et al. (1987) suggested that the Palau and Fiji populations have distinctly diverged from the ancestral form of

N. pompilius by peripheral isolation for about 1 million years. We have no available data on the fossil record of *Nautilus* to verify this hypothesis, but if it is correct, the adult size increase or decrease in relation to the length of pre-reproductive age in the history of *N. pompilius* stock can be expressed by hypermorphosis and progenesis in terms of McNamara's (1986) definition of heterochrony.

Conclusion

The *Nautilus* populations in Palau, the Philippines and Fiji are essentially similar in overall shell morphology, ontogenetic shell variation, and jaw and radular structures. They are distinguished mainly by the dimensions of adult animals. From these morphological evidence and the available genetic data, the Palau and the other two populations are regarded as either summarizing into the widespread species, *Nautilus pompilius*, or belonging to the closely related sibling species, *N. belauensis* and *N. pompilius* respectively. The size difference among the adult animals from the three populations probably results from the difference in their pre-reproductive ages.

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CROSS SECTIONAL MORPHOLOGY OF THE GLADIUS IN THE FAMILY
OMMASTREPHIDAE (CEPHALOPODA: TEUTHOIDEA) AND ITS BEARING ON
INTRAFAMILIAL SYSTEMATICS

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ABSTRACT

The cross sectional morphology of the ommastrephid gladius is compared among 15 species in 11 genera of the three currently recognized subfamilies. The three axial complexes of the free rachis are shown to comprise a suite of characters of systematic importance. Intrafamilial relationships derived from characters of the gladius generally conform to the traditional classification of the family based on a synthesis of traditional characters, with the exception of subfamilial organization. The depositional layering of chitin which occurs as part of the accretive growth of the gladius is easily seen in cross section using either light or scanning electron microscopy. Examination of these layers can provide information on ontogenetic changes in gladius construction because the early morphology is covered but apparently not altered during subsequent depositional events.

Key words: Teuthoidea, Oegopsida, Ommastrephidae, gladius morphology, phylogeny, shell, squid.

INTRODUCTION

Squids of the family Ommastrephidae are robust, muscular, powerful swimmers. Adults range in size from about 8.0 cm (*Hyaloteuthis pelagica*) to over 1.0 m (*Dosidicus gigas*) in mantle length (Wormuth, 1976; Nesis, 1983). The majority of taxa are open ocean epipelagic animals while some (e.g. *Illex* and *Todarodes*) range over continental shelves. The ommastrephids are predaceous carnivores that feed primarily on finfishes and other squids. They are prey to many predator species including marine mammals and finfishes. Many ommastrephids are commercially exploited for both human consumption and for bait in finfish fisheries and as such form the basis of substantial fisheries in many areas of the world (Clarke, 1966; Roper, 1983; Rathjen & Voss, 1987).

Roper (1983) included the Ommastrephidae as one of the four families of cephalopods (along with the Sepiidae, Octopodidae, and Loliginidae) most critically in need of comprehensive systematic revision based on four criteria. The groups are: (1) speciose and occur in greatest abundance in shallow waters; (2) support major fisheries; (3) support biomedical, ecological and other biological research; (4) poorly known systematically. Prior to and as a result of Roper's (1983) listing of

these four groups, the systematics of the Ommastrephidae represents an area of considerable recent research (e.g. Roper, et al., 1969; Adam, 1975; Zuev et al., 1975; Wormuth, 1976; Nesis, 1978, 1983; Lu & Dunning, 1982; Roeleveld, 1982, 1988; O'Dor, 1983; Okutani, 1983). A variety of morphological and meristic characters have been used in the systematic study of ommastrephids. Traditionally, the three subfamilies, Ommastrephinae, Todarodinae, and Illicinae, have been separated on characters associated with the funnel groove, specifically the occurrence of side pockets and foveolae. Below the subfamilial level, characters used to delineate taxa include fin angle, club sucker arrangement and dentition, spermatophore morphology, arm protective membrane development, condition of the funnel-mantle locking cartilages, type and distribution of light organs, hectocotylus morphology, and various morphometric relationships of the arms, tentacles, clubs, fins, etc. Details of the gladius or pen have been absent from the descriptions and systematic analyses of most of the recent systematic contributions to the Ommastrephidae. In contrast, in many of the older contributions to ommastrephid systematics (e.g. Pfeffer, 1912; Sasaki, 1929) the gladius is described, sometimes in great detail, and often illustrated. Collectively, these reports, in

particular Pfeffer's (1912) monumental monograph of the Oegopsida, which contains detailed illustrations of the gladius of many ommastrephid taxa, suggest that the ommastrephid gladius is a highly conservative structure, exhibiting little morphologic variation across the family, with the exception of relatively minor differences in the width of the free rachis and the length of the cone field. An exception to this perceived homogeneity among ommastrephid gladii is the unique, layered deposit of chitin within the concavity of the cone field of *Dosidicus gigas* (Steenstrup, 1857; Pfeffer, 1912; Toll, 1982). The existence of the widely held assumption that the ommastrephid gladius is of little value to systematic study is probably the cause of the relative lack of interest in this structure as reflected by more recent systematic contributions to this group. Indeed, the descriptive accounts of two recently described species lack any mention of the gladius whatsoever (*Ornithoteuthis antillarum* Adam, 1957; *Todaropsis filippovae* Adam, 1975).

The examination of cross sections of the ommastrephid gladius is not new. Lesueur (1821), Ball (1841), Posselt (1890), Verrill (1882), Naef (1923), Sasaki (1929), and Rancurel (1970) included variously detailed mention of the cross sectional shapes of the gladius or described the characteristics of the axes along the free rachis allowing inferences of cross sections to be made. Indeed, Naef (1923) used aspects of the cross sectional structure of the gladius as part of species diagnoses. Toll (1982) demonstrated that cross sections of ommastrephid gladii contained hitherto unknown systematic characters that could be useful in phylogenetic reconstructions. The same characters could be valuable in identifying fragmentary ommastrephid remains encountered in stomach contents of predators. This paper presents the results of a comparative study of ommastrephid gladius cross sections. The results show that while the gross shape of the ommastrephid gladius is similar throughout the family, there is consistent variation in cross sectional shape. This variation should be assessed as part of future studies regarding ommastrephid systematics. Finally, overall shape and structure of the gladius are two of the few anatomical characters of squids that allow direct comparison between fossil and Recent teuthoids and could prove useful in establishing phylogenetic relationships to fossil ommastrephid antecedents (see Donovan & Toll, 1988).

MATERIALS AND METHODS

Gladii were dissected out of preserved specimens by means of a longitudinal incision along the ventral midline. The cut edges of the mantle wall were reflected back to expose the viscera. The left gill was severed from its attachment to the inner surface of the mantle musculature. Beginning anteriorly and progressing posteriorly, the visceral mass was freed from the mantle wall along its left side and reflected to the right exposing the gladius, still in the shell sac, below it. Once completely exposed, the shell sac was cut open ventrally and laterally to allow the gladius to be removed from the inner surface of the dorsal mantle musculature. As necessary, the nuchal muscles, which extend from the nuchal cartilage to the ventral surface of the anterior free rachis, were severed from their insertion on the shell sac. The narrowest part of the gladius, that area at the posterior limit of the free rachis, is sometimes completely buried in the mantle musculature and further dissection is required to free it. Also, in some taxa, the musculature of the tail region must be opened in order to free the apex of the conus. The procedure for extraction of the gladius described here is preferable to excision of the gladius via dissection through the dorsal mantle musculature. When carefully executed, the ventral removal method results in little substantive damage to the specimen. Excised gladii were kept in either 40% isopropyl or 70% ethyl alcohol and stored in separate vials or bottles along with the specimen from which it was removed.

Because this study represented the first extensive, comparative examination of cross sections of ommastrephid gladii, a convention needed to be established regarding the choice and standardization of levels of section to be examined. Four cross sections were selected and named as follows: level A, level B, level C, and level D. The anterior three levels (A, B, and C) were established at discrete proportional distances from the anterior tip of the gladius. These are 0.10 GL (one-tenth of the length of the gladius measured from its anterior tip), 0.25 GL (one-quarter of the length of the gladius measured from its anterior tip), and 0.60 GL (six-tenths of the length of the gladius measured from its anterior tip), respectively. Level D coincides with the posterior limit of the free rachis where it meets the cone field. Cross sections were made using a new single edge razor blade

with the gladius held firmly on a hard rubber block. The cross sections of different taxa are drawn approximately to the same size to facilitate direct comparisons. All sections are oriented with the dorsal surface toward the top of the page. In each set, level A is at the top and levels B, C, and D are in ordered sequence below. Each set of cross sections is based on near mature or fully mature individuals and represents a composite, typical for that species. Variation is discussed along with the treatment of individual taxa and in the General Discussion.

Abbreviations used in the text are as follows: M, male; F, female; ML, dorsal mantle length; GL, gladius length; ANSP, Academy of Natural Sciences of Philadelphia; BCF, Bureau of Commercial Fisheries (now National Marine Fisheries Service); IATTC, Inter-American Tropical Tuna Commission; MCZ, Museum of Comparative Zoology, Harvard University; UMML, Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami; USNM, National Museum of Natural History, Smithsonian Institution; DISC, R/V DISCOVERER; ELT, USNS ELTANIN; ORE, M/V OREGON; P, R/V JOHN ELLIOTT PILLSBURY; TC, R/V TOWNSEND CROMWELL; ET, Engel Trawl; IKMT, Issacs-Kidd midwater trawl; MWT, midwater trawl; OT, otter trawl.

MORPHOLOGY AND ANATOMICAL RELATIONSHIPS OF THE OMMASTREPHID GLADIUS

The free rachis (Fig. 1) is long, broadest anteriorly, tapered posteriorly and terminates anteriorly in a stiff point. Anteriorly, there are three axial complexes, one medial and two lateral, each with three primary components; a ventrally displaced axis, a dorsal plate, and a commissure that joins the axis to the plate (Fig. 2). The plates and commissures can vary in thickness and width. Laterally, the plates are rounded or tapered to a point and ventrally recurved. The two lateral plates are connected to the central one by a pair of broad, thin, lateral fields. The lateral axes can be bifurcated anteriorly. The lateral axis, plate, and commissure progressively coalesce posteriorly to level C where the lateral axial complex varies from lobate to hook-shaped with an admedial cleft. The three axial complexes (hereafter referred to as the medial complex and lateral complexes) converge

posteriorly to form a single complex of variable shape at level D. This single axis extends to the posterior tip of the gladius. The vanes are reduced to a small, spindle-shaped cone field that accounts for 10% to 25% of the total GL. Fine, radiating striae converge anteriorly from the anterolateral portions of the cone field toward the rachis. There is a small, conical primary conus.

The gladius is partially embedded in the ventral surface of the dorsal mantle musculature along the dorsal midline. In some taxa, the anterolateral edges of the free rachis are overlain by muscle. In many, the narrow posterior portion of the free rachis, including part or all of the cone field, is completely buried within the mantle musculature. The nuchal muscles insert on the shell sac covering the ventral surface of the medial rachis fields posterior to the widest part of the free rachis. The insertion sites are oval. The gladius does not invade the posterior tail-like extension of the mantle as found in *Ornithoteuthis*, among others.

DESCRIPTIVE ACCOUNTS

Subfamily Ommastrephinae Steenstrup, 1857

Genus *Ommastrephes* d'Orbigny, 1835

Ommastrephes bartramii (Lesueur, 1821)

Material examined.—4M, ML = 283-205 mm, GL = 287-108 mm, R/V VELERO, no data (probably eastern Pacific Ocean), UMML 31.1770. —1F, ML = 241 mm, GL = 237 mm, Naples, Italy, ANSP A6474. —1F, ML = 142 mm, GL = 149 mm, R/V ATLANTIS, off Bermuda, surface night light, 11 Oct. 1937, MCZ 293702.

Description.—Cross sections (Fig. 3): **Level A**—The medial axis is subellipsoid, wider than deep, and broadly attached to the thin, medial plate. The lateral plates are moderately thick, distally tapered to blunted points or rounded tips and ventrally recurved. There are paired lateral axes. The proximal axis is digitiform and curved in some specimens. The distal axis is subovoid and wider than deep. Both axes are broadly attached to the lateral plate; **Level B**—The medial complex is similar in size and shape to that of level A. The lateral complexes are irregularly multi-lobed; **Level C**—The medial complex is small and fusiform. The lateral complexes are an inflated hook-shape. The admedial cleft is quadrangular to triangular and about one-third to one-half as wide as the complex.

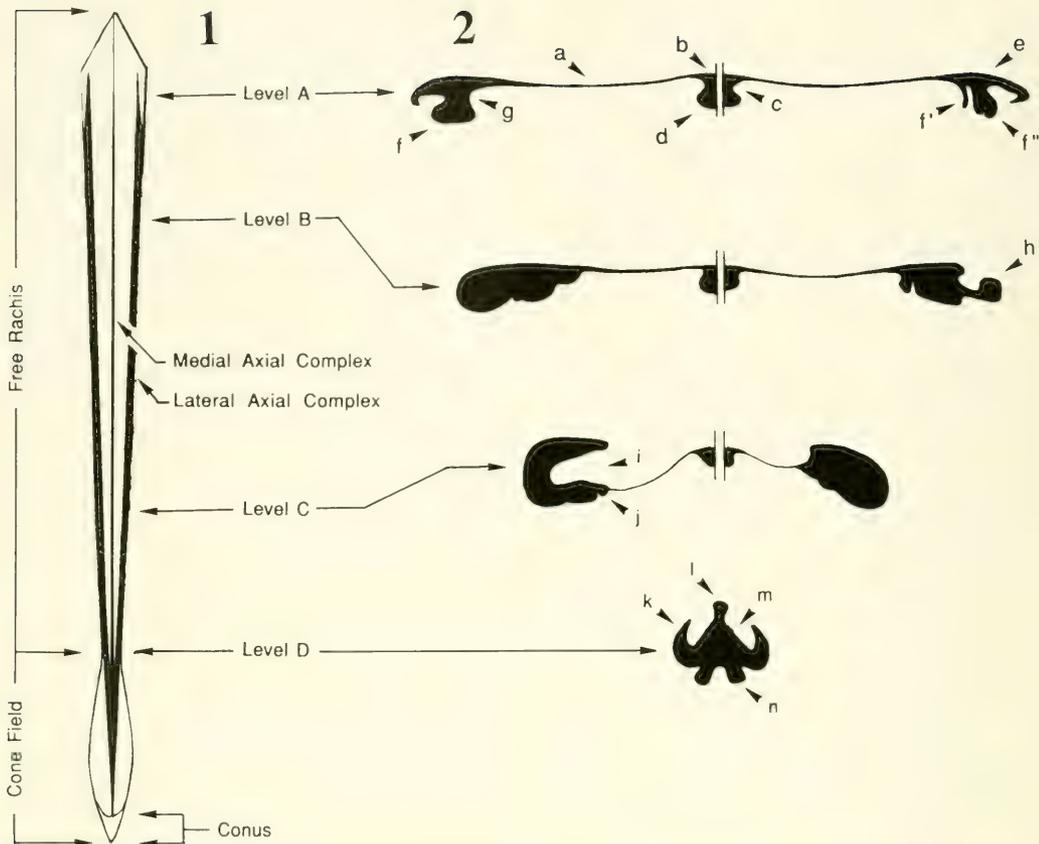


FIG. 1. Diagrammatic ventral view of ommastrephid gladius.

FIG. 2. Composite cross sections of gladius with level of sections corresponding to Fig. 1 [a-lateral field; b-medial plate; c-medial commissure; d-medial axis; e-lateral plate; f-lateral axis (single); f'-proximal lateral axis; f''-distal lateral axis; g-lateral commissure; h-accessory process; i-admedial cleft; j-ventromedial process; k-lateral process; l-dorsal carina; m-body; n-ventral keel]. All sections oriented with dorsal surface toward top of page.

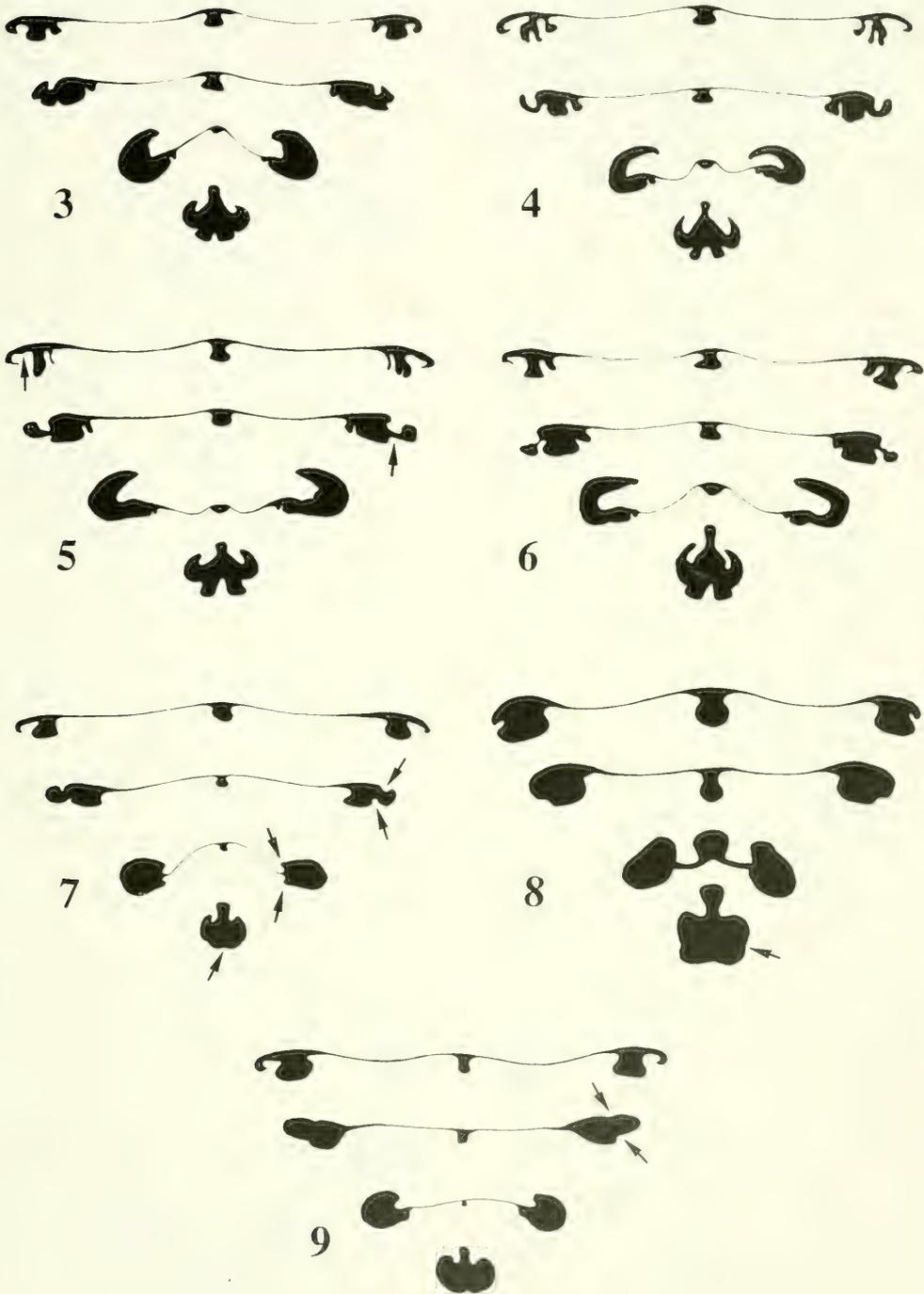
There is a small ventromedial process; **Level D**—The body is subtriangular with a pair of large quadrangular, ventral keels and stout, dorsally upswept, lateral processes that taper to blunt points. The dorsal carina is stout and slightly inflated apically.

Discussion.—The gladii show variation in the shape of the lateral thickenings at all levels and the overall shape at Level D. This variation was seen as varying degrees of thickness and shape of the axis and plate components and is greater than in any other ommastrephid species examined. The six *Ommastrephes bartramii* examined here were from distant localities—the Mediterranean Sea, western Atlantic Ocean and Pacific

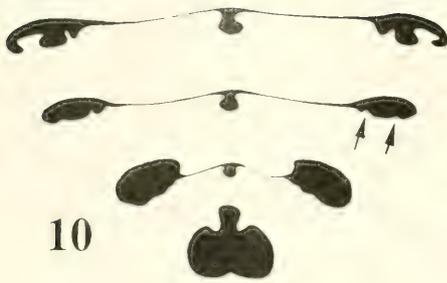
Ocean. Prevailing taxonomic uncertainties as well as geographic variation probably account for at least part of this variation.

Genus *Sthenoteuthis* Verrill, 1880
Sthenoteuthis pteropus (Steenstrup, 1855)

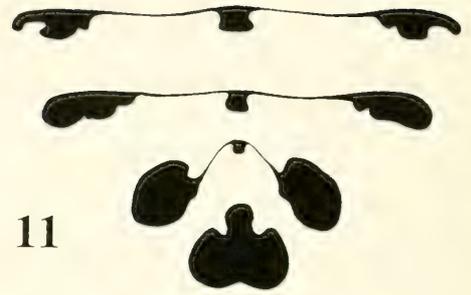
Material examined.—1F, ML = 328 mm, GL = 351 mm, DISC 425E, Atex Drift, 12°27'N, 41°21'W, dip net with night light, 12-13 Feb. 1969, UMML. —2F, ML = 288 mm, GL = 304-286 mm, DISC 425E, Atex Drift, 10°51'N, 42°21'W, dip net with night light, 14-15 Feb. 1969, UMML. —3F, ML = 305-178 mm, GL = 317-175 mm, DISC 425E, Atex Drift, 12°57'N, 40°09'W, dip net with night light, 9-10 Feb. 1969, UMML. —2F, ML =



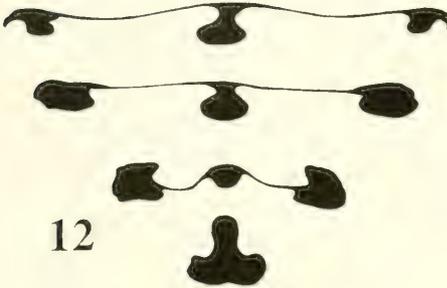
FIGS. 3-9. Stylized composite cross sections of gladius levels A-D (see text for explanations of arrows): Fig. 3. *Ommastrephes bartramii*; Fig. 4. *Sthenoteuthis pteropus*; Fig. 5. *S. oualaniensis*; Fig. 6. *Dosidicus gigas*; Fig. 7. *Eucleoteuthis luminosa*; Fig. 8. *Ornithoteuthis antillarum*; Fig. 9. *Hyaloteuthis pelagica*.



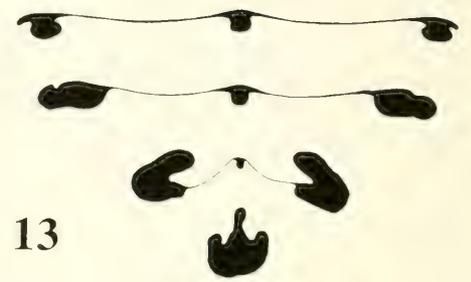
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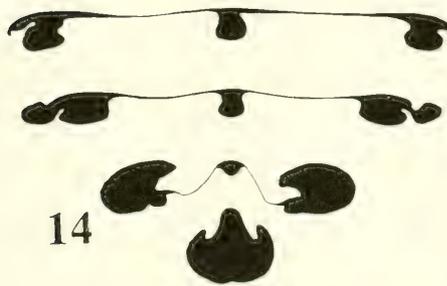
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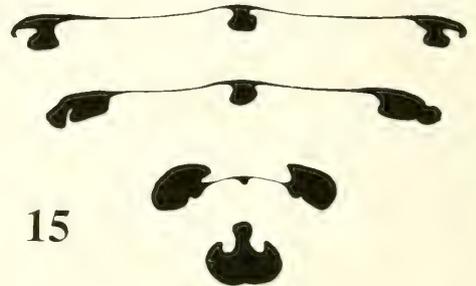
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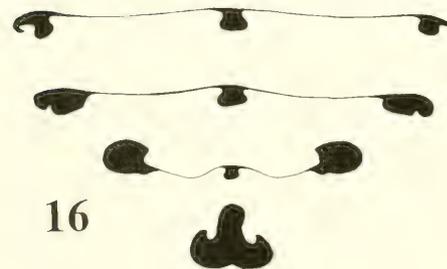
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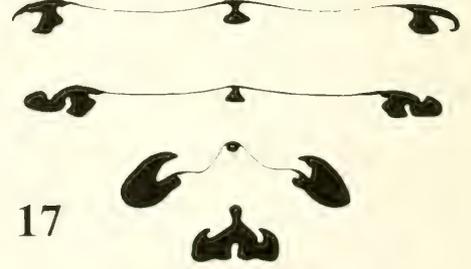
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FIGS. 10-17. Stylized composite cross sections of gladius levels A-D (see text for explanations of arrows): Fig. 10. *Illex coindetti*; Fig. 11. *I. oxygonius*; Fig. 12. *Todaropsis eblanae*; Fig. 13. *Todarodes sagittatus*; Fig. 14. *T. pacificus*; Fig. 15. *Nototodarus sloani*; Fig. 16. *N. hawaiiensis*; Fig. 17. *Martialia hyadesi*.

265—134 mm, GL = 256-132 mm, DISC 425E, Atex Drift, 12°45'N, 40°38'W, dip net with night light, 10-11 Feb. 1969, UMML. — 1F, ML = 211 mm, GL = 207 mm, DISC 425E, Atex Drift, 13°43'N, 38°58'W, dip net with night light, 6-7 Feb. 1969, UMML.

Description.—Cross sections (Fig. 4):

Level A—The medial axis is subellipsoid and wider than deep. The medial commissure is only slightly constricted. The lateral plates are broad, thin, and distally tapered to narrow points and ventrally recurved. The two paired lateral axes are spindly. The distal one is bifid. The proximal lateral axis is digitiform, curved medially and swollen apically in some specimens. The lateral commissures are constricted; **Level B**—The medial complex is similar in shape and slightly smaller than that of level A. The proximal lateral axis is broader than that of level A. The distal lateral axis is subquadrangular, wider than deep, broadly joined to the lateral plate, and slightly incised ventrally in some specimens. The accessory process is most commonly "U"-shaped, concave dorsally, but is lobate in one specimen; **Level C**—The medial complex is spindle-shaped. The lateral complexes are hook-shaped. The deep, medially facing subtriangular to sickle-shaped admedial cleft is about two-thirds to three-quarters of the width of the complex. There is a small ventromedial process; **Level D**—The body is subtriangular, broadest ventrally, with a pair of subquadrangular to lobate, ventral keels and a pair of dorsally curved lateral processes that taper to acute points. The dorsal carina is inflated apically.

Sthenoteuthis oualaniensis (Lesson, 1830)

Material examined.—1F, ML = 317 mm, GL = 341 mm, IIOE Cr. 4B, 273B, 20°50'N, 59°10'E, 4 Dec. 1963, night light and handline, UMML 31.1812. —1F, ML = 170 mm, GL = 178 mm, 10°N, 92°30'E, night light and dipnet, Nov.-Dec. 1961, USNM 656967. —1F, ML = 138 mm, GL = 143 mm, Moorea Island, Society Islands, 15 Apr. 1937, ANSP A6364. —1M, ML = 123 mm, GL = 128 mm, Moorea Island, Society Islands, 15 Apr. 1937, ANSP A6357. —1F, ML = 115 mm, GL = 121 mm, Moorea Island, Society Islands, 15 Apr. 1937, ANSP A6347. —1sex?, ML = 42 mm, GL = 45 mm, SHOYO MARU Sta. 12, 23°25.5'S, 104°36.8'W, 21 Jan. 1963, in stomach of *Alepisaurus*, UMML 31.1360.

Description.—Cross sections (Fig. 5):

Level A—The medial axis is ellipsoid, wider than deep, and attached to the medial plate by a commissure that is about one-half to two-thirds of the axis width. The lateral plates are broad, thin, tapered distally to a narrow point and ventrally recurved. There are paired lateral axes. The proximal lateral axis is digitiform and slightly curved medially. The distal one is narrow, deep, and slightly constricted basally. In two specimens, the proximal lateral axes are absent. In another specimen, the distal lateral axes are slightly bifurcated ventrally. There is a small, domelike protuberance on the ventral surface of the lateral plates distal to the distal lateral axis (arrow); **Level B**—The medial axis is similar in shape and size to that in level A but is more broadly attached to the medial plate. The lateral plate and distal lateral axis are fused into a single, quadrangular axis. A digitiform proximal axis is present in those specimens with a proximal lateral axis in level A. The lateral process is bulbous and connected to the distal surface of the lateral complex by a stalklike commissure (arrow); **Level C**—The medial complex is fusiform. The lateral complexes are hook-shaped. The deep, broadly excavated admedial cleft is subtriangular to irregularly polygonal and equal in depth to about one-half of the width of the complex. A small, ventromedial process is present; **Level D**—The body is roughly triangular, broadest ventrally, with a pair of stout, angular, ventral keels and a single dorsal carina that is slightly expanded apically. The stout lateral processes are dorsally curved and taper to rounded tips.

Remarks.—The absence of proximal lateral axes in two specimens is peculiar in comparison with the levels of intra-specific variability exhibited in all other taxa examined. I suspect that the difference is the result of prevailing systematic problems that could have confused proper species-level identification.

Genus *Dosidicus* Steenstrup, 1857
Dosidicus gigas (d'Orbigny, 1835)

Material examined.—1 sex?, ML = 360 mm, GL = 412 mm, Chinchua Norte, Peru, 16 Oct. 1941, MCZ 293699. —1M, 1F, ML = 349—298 mm, GL = 315—299 mm, R/V ALASKA Cr. 74A6, Sta. 59, "coastal waters" off La Jolla, California, USNM 729467. —2F, ML = 224—174 mm, GL = 254-204 mm, IATTC (28), off Manta, Ecuador, Apr. 1962, UMML 31.1769.

Description.—Cross sections (Fig. 6):

Level A—The ellipsoid medial axis is relatively shallow and narrow, wider than deep and attached to its plate by a commissure that is about one-half of the axis width. The lateral plates are relatively thick, distally attenuate and strongly ventrally recurved. There are paired lateral axes. The proximal lateral axis is digitiform. The distal lateral axis is subellipsoid to subtriangular, wider than deep, and attached to the lateral plate by a constricted commissure that is about one-half of the width of the axis; **Level B**—The medial complex is similar in shape and slightly smaller than that of level A. Both lateral axes are broadly fused dorsally to the lateral plate. The lobate accessory process is joined by a narrow, stalk-like commissure; **Level C**—The medial complex is fusiform. The lateral complexes are a deeply excavated C-shape. The ventromedial process is small; **Level D**—The body is subtriangular, broadest ventrally, with a pair of stout, quadrangular, ventral keels. There is a tall, medially constricted, dorsal carina. The dorsally curved lateral processes are relatively long and taper to rounded tips.

Genus *Eucleoteuthis* Berry, 1916

Eucleoteuthis luminosa (Sasaki, 1915)

Material examined.—1F, ML = 177 mm, GL = 170 mm, WH-455-II-71, 13°12'S, 8°58'W, 6 Apr. 1971, USNM 730198. —1M, ML = 151 mm, GL = 155 mm, ANTON BRUUN Cr. 17, 29°22'S, 79°57'W, dip net with night light, July 1966, MCZ 278110. —1sex?, ML = 98 mm, GL = 99 mm, SHOYO MARU Sta. 16, 16°25.0'S, 96°58.3'W, 13 Jan. 1963, in stomach of *Alepisaurus*, UMML 31.1558. —4sex?, ML = 96-89 mm, GL = 101-89 mm, SHOYO MARU Sta. 16, 16°25.0'S, 96°58.3'W, 13 Jan. 1963, in stomach of *Thunnus obesus*, UMML 31.1557.

Description.—Cross sections (Fig. 7): **Level A**—The medial axis is ovoid to subellipsoid, wider than deep, and is broadly attached to the medial plate. The lateral plates are broad, distally tapered to a narrow rounded tip and ventrally recurved. The single lateral axis is subovoid, wider than deep, and broadly attached to the plate; **Level B**—The medial complex is similar in shape and about one-half to one-third of the size of that in level A. The lateral axis and plate are broadly fused. The lobate accessory process is separated from the plate by an offset pair of proximal, ventral and distal, dorsal sulci (arrows); **Level C**—The medial

complex is subcylindrical and minute. The lateral complexes are bullet-shaped to lobate, rounded laterally with a pair of small, ventro- and dorsomedial processes (arrows). An ad-medial cleft is absent; **Level D**—The body is subcylindrical with a shallow, ventral sulcus (arrow) between a pair of low, dome-like ventral keels. The lobate, slightly dorsally curved lateral processes are broadly attached to the body. The short, relatively broad, dorsal carina is slightly inflated apically.

Genus *Ornithoteuthis* Okada, 1927

Ornithoteuthis antillarum Adam, 1957

Material examined.—1M, ML = 179 mm, GL = 175 mm, ORE II Cr. 43, Sta. 123, 12°54'N, 70°31'W, 0-732m, 24 Feb. 1973, trawl, UMML 31.1726. —4F, ML = 164-123 mm, GL = 147-125 mm, ORE 3250, 29°14'N, 87°40'W, 0-732 m, 60' MWT, 26 Apr. 1961, UMML 31.397. —1M, 1F, ML = 157-129 mm, GL = 147-116 mm, ORE 3670, 20°00.5'N, 88°22'W, 732 m, 40' flat trawl, 30 July 1962, UMML 31.438. —1M ML = 155 mm, GL = 133 mm, ORE 2944, 27°40'N, 90°50'W, 60' MWT, 183-229 m, 24 Aug. 1960, UMML 31.253. —1M, 1F, ML = 153-126 mm, GL = 136-115 mm, ORE 3254, 29°00'N, 88°02'W, 247 m, 60' MWT, 27 Apr. 1961, UMML 31.476. —2F, ML = 149-104 mm, GL = 129-91 mm, ORE 5449, 19°55'N, 68°57'W, night light, 1 June 1971, UMML 31.1618. —1M, ML = 101 mm, GL = 95 mm, CI-264, 23°53.4'N, 77°08.9'W to 23°54.7'N, 77°11.7'W, 1301-1329 m, 41' Standard Blake Trawl, 3 Nov. 1974, UMML 31.1670. —1M, ML = 75 mm, GL = 70 mm, ORE 1959, 26°55'N, 89°10'W, 2269 m, 23 Sept. 1957, UMML 31.213.

Description.—Cross sections (Fig. 8):

Level A—The medial axis is massive, subcylindrical, broader than deep, and broadly attached to the medial plate. The lateral plates are thick, slightly recurved ventrally and broadly rounded laterally. The single lateral axis is massive, ovoid, broader than deep, with a broad commissure; **Level B**—The medial complex is similar in shape and about one-third smaller than that of level A. The lateral complexes are massive, subovoid, with a broad, shallow, ventrolateral sulcus; **Level C**—The lateral fields are narrow, thick, and extend from the ventrolateral borders of the massive subovoid medial complex. The lateral complexes are subovoid and slightly concave laterally. An admedial cleft is absent;

Level D—The body is rectangular, wider than deep, with shallow, broad, ventral and lateral sulci (arrow). The carina is relatively tall and broadly inflated dorsally.

Remarks.—The narrow, thick lateral fields reflect the greater tapering of the posterior portion of the free rachis in this species as compared to all other ommastrephids.

Genus *Hyalotuthis* Gray, 1849
Hyaloteuthis pelagica (Bosc, 1802)

Material examined.—3M, 1F, ML = 73—50 mm, GL = 79 - 56mm, DEL II, Acre 12-81-N, 32°09'N, 64°07'W, 0-150 m, 1400 mesh ET, 24 Aug. 1971, USNM 728882. —1M, 2F, ML = 72—68 mm, GL = 76—75 mm, DEL II, Acre 12-79-N, 32°08'N, 64°09'W, 0-450 m, 1400 mesh ET, 23 Aug. 1971, USNM 728881. —1F, ML = 64 mm, GL = 71 mm, SHOYO MARU Cr. 12, Fish Sta. 20, 23°25.5'S, 104°36.8'W, 21 Jan. 1963, in stomach of *Alepisaurus*, UMML 31.1561. —2F, ML = 61—57 mm, GL = 65—63mm, SHOYO MARU Cr. 17, Fish Sta. 19, 19°37.7'W, 108°27.7'W, 19 Jan. 1963, in stomach of *Alepisaurus*, UMML 31.1560.

Description.—Cross sections (Fig. 9):

Level A—The medial axis is small, subovoid to subcylindrical and broadly attached to the narrow medial plate. The lateral plates are ventrally recurved distally and taper to rounded points. The single lateral axis is large, three to four times as wide as the medial axis, subovoid, broader than deep, and broadly attached to the plates; **Level B**—The medial axis is broadly joined to the medial plate. The lateral complexes are unequally bilobed with a dorsal and ventral pair of opposing, shallow, broad sulci (arrows); **Level C**—The medial axis is minute and subcylindrical. The medial plate is highly reduced. The lateral complexes are subovoid with a "U"-shaped admedial cleft equal in depth to about one-quarter of the complex width. The ventromedial process is small and dome-like; **Level D**—The body is broadly contiguous with the lobate, slightly dorsally curved lateral processes. The ventral sulcus is broad and shallow. The carina is slightly inflated apically.

Subfamily Illicinae Posselt, 1890
Genus *Illex* Steenstrup, 1880
Illex coindetti (Verany, 1837)

Material examined.—1F, ML = 189 mm, GL = 222 mm, Cette, France, June 1861,

MCZ 2304. —2M, 2F, ML = 185—122 mm, GL = 180—128 mm, P-82, 4°57'N, 9°30'W to 4°58'N, 9°32'W, 144m, 5 June 1964, UMML 31.1335. —1F, ML = 171 mm, GL = 178 mm, Naples, Italy, ANSP A8008.

Description.—Cross sections (Fig. 10):

Level A—The medial axis is subellipsoid, wider than deep, with a narrow commissure. The lateral plates are broad and thick, ventrally recurved distally, and tapered to rounded tips. There are paired lateral axes. The proximal one is subtriangular and rounded apically. The distal lateral axis is subovoid, wider than broad, and attached to the plate via a slightly constricted commissure; **Level B**—The medial complex is similar in shape and slightly smaller than that in level A. The lateral complexes are broad, irregularly lobate with two, shallow, ventral sulci (arrows); **Level C**—The medial axis is subcylindrical and broadly fused to the reduced plate. The lateral complexes are large and subovoid and with a weakly scalloped ventral outline. The ventromedial process and admedial cleft are highly reduced to absent; **Level D**—The body and weakly dorsally curved lateral processes are broadly contiguous and collectively bilobed with a shallow ventral sulcus. The dorsal carina is inflated apically.

Illex oxygonius Roper, Lu, & Mangold, 1969

Material examined.—1M, 1F, ML = 205—184 mm, GL = 209-193mm, ORE 5784, 24°28'N, 83°39'W, 567m, UMML 31.899. —2F, 1M, ML = 148—108 mm, GL = 162—118 mm, TRITON, south of Palm Beach Inlet, Florida, 165 m, 26 May 1953, ANSP A8079.

Description.—Cross sections (Fig. 11):

Level A—The medial axis is ovoid to ellipsoid, twice as wide than deep, and broadly attached to the medial plate. The lateral plates are thick, ventrally curved distally and taper to broadly rounded tips. There are paired lateral axes. The proximal lateral axis is broad, low and apically rounded. The distal lateral axis is irregularly lobate to subrectangular with rounded edges and broadly joined to the lateral plate; **Level B**—The medial complex is similar in shape and one-third to one-half the size of that of level A. The lateral complexes are large, laterally rounded, with two or three ventral sulci; **Level C**—The medial complex is similar in shape and about one-third smaller than that of level B. The lateral complexes are massive and subovoid. The ventromedial pro-

cess is dome-like. The admedial cleft is highly reduced to absent; **Level D**—The body and weakly dorsally curved lateral processes are broadly contiguous and collectively bilobed with a shallow ventral sulcus. The dorsal carina is inflated apically.

Genus *Todaropsis* Girard, 1890
Todaropsis eblanae (Ball, 1841)

Material examined.—1M, 1F, ML = 131—114 mm, GL = 133—120 mm, Atlantique Sud Sta. 154. 0°15'S, 8°47'E, 239 m, 15 Mar. 1949, UMML 31.1351. —2M, 1F, ML = 89—78 mm, GL = 90—76 mm, Geronimo Sta. 2-236. 4°03'S, 10°22'E, 0-201 m, bottom trawl, 8 Sept. 1963, USNM 730204. —2M, 3F, ML = 68—46 mm, GL = 70—46 mm, P-254, 3°50'N, 7°08'E to 3°51'N, 7°12'E, 172-148 m, 14 May 1965, 40' OT, USNM 727408.

Description.—Cross sections (Fig. 12): **Level A**—The medial axis is massive, subellipsoid and twice as wide than deep. The medial commissure is about one-third as wide as its axis. The lateral plates are relatively narrow, ventrally recurved distally and taper to a narrow rounded tip. The single lateral axis is subovoid to subellipsoid, wider than deep, about one-half as wide as the medial axis, and broadly joined to the lateral plate; **Level B**—The medial complex is similar in shape and size to that in level A. The lateral complexes are irregularly lobate and subequal in width to the medial complex; **Level C**—The medial complex is large and fusiform. The lateral complexes are irregular with a shallow, admedial cleft and small ventromedial process; **Level D**—The body and lateral processes are relatively small and collectively subrectangular. The dorsal carina is stout and slightly inflated dorsally and forms a right angle with respect to the body to give an overall appearance of a “⊥” shape.

Subfamily *Todarodinae* Adam, 1960
Genus *Todarodes* Steenstrup, 1880
Todarodes sagittatus (Lamarck, 1799)

Material examined.—1M, ML = 186 mm, GL = 178 mm, R/V TRIDENT, 36°55'N, 01°04'W, 143—150 m, 10'IKMT, 21-22 Aug. 1970. USNM 727741.

Description.—Cross sections (Fig. 13): **Level A**—The medial axis is subovoid, wider than deep and broadly attached to the medial plate. The lateral plates are relatively thin, slightly curved ventrally and taper to rounded

tips. The single lateral axis is relatively small, subovoid and wider than deep; **Level B**—The medial complex is similar in shape and slightly smaller than that in level A. The lateral complexes are roughly bilobed with slightly offset dorsal, distal and proximal, ventral sulci; **Level C**—The medial complex is similar in shape and about one-half of the size of that of level B. The lateral complexes are hook-shaped. The admedial cleft is roughly “V”-shaped with a depth of about one-third of the complex width. The ventromedial process is small and dome-like, occasionally reduced; **Level D**—The body is broadly attached to the large, dorsally curved lateral processes and has a small ventral sulcus. The lateral processes terminate in rounded lobes. The carina is tall, relatively narrow, and inflated apically.

Todarodes pacificus Steenstrup, 1880

Material examined.—2F, ML = 302—287 mm, GL = 301—292 mm, 40°16'N, 133°14.5'E, night angling, 7 Sept. 1967, USNM 730206.

Description.—Cross sections (Fig. 14): **Level A**—The medial axis is irregularly ovoid, slightly wider than deep, and broadly attached to its plate. The lateral plates are thick, ventrally curved and digitiform distally. The single lateral axis is ovoid to subovoid and wider than deep. The lateral commissure is about two-thirds of the width of the axis; **Level B**—The medial complex is similar in shape and slightly smaller than that in level A. The lateral axis is subellipsoid, broader than deep. The relatively large accessory process is separated from the lateral plate by an offset pair of narrow, deep, proximal ventral, and relatively broad, shallow, distal dorsal sulci. In some specimens the accessory process is pedunculate; **Level C**—The medial complex is subfusiform. The lateral complexes are large and hook-shaped with an angular, admedial cleft equal in depth to about one-quarter of the complex width. The ventromedial process is small and dome-like; **Level D**—The body is broadly attached to the large, dorsally curved lobate, lateral processes. The carina is subtrapezoidal, broad basally and tapers apically to a broadly rounded tip.

Genus *Nototodarus* Pfeffer, 1912
Nototodarus sloanii (Gray, 1849)

Material examined.—1F, ML = 194 mm, GL = 214 mm, Tasmania, Jan. 1875, USNM 576996. —2M, ML = 170—160 mm, GL =

183—~172 mm, Auckland, New Zealand, Jan. 1953, USNM 575461.

Description.—Cross sections (Fig. 15):

Level A—The medial axis is subovoid and broader than deep. The medial commissure is about one-half as wide as the axis. The lateral plates are relatively thick, ventrally recurved and bluntly pointed laterally. The single lateral axis is subovoid, wider than deep; **Level B**—The medial axis is ovoid, subequal in width to that of level A. The commissure is only slightly constricted. The lateral axis and plate, and in some specimens the accessory process, are broadly fused into a broad, roughly bilobed lateral complex with a pair of opposing shallow, broad, dorsal and ventral sulci. In some specimens the accessory process is irregularly lobate and more distinctly set off from the plate by a deep, narrow, ventral sulcus; **Level C**—The medial complex is small and subfusiform. The lateral fields are narrow. The lateral complexes are subovoid with a small admedial cleft equal in depth to about one-fifth of the complex width. The ventromedial process is small and dome-like; **Level D**—The body is broadly fused to the large, lobate, dorsally curved lateral processes. The ventral sulcus is shallow and broad. The carina is inflated apically.

Remarks.—In a single specimen (USNM 576996), the cross sections at levels B and D were grossly asymmetrical and anomalous. The cause of this condition is unknown. The animal was normal in all other respects and was apparently unaffected by this condition.

Nototodarus hawaiiensis (Berry, 1912)

Material examined.—1F, ML = 104 mm, GL = 122 mm, TC-36, Sta. 24, 21°09.7'N, 157°29.3'W to 21°09.8'N, 157°24.6'W, 183 m, 4-5 May 1968, USNM 730203. —2F, ML = 114—93 mm, GL = 114—99 mm, TC-35, Sta. 15, 21°05'N, 156°26'W to 21°05'N, 156°32'W, 361 m, 1 Apr. 1968, USNM 730201. —1M, ML = 88 mm, GL = 92 mm, TC-32, Sta. 2, 21°21.9'N, 158°12.4'W, 65-110 m, 12 July 1967, USNM 730202.

Description.—Cross sections (Fig. 16):

Level A—The medial axis is subellipsoid, wider than deep, and broadly attached to the medial plate. The lateral plates are ventrally recurved distally and end in narrow blunted tips. The single lateral axis is small, subovoid, wider than deep, and broadly attached to the plate; **Level B**—The medial complex is simi-

lar in shape and size to that of level A. The lateral axis is subrectangular, wider than deep. The accessory process is lobate to subspherical and separated from the lateral axis and plate by a single narrow, "V"-shaped ventral sulcus; **Level C**—The medial complex is similar in shape and about one-half of the size of that of level B. The lateral complexes are ovoid to lobate. The admedial cleft is small and rounded. The medial process is small and dome-like; **Level D**—The body is small. The lateral processes are relatively small, dorsally curved and bluntly rounded apically. The ventral sulcus is shallow and broad. The dorsal carina is rectangular, stout, and slightly inflated apically.

Genus *Martialia* Rochebrune & Mabile, 1889
Martialia hyadesi Rochebrune & Mabile, 1889

Material examined.—3M, 3F, ML = 338—286 mm, GL = 340-288 mm, ELT Cr. 23, Sta. 8c, 59°29'S, 102°30'W, rod and reel, 18-19 Apr. 1966, UMMML 31.1768.

Description.—Cross sections (Fig. 17):

Level A—The medial axis is subellipsoid, two to three times wider than deep. The medial plate is reduced. The medial commissure is narrow, about one-third the width of the medial axis. The lateral plates are ventrally recurved distally and taper to blunt points. The single lateral axis is subovoid to irregular. The lateral commissure is narrow, about one-half the width of the axis; **Level B**—The medial axis is small, subtriangular, and wider than deep. The medial plate is reduced. The lateral axis is polygonal to irregular. The lateral commissure is constricted, about one-half the width of the axis. The irregularly lobate lateral process is separated from the lateral plate by a pair of deep, offset proximal, ventral and dorsal, distal sulci; **Level C**—The medial complex is subfusiform. The lateral complexes are subovoid with a "V"-shaped admedial cleft that is equal in width to about one-third to one-quarter of the complex width. The ventromedial process is small; **Level D**—The body is subtriangular, broader than deep, with a narrow, deep, ventromedial sulcus. The dorsally upswept lateral processes are moderately angular and taper to rounded tips. The dorsal carina is narrow and inflated apically.

GENERAL DISCUSSION

The overall shape of the ommastrephid gladius is strikingly conservative as compared to

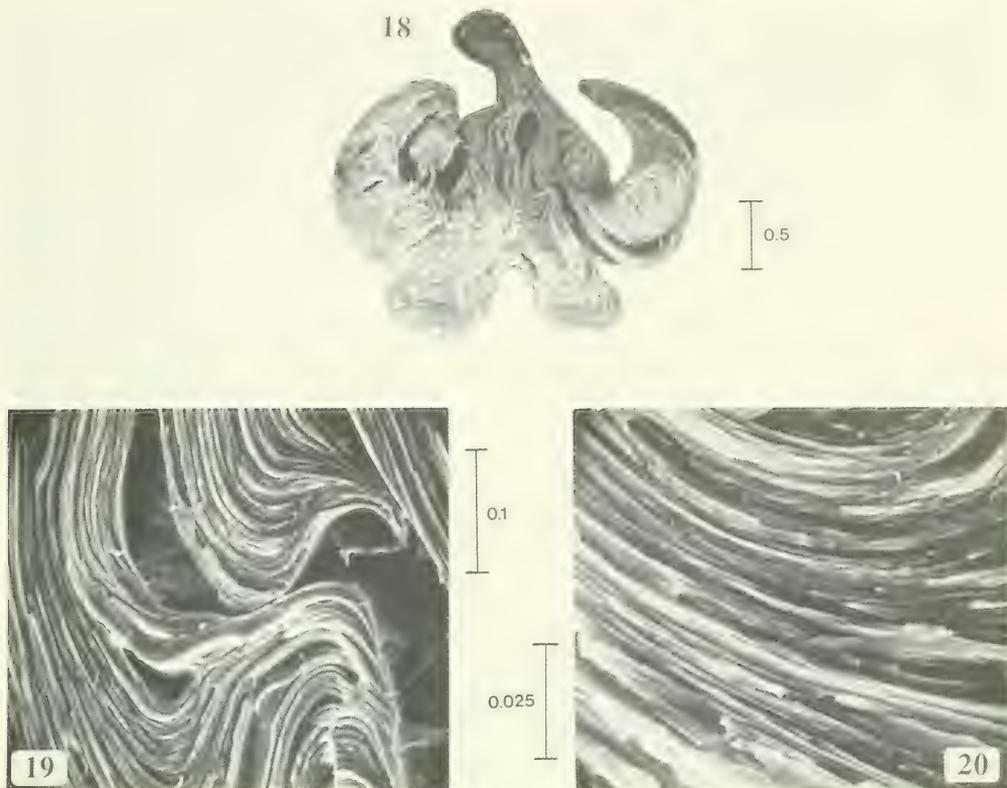
all other speciose, and many of the less speciose, teuthoid families, which show a greater range of intrafamilial variation (Toll, 1982). Therefore, the degree of variability in the structure of the gladius, as evidenced by cross sectional morphology, is surprising, even in light of earlier reports that provided some information on cross sections. Sample sizes of the 15 species treated here ranged from one to 14 specimens. Moreover, the collection of specimens from several taxa were heterogeneous with respect to geographical distribution, sex, and to a limited extent, size. As a result, intraspecific variability cannot be rigorously assessed here. However, several preliminary statements can be made at this time. The major diagnostic features associated with each taxon do not vary within that taxon. These include the single vs. double (i.e. proximal and distal) lateral axes along the anterior region of the free rachis (level A) (with the exception of two specimens of *Sthenoteuthis oualaniensis*, see Remarks, that taxon), accessory processes along this same region, hook-shaped vs. lobate lateral complexes along the posterior portion of the free rachis (level C), presence or absence of keels and carina and the basic shape of the axial axis at the posterior terminus of the free rachis (level D), relative sizes of the medial and lateral axes, and degree of posterior tapering of the medial axis. Intra-specific variability was recognized in terms of the precise shape of free rachis axes, and depth and distinctiveness of sulci dividing free rachis axes and separating the accessory processes from the lateral plates. Out of a total 89 ommastrephid gladii, one (1.1%) showed gross structural anomalies (see *Nototodaros sloanii*).

Relationships among species and genera of ommastrephids are immediately apparent based on the cross sectional shape of their gladii. *Ommastrephes bartramii*, *Sthenoteuthis pteropus*, *S. oualaniensis*, and *Dosidicus gigas* form a distinct clade sharing a digitiform to vermiform proximal lateral axis at level A (with the exception of the two variant specimens of *S. oualaniensis*) and paired, quadrangular keels at level D. *Eucleoteuthis luminosa* and *Hyaloteuthis pelagica* form a second clade sharing a small medial axis at level A that tapers to become minute at level D. The remaining ommastrephine, *Ornithoteuthis antillarum*, is unique in the relative and absolute sizes of the medial and lateral axes at levels A through C and the rectangular body at level D. In support of their congeneric

placement, *Illex coindetti* and *I. oxygonius* form a clade sharing a broadly rounded distal terminus of the lateral plate at level A, general shape of the lateral axes and relative sizes of the medial and lateral axes at levels B and C, and overall shape at level D. *Todaropsis eblanae* is distinct from *Illex* based on many characters, the most salient being the relative sizes of the medial and lateral axes at levels A through C and the overall shape of level D. Clear relationships among the Todarodinae are more difficult to establish based on characters of the gladius alone. *Martialia* is unique in the degree of constriction of the medial commissure at levels A and B and the deep ventral sulcus at level D. The two species of *Todarodes* and the two species of *Nototodaros* studied here show no more similarity between congeners than between noncongeners. Therefore, based on these characters, these two genera appear to be closely related.

Some of these groupings are congruent with some of the findings of Zuev et al. (1975), Wormuth (1976) and Roeleveld (1988), all based on a suite of traditional soft tissue characters. In particular, Wormuth's groups A (*Symplectoteuthis* [= *Sthenoteuthis*] *oualaniensis*, *Dosidicus*, and *Ommastrephes*) and B (*Symplectoteuthis* [= *Sthenoteuthis*] *luminosa* and *Hyaloteuthis*), which are equivalent to Roeleveld's (1988: fig. 1) clades based on nodes E and G, respectively, are well supported by the present findings; Wormuth's group C (*Ornithoteuthis volatilis*, *Illex illecebrosus*, and *Todarodes pacificus*) is not. The relatively isolated position of *Ornithoteuthis* within the Ommastrephinae as indicated by Roeleveld's (1988) node D is corroborated by the present study. Her findings on the interrelationships of the genera within the Todarodinae and Illicinae are supported in part, insofar as her figure 1 shows an unresolved tricotomy including all three subfamilies at node A. (However, in the text (p. 287) she indicates that the Illicinae are separable on the basis of several characters, in particular the condition of eight sucker rows on the dactylus of the tentacular club.) Based on characters of the gladius alone, there is no support for the current subfamilial classification within the Ommastrephidae.

Cross sections of ommastrephid gladii clearly show laminae indicative of accretive growth. This can be seen easily with either light or scanning electron microscopy. The particular distinctiveness of this layering in the



FIGS. 18-20. *Sthenoteuthis pteropus*, scanning electron micrograph of gladius level D. Fig. 18 whole view; Fig. 19. Enlargement of Fig. 18 in body area near basal portion of ventral keel; Fig. 20. Enlargement of Fig. 19 to show changes in radius of arc of depositional layers during ontogeny.

Ommastrephidae, as compared to most teuthoid gladii wherein laminations are more difficult to resolve, allows easy observation of the change in the shape of cross sections during ontogeny. For example, the strong quadrangular keels at level D of the gladius of *Sthenoteuthis pteropus* begin as small, rounded, dome-like protuberances (Figs. 18-20). Also, examination of the whole cross section immediately suggests longitudinal structural continuity between the hook-shaped lateral complexes at level C and the lateral processes at level D. The same conclusion applies to the medial axis of levels A through C, which forms the nucleus of the dorsal carina at level D. Future examination of layering patterns could provide valuable evidence relating to ontogenetic precedence of cross sectional shape that could in turn be used to establish evolutionary polarity of these character states for incorporation in phylogenetic analyses.

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COMPARISON OF RECENT CLASSIFICATIONS OF STYLOMMATOPHORAN LAND-SNAIL FAMILIES, AND EVALUATION OF LARGE-RIBOSOMAL-RNA SEQUENCING FOR THEIR PHYLOGENETICS

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ABSTRACT

Morphological approaches to the phylogenetic relationships among stylommatophoran families have not reached a consensus. We compare in tabular form the recent classifications of Solem, Boss, Schileyko, Nordsieck, and Tillier, and find that they differ up to 52%, 79% and 74% at the ordinal, subordinal, and superfamilial levels.

To explore the utility of molecular sequence data for resolving stylommatophoran phylogeny, we sequenced regions of large ribosomal RNAs (LrRNAs) of 10 species, exemplars of Archaeogastropoda, Mesogastropoda, Basommatophora, Holopodopes, Aulacopoda, and Holopoda. One divergent domain, D6, its conserved flanking regions, and the highly conserved 5' end of LrRNA were sequenced by a rapid and versatile primer-directed method.

Sequencing a total of 177 nucleotide sites yielded 61 variable positions. Four polygyrids (two polygyrines and two triodopsines) had identical sequences, and two zonitids differed at a single position. Three different phylogenetic analyses (maximum parsimony, and UPGMA on simple and K_{nuc} distance matrices) resulted in the same topology: (*Helicina* (*Oncomelania* (*Bi-omphalaria* (*Neohelix-Triodopsis-Mesodon* (*Haplotrema* (*Ventridens-Mesomphix*)))))), except that the phenograms did not resolve the final three taxa. Standard errors for K_{nuc} values indicated no significant resolution of the four stylommatophoran families, however.

Among the three stylommatophoran families (Polygyridae, Haplotrematidae, and Zonitidae), only 1% of nucleotide positions were variable in the 5'-terminal and the D6-flanking regions, but fully 13% of nucleotide positions were variable within the D6 divergent domain. Our results demonstrate the potential usefulness of this approach, and we predict that divergent domains of the LrRNA molecule will be of some value in resolving stylommatophoran phylogeny.

Key words: land snail families, phylogenetics, RNA, nucleotide sequences, Stylommatophora, Archaeogastropoda, Mesogastropoda, Basommatophora.

INTRODUCTION

There are probably more species of land snails (estimated 30,000–35,000) than of land birds, mammals, reptiles and amphibians combined (Solem, 1984). The vast majority of land snails are stylommatophoran pulmonates, of which there are 71 to 92 families, according to recent classifications. Stylommatophorans are ancient; fossils date from the mid Paleozoic, and most seem assignable to Recent families, implying that radiation into higher taxa occurred soon after invasion of land (Solem & Yochelson, 1979). Large land snails and some small ones are relatively poor dispersers. This combination of ancient origin, slow evolution at higher taxonomic levels, and often low vagility makes

pulmonate land snails superb biological indicators of early tectonic and geomorphological events (Peake, 1978; Solem, 1979a, 1979b, 1981; Nordsieck, 1986).

The biogeographic value of pulmonate land snails has been severely limited, however, by the lack of a robust phylogenetic inference for their families. Thus there are major discrepancies among the five suprafamilial classifications of pulmonate land snails that have been published within the past 12 years. These classifications differ in the data used, the methodology employed, or both. Solem (1978) presented a slightly modified version of the traditional Pilsbry-Baker scheme, based primarily on excretory, locomotory, and genitalic gross anatomy, using an evolutionary approach, presenting no formal phylog-

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eny but a hierarchically arrayed classification. Boss (1982) gave an apparently strictly phenetic classification. Sharply departing from these was Schileyko's basically evolutionary approach (1979; edited and translated into English by Boss & Jacobson, 1985) based primarily on shell and reproductive morphology. The first overtly cladistic approach was by Nordsieck (1985, 1986), who reintegrated and reinterpreted the widely scattered literature primarily on reproductive and excretory characters and secondarily on shell features. The most recent and most thorough effort to date was Tillier's (1989) presentation of major new data sets on the digestive, nervous, and excretory systems, which he subjected to a kind of cladistic analysis. In sum, the systematics methods have ranged from evolutionary to phenetic to cladistic; and the data bases have ranged from primary emphasis on, to no emphasis on, reproductive morphology, all incorporating only subsets of available anatomical data. No molecular data yet exist for family comparisons.

The efficacy of large ribosomal RNA sequencing for resolving evolutionary relationships among taxa has been well demonstrated (e.g., Qu et al., 1989; Guadet et al., 1989; Larson & Wilson, 1989; Lenaers et al., 1989). This molecule consists of rapidly evolving segments (divergent domains) interspersed among extraordinarily conserved segments. These conserved regions yield phylogenetic information at several higher taxonomic levels, and can also be used to target and to establish the homologies of divergent domains. The taxonomic level at which divergent domains are useful as sources of phylogenetic information differs widely among organisms: for example, at the family level in salamanders (Larson & Wilson, 1989), but at the species level in both the fungus *Fusarium* (Guadet et al., 1989) and the prosobranch gastropod *Truncatella* (Rosenberg & Kuncio, in preparation). Among the logistic advantages of the LrRNA molecule for land-pulmonate studies are its presence in high concentrations in all tissues (allowing small samples to be used), and the rapidity with which it can be extracted and sequenced under various states of preservation (allowing efficient accumulation of data).

The purposes of this paper are (1) to assess quantitatively the levels of discrepancy among the family-level stylommatophoran classifications of Solem, Boss, Schileyko, Nordsieck, and Tillier; and (2) to evaluate the

applicability to stylommatophoran family-level phylogenetics of LrRNA sequencing.

MATERIALS AND METHODS

Distances Among Classifications

The five stylommatophoran classifications (Appendix) were compared at three taxonomic levels: superfamily, suborder, and order. At each level, the distance between each pair of classifications was calculated as the number of families differently classified, divided by the total number of families classified by both. Whenever the taxonomic names differed, names were equated in such a way as to maximize the similarities of their grouped families. Thus the following equations were used, with the authors' names abbreviated So for Solem, Sh for Schileyko, B for Boss, N for Nordsieck, and T for Tillier. At the ordinal level (called subordinal by B and T): Sh Geophila and Athoracophora = T Dolichonephra and Brachynephra; B Heterurethra = N Elasmognatha; B and So Sigmurethra and Mesurethra = T Dolichonephra and Brachynephra; Sh Geophila = So Sigmurethra; Sh Geophila and Succineida = B Sigmurethra and Heterurethra; Sh Geophila and Succineida = N Sigmurethra and Elasmognatha; and N Sigmurethra and Elasmognatha = T Dolichonephra and Brachynephra. At the subordinal level (called infraordinal by B): So Orthurethra, Holopodopes, and Aulacopoda = Sh Achatinina, Pupillina, and Helixina; So Holopodopes and Holopoda = N Achatinida and Helicida; Sh Pupillina, Achatinina, Helixina, and Succineida = B Orthurethra, Holopodopes, Aulacopoda, and Heterurethra = N Orthurethra, Achatinida, Helicida, and Elasmognatha; Sh Pupillina = T Orthurethra; and B Holopodopes, Holopoda, and Heterurethra = N Achatinida, Helicida, and Elasmognatha. At the superfamily level: Sh Vitrinoidea and Limacoidea = So Limacacea A and B; So Succinacea = B unnamed subfamilies of suborder Heterurethra; N Cochliocopoidea, Orthalicoidea, Helixarionioidea, and Mesodontoidea = So Cionellacea, Bulimulacea, Limacacea A, and Polygyracea; T Zonitoidea = So Limacacea B; Sh and B Succineidae were judged the same ranking for both, though unnamed by either; N Cochliocopoidea = Sh Cionelloidea; N Cochliocopoidea, Orthalicoidea, and Mesodontoidea = B Cionellacea, Bulimulacea, and Polygyra-

cea; and T Zonitoidea = B Limacacea. We emphasize that these are **not** taxonomic decisions, but simple expedients—often Procrustean—for calculating differences among the five classification schemes. Each of the three resulting distance matrices was analyzed by UPGMA clustering, using a hand calculator.

RNA Sequence Analysis

LrRNA sequences were obtained from 10 snail species representing the stylommatophoran suborders (according to Solem, 1978) Holopodops [one lot the haplotrematid *Haplotrema concavum* (Say) (ANSP A12650, KCE32, collected Madison County, Alabama, 5–7 May 1988 by K. C. Emberton)], Aulacopoda [one lot each of the zonitids *Ventridens cerinoideus* (Anthony) (KCE24, collected McIntosh County, Georgia, 15 April 1988 by K. C. Emberton) and *Mesomphix latior* (Pilsbry) (ANSP A12649, KCE32, collected Madison County, Alabama, 5–7 May 1988 by K. C. Emberton)], and Holopoda [one lot each of the triodopsine polygyrids *Neohelix* (= *Xolotrema* = *Triodopsis*) *albolabris* (Say) (ANSP 373132, collected Gilchrist County, Virginia, June 1987 by T. Asami) and *Triodopsis hopetonensis* (Shuttleworth) (= *T. fallax hopetonensis*) (ANSP 373135, collected Whitley County, Kentucky, 1 December 1987 by D. Stephens), and of the polygyrine polygyrids *Mesodon normalis* (Pilsbry) (ANSP 373133, collected Gilchrist County, Virginia, June 1987 by T. Asami) and *Mesodon inflectus* (Say) (ANSP 373134, collected Jessamine County, Kentucky, 30 November 1987 by D. Stephens)], as well as the outgroup taxa Archaeogastropoda [one lot of the helicimid *Helicina orbiculata* (Say) (ANSP A12648, KCE32, collected Madison County, Alabama, 5–7 May 1988 by K. C. Emberton)], Mesogastropoda [one lot of the pomatiopsid *Oncomelania hupensis* (Gredler) (ANSP 375731, collected Hanyang, Hubei, People's Republic of China, 25 November 1985 by G. M. Davis & Y. H. Guo)], and Basommatophora [one lot of the planorbid *Biomphalaria glabrata* (Say) (= *B. guadeloupensis*) (ANSP A12651, from aquarium culture, Department of Medicine, University of Pennsylvania)].

Specimens were prepared for RNA extraction in one of the following ways: (1) snails were killed and immediately stored by freez-

ing at -80°C . Feet and terminal genitalia were later dissected from semi-thawed snails, frozen directly in liquid nitrogen, and re-stored at -70°C until homogenized (*Neohelix albolabris*, *Mesodon normalis*); (2) feet and terminal genitalia were dissected from live snails and stored directly in liquid nitrogen until homogenized (*Biomphalaria glabrata*, *Mesodon inflectus*, some *Triodopsis hopetonensis*); (3) snails were killed and stored by freezing at -80°C , then homogenized whole, shell and all (*Oncomelania hupensis*, *Ventridens cerinoideus*, *Mesomphix latior*, *Haplotrema concavum*, *Anguispira alternata*); and (4) live, whole snails were homogenized, shell and all (some *Triodopsis hopetonensis*). RNA analysis was performed on both single snails and several specimens for most species.

Total RNA was extracted by a modification of the method of Auffray & Rougeon (1980). One to two grams of tissue were homogenized using a polytron (Brinkmann) in 6 M urea, 3 M LiCl. Debris was removed by low-speed centrifugation. The supernatant was stored overnight at 4°C . The formed RNA precipitate was collected by centrifugation. The RNA was then solubilized and exhaustively extracted with phenol-chloroform (1:1), chloroform, then ether. Following ethanol precipitation, the RNA was collected by high speed centrifugation and was resuspended in water to a concentration of approximately 1 mg/ml.

Sequencing of the LrRNAs was performed using methods modified from Qu et al. (1983) and Lane et al. (1985). Oligonucleotide primers were synthesized at the DNA Synthesis Facility of the University of Pennsylvania. The two primers used correspond to sequences that are extremely conserved in LrRNAs throughout all five kingdoms of life and are complements of the mouse sequence (Hassouna et al., 1984) as follows:

5'-terminus: nucleotides 52 through 66

D6 region: nucleotides 2099 through 2118

For sequencing purposes each primer was end-labelled with ^{32}P under standard conditions with T4 polynucleotide kinase and gamma-AT ^{32}P (Maniatis et al., 1982), annealed to total RNA, and elongated with AMV reverse transcriptase in the presence of deoxy- and dideoxy-nucleoside triphosphates at 50°C . Samples were electrophoresed, the gel dried and autoradiographed. Following film development, the sequences were read and entered into the computer using the IBI/Pustell DNA Sequence Analysis software. Initial alignment of sequences was performed

using this program; the results were then modified manually.

Multiple sequencing runs were made for each species. Replicate runs were used to resolve sequence ambiguities where possible. In some cases, the identification of an individual base could not be determined, and these bases were not used in phylogenetic analyses. We estimate the error rate for identification of the bases used in the analysis to be well under 1%.

Variable nucleotide positions among the aligned sequences were analyzed both cladistically and phenetically. Cladistic analysis employed the Wagner criterion of unrestricted parsimony (Kluge & Farris, 1968; Farris, 1970), with character states unordered. *Helicina orbiculata* was used as the outgroup for rooting the cladogram. For tree construction, we chose the branch-and-bound algorithm (Hendy & Penny, 1982), which assures maximum parsimony (Swofford, 1985). Trees were generated not only of minimum length n , but also of lengths $n+1$ and $n+2$. PAUP programs (Swofford, 1985), run on a personal computer, were used for all cladistic analyses.

For phenetic analysis of the sequence data, two separate UPGMA clusterings were performed from distinctly different distance matrices. The first distance measure used was the proportion of common nucleotide positions showing any kind of difference. This was calculated for each pair of taxa by counting the number of nucleotide differences between them, without correction for multiple changes at one given site, and then by dividing this count by the total number of comparable nucleotide positions for the pair. The second distance measure was Kimura's (1980) K_{nuc} index, which incorporates the possibility of transitions occurring more frequently than transversions. For this index, the proportion of different sites was partitioned into that due to transitions (i.e. purine to purine or pyrimidine to pyrimidine) versus that due to transversions (purine to pyrimidine and vice versa), deletions, and insertions. These proportions were used to calculate values of not only K_{nuc} but also its standard error, using formulae given in Kimura (1980).

The relative rates of nucleotide substitution in divergent domains and conserved regions of stylommatophorans were compared by calculating the percent variable positions in the D6 domain versus the 5' terminus plus the D6 flanker regions.

RESULTS

Distances Among Classifications

The five stylommatophoran classifications are summarized in the Appendix. The discrepancies among them are analyzed in Table 1 in the form of distance matrices, and in Figure 1 in the form of UPGMA phenograms, at three levels of classification: order (or suborder), suborder (or infraorder), and superfamily. Even using the most conservative possible estimates (e.g. equating differently named largest categories), differences ranged to 52%, 79%, and 74% at the ordinal, subordinal, and superfamilial levels respectively (Table 1). The Solem and Boss classifications cluster closest at all three taxonomic levels, since both are based primarily on the Pilsbry-Baker scheme; nevertheless, they differ substantially (20%) in superfamilial assignment. Nordsieck's reclassification produced little change at the ordinal level, but major change at the subordinal and superfamilial levels. Both Schileyko's conchological-reproductive and Tillier's non-reproductive anatomical revisions differ greatly from these three classifications and from each other at all three levels (Table 1, Fig. 1).

RNA Sequence Analysis

Nucleotide-sequence data for the 10 gastropod species are presented in Figure 2. No differences were detected within species. At the 5' termini of LrRNAs, 39 nucleotides were sequenced, of which five (13%) were variable among the 10 taxa. The D6 region showed much greater variability (41%), with 56 variable positions among the 138 that were sequenced. There was greater variability in the D6 region itself (positions 1 to 41) than on either side of it (positions -42 to -1 and 42 to 96), with 83% and 23% variable nucleotide sites respectively.

The great majority of this variation lay between the set of stylommatophorans and the set of outgroups. No differences whatever were detected among the four species of polygyrids.

Cladistic analysis of this variation produced a single most parsimonious tree with a consistency index of 0.90 (0.74 if all autapomorphies were removed), which is presented in Figure 3 and Table 2. This cladogram had a tree length of 72. Three cladograms were also produced with tree lengths of 73 (consistency

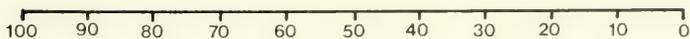
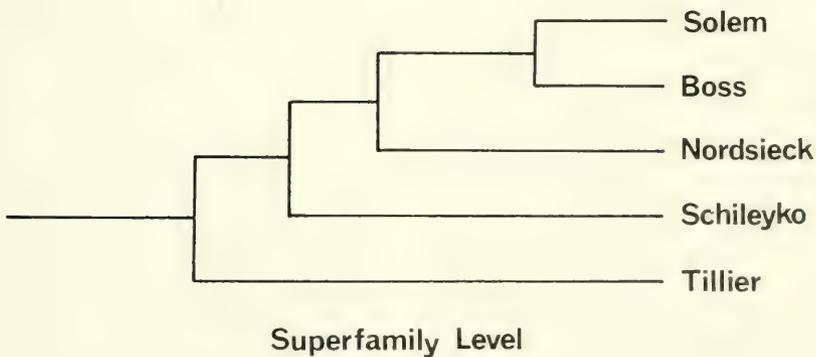
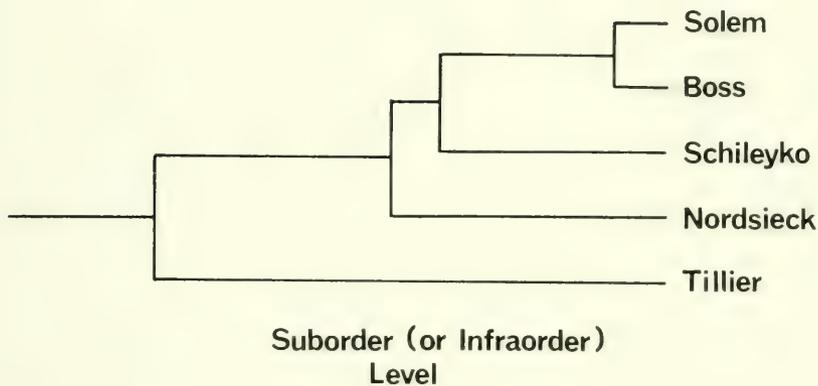
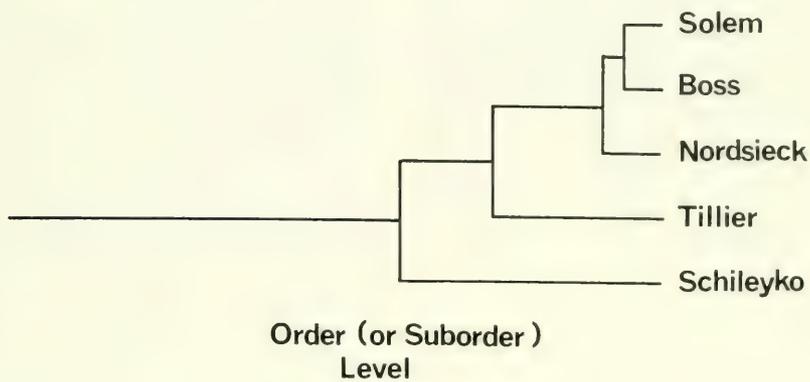


FIG. 1. UPGMA phenograms of the past decade's five classifications of pulmonate land-snail families, by author, at three taxonomic levels. The common scale is percent difference in classification of all families common to each pair of classifications, as conservatively calculated from the Appendix.

TABLE 1. Distances among recent stylommatophoran classifications at the superfamilial, subordinal, and ordinal levels. So = Solem (1978), Sh = Schileyko (1979), B = Boss (1982), N = Nordsieck (1985, 1986), and T = Tillier (1989). The upper matrix gives the number of families compared; the lower matrix is the proportion of compared families differently classified.

	Ordinal				
	So	Sh	B	N	T
So	—	64	65	67	56
Sh	0.31	—	62	69	54
B	0.06	0.32	—	64	52
N	0.09	0.22	0.09	—	56
T	0.23	0.52	0.27	0.27	—

	Subordinal				
	So	Sh	B	N	T
So	—	60	65	63	56
Sh	0.38	—	61	69	53
B	0.08	0.30	—	64	52
N	0.44	0.38	0.45	—	55
T	0.77	0.79	0.75	0.78	—

	Superfamilial				
	So	Sh	B	N	T
So	—	64	64	66	55
Sh	0.61	—	63	68	54
B	0.20	0.59	—	63	51
N	0.39	0.53	0.48	—	54
T	0.62	0.74	0.61	0.74	—

index = 0.890). Each of these differed from Figure 3 in only a single detail: pairing *Oncomelania* with *Biomphalaria*, pairing *Haplotrema* with *Mesomphix*, and pairing *Haplotrema* with *Ventridens*, respectively. Four slightly less parsimonious cladograms (length = 74, consistency index = 0.878) were also produced. Two of these paired *Oncomelania* with *Biomphalaria*, one also pairing *Haplotrema* with *Mesomphix*, the other also pairing *Haplotrema* with *Ventridens*. The third 74-length cladogram differed from Figure 3 by placing *Biomphalaria* between the Polygyridae and the remaining stylommatophorans, and the fourth cladogram differed by pairing *Biomphalaria* with the Polygyridae.

Phenetic analyses of sequence data are presented in Tables 3, 4, and 5; and in Figure 4. Table 3 presents, for each pair of taxa, the numbers of nucleotide site differences and of total sites compared, used in calculating simple distance coefficients. Table 4 partitions the proportion of different sites into that due to

transitions versus that due to transversions, deletions, and insertions. Kimura's (1980) evolutionary distance K_{nuc} and its standard error are presented in Table 5.

UPGMA clustering from Table 5 yielded the phenogram in Figure 4, which includes standard error bars. This tree is almost identical in topology to the cladogram in Figure 3, with the exception that *Haplotrema*, *Mesomphix*, and *Ventridens* form an unresolved trichotomy. The standard error bars in Figure 4 indicate significant differences among all branch points, except the branch point between the Polygyridae and the three other stylommatophoran families.

UPGMA clustering from values of the proportion of different sites (Tables 3 and 4) resulted in a phenogram identical in topology to Figure 4, and virtually identical to it in branch-point distances as well. In Figure 4, the branch-point distances, from top to bottom, are 0.020, 0.038, 0.104, 0.187, and 0.283; whereas in the phenogram based on proportion of different sites (not figured), the branch-point differences are 0.020, 0.030, 0.097, 0.165, and 0.232.

Among the seven species of stylommatophorans sequenced, there was variation at five of the 40 positions of the D6 divergent domain (positions #16, 27, 29, 31, and 36). At these positions there were five interfamilial differences and one intrafamilial difference (position #16 in Zonitidae). Thus in this region of the molecule, 13% of the sites were phylogenetically informative. The conserved regions, on the other hand, had only 1% informative sites: sequencing 137 positions in the 5'-terminus and in the flanker regions of D6 yielded only one position (#83) that differed among the stylommatophorans.

DISCUSSION

Comparison of Classifications

A systematic discussion of the recent classifications of the stylommatophorans (compared in Appendix) is beyond the scope of this paper. All we have done is point out the high degree of taxonomic discrepancies among them (Table 1, Fig. 1). These discrepancies can be attributed to a number of factors: (1) use of different characters (e.g. Tillier's unique use of the digestive and nervous systems but not the reproductive system); (2) emphasis on different characters (e.g. Schil-

Selected Large Ribosomal RNA Sequences

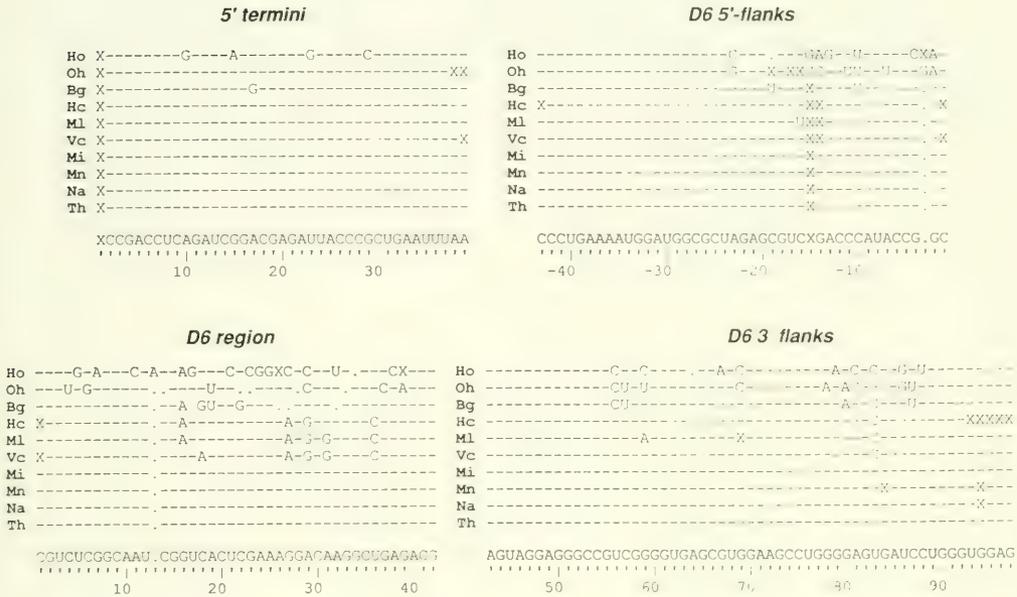


FIG. 2. Nucleotide sequence data for 10 species of gastropods from the 5' termini and the D6 regions of large ribosomal RNA molecules. Ho = *Helicina orbiculata*, Oh = *Oncomelania hupensis*, Bg = *Biomphalaria glabrata*, Hc = *Haplotrema concavum*, Ml = *Mesomphix latior*, Vc = *Ventridens cerinoideus*, Mi = *Mesodon infectus*, Mn = *Mesodon normalis*, Na = *Neohelix albolabris*, and Th = *Triodopsis hopetonensis*. Dash = same as polygyrids (given below, with position numbers), X = unknown, period = absent.

eyko's strong emphasis on shell characters); (3) different interpretation of the same characters (e.g. Nordsieck's and Schileyko's different opinions on the homologies of genital appendages); and (4) different methodologies (e.g. Solem's intuitive evolutionary approach versus Tillier's more objective cladistic approach). At least partial resolution of these factors is possible by careful analysis of all available characters in order to construct an integrative phylogenetic hypothesis, which is urgently needed. Accurate detection of homologies in many anatomical and conchological characters, however, may never be possible. Stylommatophoran families are simply so old, and their environmental selective pressures so similar (see Solem, 1978), that convergences and parallelisms are pervasive (e.g. Tillier, 1989). If there is any remedy for this systematic dilemma, it probably lies in the application of new, independent data sets, of which molecular sequences currently seem most promising.

RNA Sequence Analysis

There is a burgeoning literature on the phylogenetic interpretation of nucleotide sequence data, with many alternative approaches (e.g. Felsenstein, 1982; Wolters & Erdmann, 1986; Sourdis & Krimbas, 1987; Saitou & Nei, 1987; Lake, 1987a, 1987b; Saitou, 1988; Sourdis & Nei, 1988; and references therein). We chose three approaches (maximum parsimony, simple distance UP-GMA, and K_{nuc} distance UPGMA) that have held their own in the ongoing controversy or have been applied recently to LrRNA (Guadet et al., 1989; Larson & Wilson, 1989; Qu et al., 1989) or other rRNA data (Bremer & Bremer, 1989). We did not adjust either for compensatory changes in the D6 stem region (see Wheeler & Honeycutt, 1988) or for possible multiple changes at a given site (e.g. Holmquist, 1983), and we do not know whether these would substantially change our results.

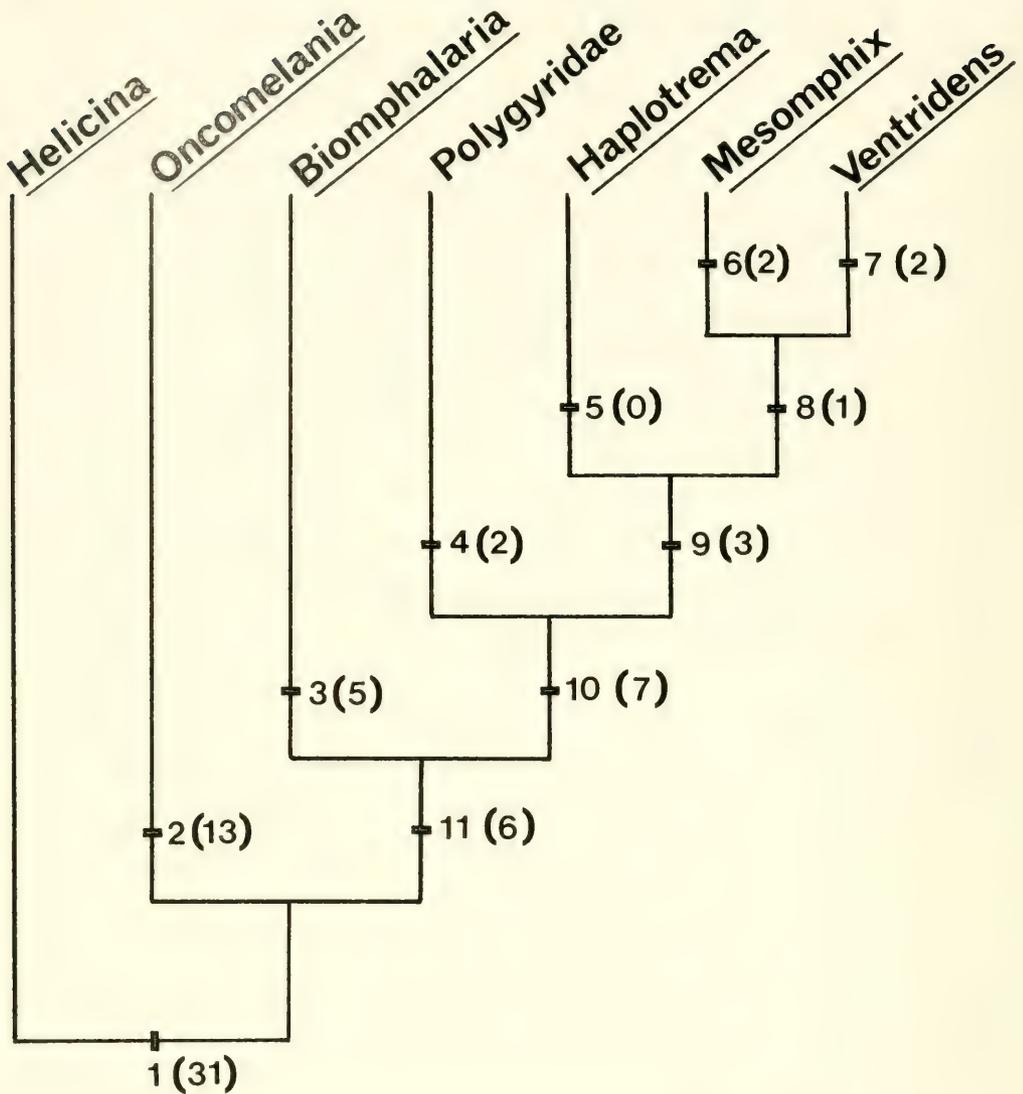


FIG. 3. Maximum-parsimony cladogram from the nucleotide sequence data presented in Fig. 2. The consistency index is 0.90 (but is 0.74 if all autapomorphies are removed). The numbers refer to the lists of apomorphies as listed in Table 2, with the number of apomorphies in parentheses.

The three phylogenetic approaches gave identical results (Figs. 3, 4), with the exception that maximum parsimony cladistics resolved the trichotomy among *Haplotrema*, *Ventridens*, and *Mesomphix*, by pairing the latter two by means of a single synapomorphy (Table 2, #8). This agreement among methodological approaches provides reasonable confidence that Figure 3 is a robust interpretation of the sequence data at hand.

Haszprunar (1988) recently presented a

cladistic analysis of the major gastropod groups, with explicit and thorough character analyses from a range of sources. For the taxa we have analyzed, his phylogram agrees with all previous hierarchically arranged classifications (e.g. Taylor & Sohl, 1962) in the arrangement: (*Helicina* (*Oncomelania* (Pulmonata))), which appears as (*Archaeogastropoda*: Neritimorpha (*Apogastropoda*: *Neotaenioglossa* (Euthyneura))) in Haszprunar's (1988) figure 5 and as the more

TABLE 2. Character-state transformations in the 5' and D6 regions of large ribosomal RNAs of stylommatophoran gastropods and three outgroups. Numbers 1-11 refer to the cladogram in Figure 3. Derived from sequences given in Fig. 2, and presented here by region, nucleotide position(s), and suggested transformation.

	5' end	D6 5' flank	D6region	D6 3' flank
1.	10 G<>A 15 A<>G 23 G<>U 29 C<>G	-23 C<>A -19 D<>U -13 G<>A	5 G<>U 7 A<>G 11 C<>A 13 A<>D 17 G<>U 19 A<>U 21 C<>U 23 C<>G 24 G<>A 25 G<>A 27 C<>G 32 U<>A 34 C<>G 35 U<>C 36 D<>U 38 C<>A	57 C<>U 59 C<>U 64 D<>A 67 A<>G 79 A<>G 80 G<>A 87 C<>U 88 U<>C
2.		-11 C >U -7 A >U -3 D >G	4 C >U 6 C >G 14 C >D 16 A >G 22-23 P >D 33 G >D 37 G >C 39 G >A 18 C >G 22 C >G 26-27 P >D 32 A >D 16 A >G	78 G >A 83 C >U
3.	17 A >G			
4.				
5.	no transformations			83 C >U
6.			16 A >G	59 G >A
7.			16 A >G 18 C >A	
8.			31 A >G	
9.			27 G >A 29 A >G 36 U >C	
10.		-19 U >C -10 U >C	19 U >A	56 C >U 57 U >C 80 A >G 87 U >C
11.		-2 A >G	29 C >A	59 U >G 69 C >G 81 C >A 86 G >U

familiar (Archaeogastropoda (Mesogastropoda (Pulmonata))) in, for example, Taylor & Sohl (1962). Our LrRNA data confirm this phylogenetic hypothesis (Figs. 3, 4). This corroboration between anatomical and molecular data lends credence to both.

Within the Pulmonata we sequenced, the resulting topology is summarized by the cen-

tral tree in Figure 5, namely: (Basommatophora (Polygyridae (Haplotrematidae (Zonitidae))). For comparison, Figure 5 also presents the trees for these taxa as presented in Schileyko (1979: fig. 7, as translated by Boss & Jacobson, 1985) and Tillier (1989: text-figs. 25 and 29b), and as inferred from the hierarchical classifications of Solem

TABLE 3. Number of nucleotide differences (upper matrix) and total number of comparable nucleotide positions (lower matrix) between pairs of sequences aligned in Fig. 2. "Polygyridae" pools the four species that were sequenced and found to be identical at all 177 positions examined.

	He.	On.	Bi.	Ha.	Me.	Ve.	Po.
<i>Helicina</i>	—	43	39	24	35	37	36
<i>Oncomelania</i>	170	—	28	29	29	31	27
<i>Biomphalaria</i>	174	172	—	16	19	18	16
<i>Haplotrema</i>	165	163	168	—	3	3	5
<i>Mesomphix</i>	172	170	175	167	—	4	8
<i>Ventridens</i>	170	169	173	167	172	—	6
Polygyridae	174	172	177	168	175	173	—

TABLE 4. Proportions of compared nucleotide sites different due to transitions (upper matrix) and transversions plus deletions/insertions (lower matrix).

	He.	On.	Bi.	Ha.	Me.	Ve.	Po.
<i>Helicina</i>	—	0.112	0.092	0.085	0.093	0.094	0.092
<i>Oncomelania</i>	0.141	—	0.047	0.086	0.088	0.089	0.064
<i>Biomphalaria</i>	0.132	0.116	—	0.054	0.069	0.069	0.051
<i>Haplotrema</i>	0.121	0.092	0.042	—	0.018	0.012	0.030
<i>Mesomphix</i>	0.110	0.082	0.040	0.000	—	0.017	0.046
<i>Ventridens</i>	0.124	0.095	0.035	0.006	0.006	—	0.029
Polygyridae	0.115	0.093	0.040	0.000	0.000	0.006	—

TABLE 5. Values of Kimura's (1980) evolutionary distance K_{nuc} (upper matrix) and its standard error (lower matrix) between pairs of sequences aligned in Fig. 2.

	He.	On.	Bi.	Ha.	Me.	Ve.	Po.
<i>Helicina</i>	—	0.310	0.267	0.241	0.238	0.258	0.243
<i>Oncomelania</i>	0.051	—	0.184	0.204	0.195	0.211	0.176
<i>Biomphalaria</i>	0.045	0.036	—	0.102	0.118	0.113	0.097
<i>Haplotrema</i>	0.044	0.040	0.026	—	0.018	0.018	0.031
<i>Mesomphix</i>	0.043	0.038	0.028	0.011	—	0.024	0.048
<i>Ventridens</i>	0.045	0.040	0.028	0.011	0.012	—	0.036
Polygyridae	0.043	0.035	0.025	0.014	0.017	0.015	—

(1978) and Nordsieck (1986). (No tree is presented for Boss [1982], because his classification is not explicitly hierarchical, but if it were, the tree would probably equal that for Solem [1978].)

In these four trees from the literature, the Basommatophora appear as the sister group to the three stylommatophoran families, in Schileyko's tree by explicit inclusion, in the other three trees by implicit assumption, because that is the traditional taxonomic position of the Basommatophora. The LrRNA sequence data corroborate this relationship (Fig. 5, center), with the Basommatophora (as represented by *Biomphalaria glabrata*) joining the base of the stylommatophoran clade.

This sister-group status of the Basommatophora to the Stylommatophora has been

called into question by Solem (1985; see also Solem & Yochelson [1979]) because (a) the earliest known basommatophoran fossils appear about 150 million years later than the earliest known stylommatophoran fossils, and (b) there is no convincing anatomical evidence of a sister-group relationship. Our data do not contradict this opinion; the real test will require sequencing at least one of the four Recent stylommatophoran families that appear in the Paleozoic (Tornatellinidae, an unassigned pupillacean family, Enidae, and Discidae [Solem & Yochelson, 1979]). We can at least say with fair confidence that the Basommatophora are plesiomorphic to the stylommatophorans included in this study.

Concerning the relationship among the Polygyridae, the Haplotrematidae, and the

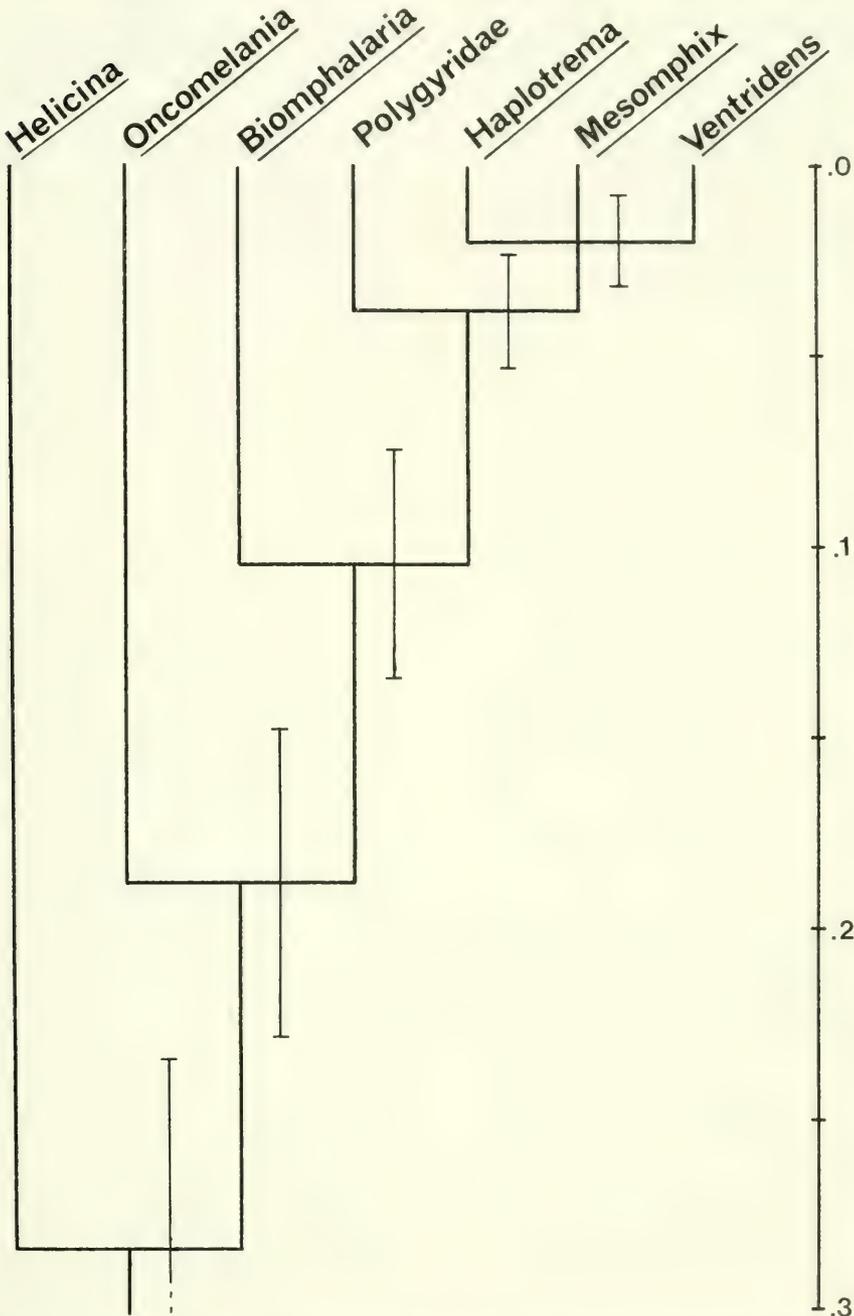


FIG. 4. UPGMA phenogram from K_{nuc} distances (Table 5, top) calculated from the nucleotide sequence data presented in Fig. 2. Standard error bars are averaged from those presented in Table 5 (bottom).

Zonitidae, our RNA sequence data do not support any recently proposed phylogeny, but are closest to that of Schileyko (1979) (Fig. 5).

These two phylogenetic hypotheses differ most strikingly from the others in placing the Polygyridae as most plesiomorphic. This

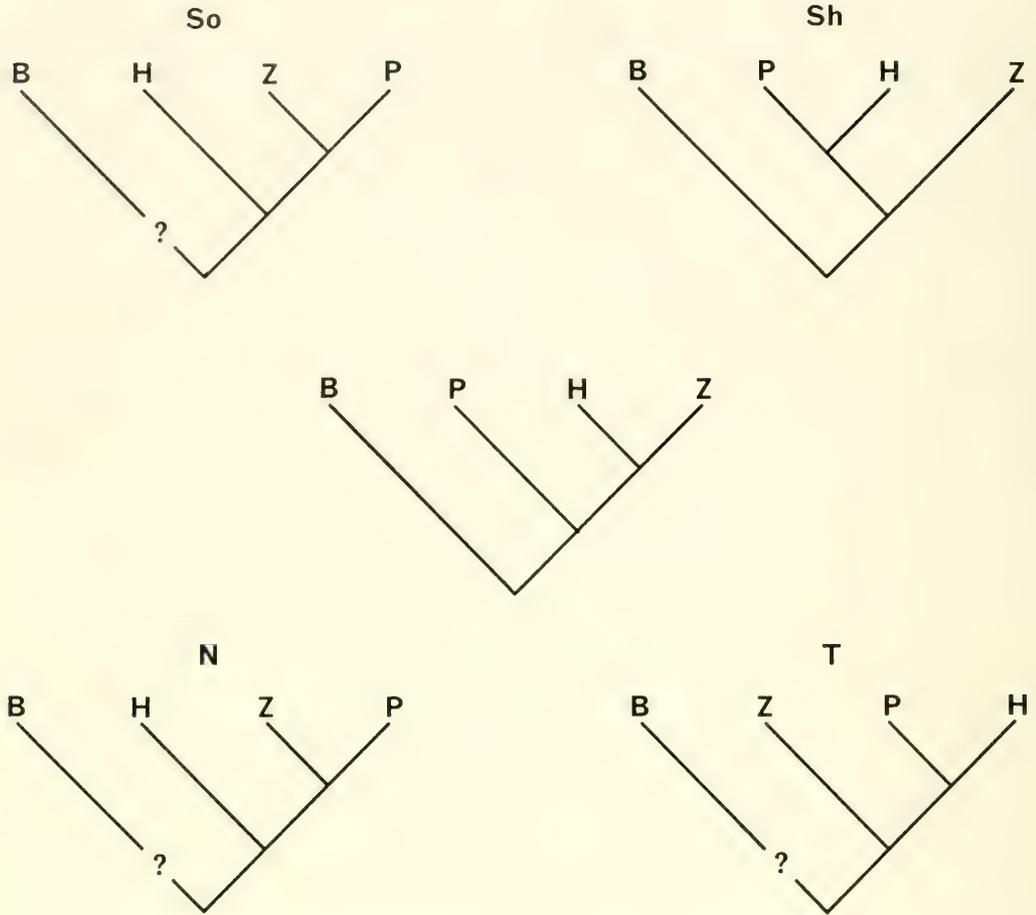


FIG. 5. Comparison of proposed phylogenies for selected pulmonate snail taxa. B = Basommatophora, P = Polygyridae, H = Haplotrematidae, Z = Zonitidae. Central tree is derived from LrRNA sequence data (Figs. 3, 4); other trees from: So = Solem (1978), Sh = Shileyko (1979), N = Nordsieck (1986), T = Tillier (1989). In each tree, taxa are arranged from the most plesiomorphic (left) to most apomorphic (right).

strong contrast from the traditional Western classification, although not statistically significant according to K_{nuc} analysis (Fig. 4), hints of many possible surprises to come as the result of future molecular sequence studies with greater numbers of phylogenetically informative positions.

Within the Polygyridae, the lack of sequence divergence between the subfamilies Triodopsinae and Polygyrinae is remarkable, considering their great anatomical differences (e.g. Emberton, 1986).

In summary, the LrRNA molecule presents many opportunities for comparative analysis at a hierarchy of taxonomic levels (Guadet et al., 1989; Larson & Wilson, 1989; Lenaers et

al., 1989; Qu et al., 1989). We chose the 5' terminus and one divergent domain for an initial analysis. It is instructive to extrapolate from our results in order to predict the potential value of the LrRNA molecule for stylommatophoran systematics. Clearly, the conserved regions are unproductive, at less than 1% informative sites among three families. It is in the divergent domains that sequencing efforts are rewarded. LrRNA contains 12 divergent domains (D1–D12), of which D6 can be assumed to be at or below average in number of nucleotide sites (e.g. Hassouna et al., 1984; Hancock et al., 1988). In D6 we found five informative sites out of 40 among the three stylommatophoran families se-

quenced. Thus, at 13% informative sites, Lr-RNA divergent domains afford a high return for the effort. Including more families would certainly increase this percentage.

Mining more of this phylogenetic information would prove a useful adjunct to the anatomical data already available (and in need of synthesis) for the Stylommatophora. Such efforts will be aided by our discoveries that (1) whole-snail preparations can be used, making it possible to include such generally minute-sized families as pupillids, ferrussaciids, and valloniids; and (2) turnaround time from sample receipt to sequence recording can be a mere three days per divergent domain, running up to 12 samples simultaneously.

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APPENDIX. Comparison of the five classifications of the families of pulmonate land snails published in the last decade. Parenthetical synonymies of families at the end of the list are according to Zilch (1960).

Family	Solem, 1978		
	Order	Suborder	Superfamily
Achatinellidae			
Gulick, 1873	Orthurethra	—	Achatinellacea
Tornatellidae			
Cooke & Kondo, 1960	Orthurethra	—	Achatinellacea ¹
Amastriidae			
Pilsbry, 1911	Orthurethra	—	Cionellacea
Cionellidae (= Cochliocopidae)			
Clessin, 1879	Orthurethra	—	Cionellacea
Pupillidae			
Turton, 1831	Orthurethra	—	Pupillacea
Vertiginidae			
Fitzinger, 1833	Orthurethra	—	Pupillacea ²
Orculidae			
Pilsbry, 1918	Orthurethra	—	Pupillacea ²
Chondrinidae			
Steenberg, 1925	Orthurethra	—	Pupillacea ²
Pleurodiscidae			
Wenz, 1923	Orthurethra	—	Pupillacea
Pyramidulidae			
Wenz, 1923	Orthurethra	—	Pupillacea ³
Valloniidae			
Morse, 1864	Orthurethra	—	Pupillacea
Strobilopsidae			
Pilsbry, 1918	Orthurethra	—	Pupillacea
Partulidae			
Pilsbry, 1900	Orthurethra	—	Partulacea
Enidae (= Buliminidae)			
Clessin, 1879	Orthurethra	—	Partulacea
Clausiliidae			
Mörch, 1864	Mesurethra	—	Clausiliacea
Cerionidae (= Ceriidae)			
Fleming, 1818	Mesurethra	—	Clausiliacea
Dorcasiidae			
Connolly, 1915	Mesurethra	—	Strophocheilacea
Strophocheilidae			
Thiele, 1926	Mesurethra	—	Strophocheilacea
Ferussaciidae			
Bourguignat, 1883	Sigmurethra	Holopodopes	Achatinacea
Subulinidae			
Crosse & Fischer, 1877	Sigmurethra	Holopodopes	Achatinacea
Spiraxidae			
Baker, 1955	Sigmurethra	Holopodopes	Achatinacea
Megaspiridae			
Pilsbry, 1904	Sigmurethra	Holopodopes	Achatinacea
Achatinidae			
Swainson, 1840	Sigmurethra	Holopodopes	Achatinacea
Streptaxidae			
Gray, 1840	Sigmurethra	Holopodopes	Streptaxacea
Haplotrematidae			
H.B. Baker, 1925	Sigmurethra	Holopodopes	Rhytidacea
Systrophiidae			
Thiele, 1926	Sigmurethra	Holopodopes	Rhytidacea
Rhytididae (= Paraphantidae)			
Pilsbry, 1893	Sigmurethra	Holopodopes	Rhytidacea
Aperidae (= Chlamydephoridae)			
Möllendorff, 1902	Sigmurethra	Holopodopes	Rhytidacea
Macrocyclidae			
Thiele, 1926	Sigmurethra	Holopodopes	Rhytidacea?
Acavidae			
Pilsbry, 1895	Sigmurethra	Holopodopes	Acavacea?
Clavatoridae			
Thiele, 1926	Sigmurethra	Holopodopes	Acavacea? ⁴
Caryodidae			
Thiele, 1926	Sigmurethra	Holopodopes	Acavacea?

(continued)

APPENDIX. (Continued)

Family	Schileyko, 1979			
	Order	Suborder	Infraorder	Superfamily
Achatinellidae	Geophila	Pupillina		
Gulick, 1873	Ferussac, 1812	Schileyko, 1979	—	Achatinelloidea
Tornatellidae				
Cooke & Kondo, 1960	—	—	—	—
Amastriidae				
Pilsbry, 1911	Geophila	Pupillina	—	Cionelloidea
Cionellidae (= Cochliocopidae)				
Clessin, 1879	Geophila	Pupillina	—	Cionelloidea
Pupillidae				
Turton, 1831	Geophila	Pupillina	—	Pupilloidea
Vertiginidae				
Fitzinger, 1833	Geophila	Pupillina	—	Pupilloidea
Orculidae				
Pilsbry, 1918	Geophila	Pupillina	—	Achatinelloidea
Chondrinidae				
Steenberg, 1925	Geophila	Pupillina	—	Pupilloidea
Pleurodiscidae				
Wenz, 1923	Geophila	Helixina	Endodontinia	Punctoidea
Pyramidulidae				
Wenz, 1923	Geophila	Pupillina	—	Pupilloidea
Valloniidae				
Morse, 1864	Geophila	Pupillina	—	Pupilloidea
Strobilopsidae				
Pilsbry, 1918	Geophila	Pupillina	—	Pupilloidea
Partulidae				
Pilsbry, 1900	Geophila	Achatinina Schileyko, 1979	—	Partuloidea
Enidae (= Buliminidae)				
Clessin, 1879	Geophila	Pupillina	—	Pupilloidea
Clausilidae				
Mörch, 1864	Geophila	Achatinina	—	Clausilioidea
Cerionidae (= Ceriidae)				
Fleming, 1818	Geophila	Pupillina	—	Cerioidea
Dorcasiidae				
Connolly, 1915	Geophila	Achatinina	—	Achatinoidea
Strophocheilidae				
Thiele, 1926	Geophila	Achatinina	—	Achatinoidea
Ferussaciidae				
Bourguignat, 1883	Geophila	Achatinina	—	Subulinoidea
Subulinidae				
Crosse & Fischer, 1877	Geophila	Achatinina	—	Subulinoidea
Spiraxidae				
Baker, 1955	Geophila	Oleacinina Schileyko, 1979	—	Testacelloidea
Megaspiridae				
Pilsbry, 1904	Geophila	Achatinina	—	Clausilioidea
Achatinidae				
Swainson, 1840	Geophila	Achatinina	—	Achatinoidea
Streptaxidae				
Gray, 1840	Geophila	Oleacinina	—	Streptaxoidea
Haplotrematidae				
H.B. Baker, 1925	Geophila	Helixina	Helixinia	Rhytidoidea
Systrophiidae				
Thiele, 1926	Geophila	Helixina	Endodontinia	Punctoidea
Rhytididae (= Paraphantidae)				
Pilsbry, 1893	Geophila	Helixina	Helixinia	Rhytidoidea
Aperidae (= Chlamydephoridae)				
Möllendorff, 1902	—	—	—	—
Macrocyclidae				
Thiele, 1926	—	—	—	—
Acavidae				
Pilsbry, 1895	Geophila	Achatinina	—	Achatinoidea
Clavatoridae				
Thiele, 1926	Geophila	Achatinina	—	Achatinoidea
Caryodidae				
Thiele, 1926	—	—	—	—

APPENDIX. (Continued)

Family	Boss, 1982			Nordsieck, 1985, 1986		
	Suborder	Infraorder	Superfamily	Order	Suborder	Superfamily
Achatinellidae Gulick, 1873	Orthurethra	—	Achatinelloidea	Orthurethra	—	Achatinelloidea
Tornatellidae Cooke & Kondo, 1960	Orthurethra	—	Achatinelloidea ¹	Orthurethra	—	Achatinelloidea ¹
Amastriidae Pilsbry, 1911	Orthurethra	—	Cionelloidea	Orthurethra	—	Cochliocopoidea
Cionellidae (= Cochliocopidae) Clessin, 1879	Orthurethra	—	Cionelloidea	Orthurethra	—	Cochliocopoidea
Pupillidae Turton, 1831	Orthurethra	—	Pupillaceae	Orthurethra	—	Pupilloidea
Vertiginidae Fitzinger, 1833	Orthurethra	—	Pupillaceae	Orthurethra	—	Pupilloidea
Orculidae Pilsbry, 1918	Orthurethra	—	Pupillaceae ²	Orthurethra	—	Pupilloidea
Chondrinidae Steenberg, 1925	Orthurethra	—	Pupillaceae ²	Orthurethra	—	Pupilloidea
Pleurodiscidae Wenz, 1923	Orthurethra	—	Pupillaceae	Orthurethra	—	Pupilloidea
Pyramidulidae Wenz, 1923	Orthurethra	—	Pupillaceae ³	Orthurethra	—	Pupilloidea
Valloniidae Morse, 1864	Orthurethra	—	Pupillaceae	Orthurethra	—	Pupillaceae
Strobilopsidae Pilsbry, 1918	Orthurethra	—	Pupillaceae	Orthurethra	—	Pupilloidea
Partulidae Pilsbry, 1900	Orthurethra	—	Achatinelloidea	Sigmurethra	Achatinida	Partuloidea
Enidae (= Buliminidae) Clessin, 1879	Orthurethra	—	Pupillaceae	Orthurethra	—	Buliminoidea
Clausiliidae Mörch, 1864	Mesurethra	—	Clausilloidea	Orthurethra	—	Clausilloidea ¹³
Cerionidae (= Ceriidae) Fleming, 1818	Mesurethra	—	Clausilloidea	—	—	—
Dorcasiidae Connolly, 1915	Mesurethra	—	Strophocheilaceae	Sigmurethra	Achatinida	Acavoidea
Strophocheilidae Thiele, 1926	Mesurethra	—	Strophocheilaceae	Sigmurethra	Achatinida	Acavoidea
Ferussaciidae Bourguignat, 1883	Sigmurethra	Holopodopes	Strophocheilaceae	Sigmurethra	Achatinida	Achatinoidea
Subulinidae Crosse & Fischer, 1877	Sigmurethra	Holopodopes	Achatinaceae	Sigmurethra	Achatinida	Achatinoidea
Spiraxidae Baker, 1955	Sigmurethra	Holopodopes	Achatinaceae	Sigmurethra	Achatinida	Oleacinoidea
Megaspiridae Pilsbry, 1904	Mesurethra	—	Clausilloidea	Sigmurethra	Achatinida	Orthalicoidea [?]
Achatinidae Swainson, 1840	Sigmurethra	Holopodopes	Achatinaceae	Sigmurethra	Achatinida	Achatinoidea
Streptaxidae Gray, 1840	Sigmurethra	Holopodopes	Streptaxaceae	Sigmurethra	Achatinida	Streptaxoidea
Haplotrematidae H.B. Baker, 1925	Sigmurethra	Holopodopes	Rhytidaceae	Sigmurethra	Achatinida	Rhytidoidea
Systrophiidae Thiele, 1926	Sigmurethra	Aulacopoda	Limacaceae	Sigmurethra	Achatinida	Rhytidoidea
Rhytididae (= Paraphantidae) Pilsbry, 1893	Sigmurethra	Holopodopes	Rhytidaceae	Sigmurethra	Achatinida	Rhytidoidea
Aperidae (= Chlamydephoridae) Möllendorff, 1902	Sigmurethra	Holopodopes	Rhytidaceae	—	—	—
Macrocyclidae Thiele, 1926	Sigmurethra	Holopodopes	Rhytidaceae	Sigmurethra	Achatinida	Acavoidea ¹⁵
Acavidae Pilsbry, 1895	Sigmurethra	Holopodopes	Rhytidaceae	Sigmurethra	Achatinida	Acavoidea
Clavatoridae Thiele, 1926	—	—	—	—	—	—
Caryodidae Thiele, 1926	—	—	—	Sigmurethra	Achatinida	Acavoidea

(continued)

APPENDIX. (Continued)

Family	Tillier, 1989	
	Suborder	Superfamily
Achatinellidae Gulick, 1873	Orthurethra	Pupilloidea
Tornatellidae Cooke & Kondo, 1960	Orthurethra	Pupilloidea ¹
Amastriidae Pilsbry, 1911	Orthurethra	Chondrinoidea
Cionellidae (= Cochliocopidae) Clessin, 1879	Orthurethra	Chondrinoidea
Pupillidae Turton, 1831	Orthurethra	Pupilloidea
Vertiginidae Fitzinger, 1833	Orthurethra	Chondrinoidea
Orculidae Pilsbry, 1918	Orthurethra	Chondrinoidea
Chondrinidae Steenberg, 1925	Orthurethra	Chondrinoidea
Pleurodiscidae Wenz, 1923	—	—
Pyramidulidae Wenz, 1923	Orthurethra	Pupilloidea
Valloniidae Morse, 1864	Orthurethra	Pupilloidea
Strobilopsidae Pilsbry, 1918	Orthurethra	Pupilloidea ¹⁸
Partulidae Pilsbry, 1900	Orthurethra	Partuloidea
Enidae (= Buliminidae) Clessin, 1879	Orthurethra	Partuloidea
Clausiliidae Mörch, 1864	Brachynephra	Clausilioidea
Cerionidae (= Ceriidae) Fleming, 1818	Brachynephra	Clausilioidea
Dorcasidae Connolly, 1915	—	—
Strophocheilidae Thiele, 1926	—	—
Ferussaciidae Bourguignat, 1883	Dolichonephra	Achatinoidea
Subulinidae Crosse & Fischer, 1877	Dolichonephra	Achatinoidea
Spiraxidae Baker, 1955	Dolichonephra	Achatinoidea ²⁰
Megaspiridae Pilsbry, 1904	Brachynephra	Clausilioidea
Achatinidae Swainson, 1840	Dolichonephra	Achatinoidea
Streptaxidae Gray, 1840	Dolichonephra	Achatinoidea
Haplotrematidae H.B. Baker, 1925	Dolichonephra	Helicoidea
Systrophidae Thiele, 1926	Brachynephra	Endodontoidea
Rhytididae (= Paraphantidae) Pilsbry, 1893	Brachynephra	Acavoidea
Aperidae (= Chlamydephoridae) Möllendorff, 1902	—	—
Macrocyclidae Thiele, 1926	—	—
Acavidae Pilsbry, 1895	Brachynephra	Acavoidea
Clavatoridae Thiele, 1926	—	—
Caryodidae Thiele, 1926	—	—

APPENDIX. (Continued)

Family	Solem, 1978		
	Order	Suborder	Superfamily
Urocoptidae			
Pilsbry & Vanatta, 1898	Sigmurethra	Holopodopes	Bulimulacea
Bulimulidae			
Tryon, 1867	Sigmurethra	Holopodopes	Bulimulacea
Orthalicidae			
Albers-Martens, 1860	Sigmurethra	Holopodopes	Bulimulacea ⁵
Amphibulimidae			
Crosse & Fischer, 1873	Sigmurethra	Holopodopes	Bulimulacea ⁵
Odontostomidae			
Pilsbry & Vanatta, 1898	Sigmurethra	Holopodopes	Bulimulacea ⁵
Punctidae			
Morse, 1864	Sigmurethra	Aulacopoda	Arionacea
Endodontidae			
Pilsbry, 1894	Sigmurethra	Aulacopoda	Arionacea
Charopidae			
Hutton, 1884	Sigmurethra	Aulacopoda	Arionacea
Otoconchidae			
Cockerell, 1893	Sigmurethra	Aulacopoda	Arionacea ⁶
Helicodiscidae			
Pilsbry, 1927	Sigmurethra	Aulacopoda	Arionacea
Discidae			
Thiele, 1931	Sigmurethra	Aulacopoda	Arionacea
Arionidae			
Gray, 1840	Sigmurethra	Aulacopoda	Arionacea
Philomycidae			
Gray, 1847	Sigmurethra	Aulacopoda	Arionacea
Succineidae			
Beck, 1837	Sigmurethra	Aulacopoda	Succineacea
Athoracophoridae			
Fischer, 1883	Sigmurethra	Aulacopoda	Succineacea?
Helicarionidae			
Bourguignat, 1888	Sigmurethra	Aulacopoda	Limacacea A
Euconulidae			
H.B. Baker, 1928	Sigmurethra	Aulacopoda	Limacacea A ⁷
Ariophantidae			
Godwin-Austen, 1888	Sigmurethra	Aulacopoda	Limacacea A ⁷
Urocyliidae			
Simroth, 1889	Sigmurethra	Aulacopoda	Limacacea A
Aillyidae			
H.B. Baker, 1930	Sigmurethra	Aulacopoda	Limacacea A
Zonitidae			
Mörch, 1864	Sigmurethra	Aulacopoda	Limacacea B
Trochomorphidae			
Möllendorff, 1890	Sigmurethra	Aulacopoda	Limacacea B ⁸
Vitrinidae			
Fitzinger, 1833	Sigmurethra	Aulacopoda	Limacacea B ⁸
Thyrophorellidae			
Girard, 1895	Sigmurethra	Aulacopoda	Limacacea B?
Parmacellidae			
Gray, 1860	Sigmurethra	Aulacopoda	Limacacea B
Limacidae			
Rafinesque, 1815	Sigmurethra	—	Limacacea B
Milacidae			
Germain, 1930	Sigmurethra	Aulacopoda	Limacacea B ⁹
Trigonochlamydidae			
Hesse, 1882	Sigmurethra	Aulacopoda	Limacacea B
Testacellidae			
Gray, 1840	Sigmurethra	Aulacopoda	Limacacea B?
Polygyridae (= Mesodontidae)			
Pilsbry, 1894	Sigmurethra	Holopoda	Polygyracea
Sagdidae			
Pilsbry, 1895	Sigmurethra	Holopoda	Polygyracea
Corillidae (= Plectopylidae)			
Pilsbry, 1905	Sigmurethra	Holopoda	Polygyracea
Oleacinidae			
Adams, 1855	Sigmurethra	Holopoda	Oleacinacea?
Camaenidae			
Pilsbry, 1894	Sigmurethra	Holopoda	Camaenacea
Ammonitellidae			
Pilsbry, 1930	Sigmurethra	Holopoda	Camaenacea (continued)

APPENDIX. (Continued)

Family	Schileyko, 1979			
	Order	Suborder	Infraorder	Superfamily
Urocoptidae				
Pilsbry & Vanatta, 1898	Geophila	Achatinina	—	Clausilioidea
Bulimulidae				
Tryon, 1867	Geophila	Achatinina	—	Achatinoidea
Orthalicidae				
Albers-Martens, 1860	—	—	—	—
Amphibulimidae				
Crosse & Fischer, 1873	Geophila	Achatinina	—	Achatinoidea
Odontostomidae				
Pilsbry & Vanatta, 1898	Geophila	Achatinina	—	Achatinoidea
Punctidae				
Morse, 1864	Geophila	Helixina	Endodontinia	Punctoidea
Endodontidae				
Pilsbry, 1894	Geophila	Helixina	Endodontinia	Punctoidea
Charopidae				
Hutton, 1884	—	—	—	—
Otoconchidae				
Cockerell, 1893	Geophila	Helixina	Helixinia	Arionoidea
Helicodiscidae				
Pilsbry, 1927	Geophila	Helixina	Endodontinia	Punctoidea
Discidae				
Thiele, 1931	—	—	—	—
Arionidae				
Gray, 1840	Geophila	Helixinia	Helixinia	Arionoidea
Philomycidae				
Gray, 1847	Geophila	Helixinia	Helixinia	Arionoidea
Succineidae				
Beck, 1837	Succineida	—	—	—
Athoracophoridae				
Fischer, 1883	Athoracophorida	—	—	—
Helicarionidae				
Bourguignat, 1888	Geophila	Helixina	Helixinia	Vitrinoidea
Euconulidae				
H.B. Baker, 1928	Geophila	Helixina	Helixinia	Gastrodontoidea
Ariophantidae				
Godwin-Austen, 1888	Geophila	Helixina	Helixinia	Vitrinoidea
Urocyclidae				
Simroth, 1889	Geophila	Helixina	Helixinia	Vitrinoidea
Aillyidae				
H.B. Baker, 1930	Aillyida	—	—	—
Zonitidae				
Mörch, 1864	Geophila	Helixina	Zonitinia Schileyko, 1979	Zonitoidea
Trochomorphidae				
Möllendorff, 1890	Geophila	Helixina	Helixinia	Vitrinoidea
Vitrinidae				
Fitzinger, 1833	Geophila	Helixina	Helixinia	Vitrinoidea
Thyrophorellidae				
Girard, 1895	Geophila	Helixina	Endodontinia	Thyrophorelloidea
Parmacellidae				
Gray, 1860	Geophila	Helixina	Zonitinia	Parmacelloidea
Limacidae				
Rafinesque, 1815	Geophila	Limaxina	Limaxinia	Limacoidea
Milacidae				
Germain, 1930	Geophila	Helixina	Zonitinia	Parmacelloidea
Trigonochlamydidae				
Hesse, 1882	Geophila	Limaxina	Trigonochlamydina Schileyko, 1979	Trigonochlamydoidea
Testacellidae				
Gray, 1840	Geophila	Oleacinina	—	Testacelloidea
Polygyridae (= Mesodontidae)				
Pilsbry, 1894	Geophila	Helixina	Endodontinia	Punctoidea
Sagdidae				
Pilsbry, 1895	Geophila	Pupillina	—	Sagdoidea
Corillidae (= Plectopylidae)				
Pilsbry, 1905	Geophila	Helixina	Helixinia	Helicoidea
Oleacinidae				
Adams, 1855	Geophila	Oleacinina	—	Testacelloidea
Camaenidae				
Pilsbry, 1894	Geophila	Helixina	Helixinia	Helicoidea
Ammonitellidae				
Pilsbry, 1930	Geophila	Helixina	Helixinia	Helicoidea

APPENDIX. (Continued)

Family	Boss, 1982			Nordsieck, 1985, 1986		
	Suborder	Infraorder	Superfamily	Order	Suborder	Superfamily
Urocoptidae						
Pilsbry & Vanata, 1898	Sigmurethra	Holopodopes	Bulimulacea	—	—	—
Bulimulidae						
Tyron, 1867	Sigmurethra	Holopodopes	Bulimulacea	Sigmurethra	Achatinida	Orthalicoidea ¹⁴
Orthalicoidea						
Albers-Martens, 1860	Sigmurethra	Holopodopes	Bulimulacea	Sigmurethra	Achatinida	Orthalicoidea
Amphibulimidae						
Crosse & Fischer, 1873	Sigmurethra	Holopodopes	Bulimulacea	Sigmurethra	Achatinida	Orthalicoidea ¹⁴
Odontostomidae						
Pilsbry & Vanatta, 1898	Sigmurethra	Holopodopes	Bulimulacea	Sigmurethra	Achatinida	Orthalicoidea ¹⁴
Punctidae						
Morse, 1864	Sigmurethra	Aulacopoda	Arionacea ¹⁰	Sigmurethra	Achatinida	Punctoidea
Endodontidae						
Pilsbry, 1894	Sigmurethra	Aulacopoda	Arionacea	Sigmurethra	Achatinida	Punctoidea
Charopidae						
Hutton, 1884	Sigmurethra	Aulacopoda	Arionacea ¹⁰	Sigmurethra	Achatinida	Punctoidea ¹⁷
Otoconchidae						
Cockerell, 1893	Sigmurethra	Aulacopoda	Arionacea	Sigmurethra	Achatinida	Punctoidea ¹⁷
Helicodiscidae						
Pilsbry, 1927	Sigmurethra	Aulacopoda	Arionacea ¹⁰	Sigmurethra	Achatinida	Punctoidea ¹⁷
Discidae						
Thiele, 1931	—	—	—	Sigmurethra	Achatinida	Punctoidea
Arionidae						
Gray, 1840	Sigmurethra	Aulacopoda	Arionacea	Sigmurethra	Helicida	Arionoidea
Philomycidae						
Gray, 1847	Sigmurethra	Aulacopoda	Arionacea	Sigmurethra	Helicida	Arionoidea
Succineidae						
Beck, 1837	Heterurethra	—	—	Elasmognatha	—	Succinoidea
Athoracophoridae						
Fischer, 1883	Heterurethra	—	—	Elasmognatha	—	Athoracophoroidea
Helicarionidae						
Bourguignat, 1888	Sigmurethra	Aulacopoda	Limacacea	Sigmurethra	Helicida	Helixarionoidea
Euconulidae						
H.B. Baker, 1928	Sigmurethra	Aulacopoda	Limacacea ¹¹	Sigmurethra	Helicida	Helixarionoidea
Ariophantidae						
Godwin-Austen, 1888	Sigmurethra	Aulacopoda	Limacacea ¹¹	Sigmurethra	Helicida	Helixarionoidea ¹¹
Urocyclidae						
Simroth, 1889	Sigmurethra	Aulacopoda	Limacacea	Sigmurethra	Helicida	Helixarionoidea
Aillyidae						
H.B. Baker, 1930	Heterurethra	—	—	Sigmurethra	Achatinida	Aillyoidea
Zonitidae						
Mörch, 1864	Sigmurethra	Aulacopoda	Limacacea	Sigmurethra	Helicida	Vitrinoidea
Trochomorphidae						
Möllendorff, 1890	Sigmurethra	Aulacopoda	Limacacea ¹²	Sigmurethra	Helicida	Helixarionoidea ¹¹
Vitrinidae						
Fitzinger, 1833	Sigmurethra	Aulacopoda	Limacacea ¹²	Sigmurethra	Helicida	Vitrinoidea
Thyrophorellidae						
Girard, 1895	Sigmurethra	Aulacopoda	Arionacea	Sigmurethra	Achatinida	Achatinoidea?
Parmacellidae						
Gray, 1860	—	—	—	Sigmurethra	Helicida	Vitrinoidea
Limacidae						
Rafinesque, 1815	Sigmurethra	Aulacopoda	Limacacea	Sigmurethra	Helicida	Limacoidea
Milacidae						
Germain, 1930	—	—	—	Sigmurethra	Helicida	Vitrinoidea
Trigonochlamyidae						
Hesse, 1882	Sigmurethra	Aulacopoda	Limacacea	Sigmurethra	Helicida	Trigonochlamydoidea
Testacellidae						
Gray, 1840	Sigmurethra	Aulacopoda	Testacellacea	Sigmurethra	Achatinida	Oleacinoidea
Polygyridae (= Mesodontidae)						
Pilsbry, 1894	Sigmurethra	Holopoda	Polygyracea	Sigmurethra	Helicida	Mesodontoidea
Sagidae						
Pilsbry, 1895	Sigmurethra	Holopoda	Oleacinacea	Sigmurethra	Helicida	Sagdoidea
Corillidae (= Plectopylidae)						
Pilsbry, 1905	Sigmurethra	Holopoda	Polygyracea	Sigmurethra	Achatinida	Plectopyloidea
Oleacinidae						
Adams, 1855	Sigmurethra	Holopoda	Oleacinacea	Sigmurethra	Achatinida	Oleacinoidea
Camaenidae						
Pilsbry, 1894	Sigmurethra	Holopoda	Helicacea	Sigmurethra	Helicida	Camaenoidea
Ammonitellidae						
Pilsbry, 1930	Sigmurethra	Holopoda	Polygyracea	Sigmurethra	Achatinida	Acavoidea ¹⁶

(continued)

APPENDIX. (Continued)

Family	Tillier, 1989	
	Suborder	Superfamily
Urocoptidae Pilsbry & Vanatta, 1898	Brachynephra	Clausilioidea
Bulimulidae Tryon, 1867	Brachynephra	Clausilioidea
Orthalicidae Albers-Martens, 1860	—	—
Amphibulimidae Crosse & Fischer, 1873	—	—
Odontostomidae Pilsbry & Vanatta, 1898	—	—
Punctidae Morse, 1864	Brachynephra	Endodontoidea
Endodontidae Pilsbry, 1894	Brachynephra	Endodontoidea
Charopidae Hutton, 1884	Brachynephra	Endodontoidea
Otoconchidae Cockerell, 1893	—	—
Helicodiscidae Pilsbry, 1927	—	—
Discidae Thiele, 1931	Dolichonephra	Zonitoidea
Arionidae Gray, 1840	Dolichonephra	Zonitoidea
Philomycidae Gray, 1847	Dolichonephra	Zonitoidea ¹⁹
Succineidae Beck, 1837	Dolichonephra	Achatinoidea
Athoracophoridae Fischer, 1883	Brachynephra	Endodontoidea
Helicarionidae Bourguignat, 1888	Dolichonephra	Helicoidea
Euconulidae H.B. Baker, 1928	Dolichonephra	Zonitoidea
Ariophantidae Godwin-Austen, 1888	—	—
Urocyclidae Simroth, 1889	—	—
Aillyidae H.B. Baker, 1930	Dolichonephra	Helicoidea ¹¹
Zonitidae Mörch, 1864	Dolichonephra Tillier, 1989	Zonitoidea
Trochomorphidae Möllendorff, 1890	Dolichonephra	Zonitoidea
Vitrinidae Fitzinger, 1833	Dolichonephra	Helicoidea
Thyrophorellidae Girard, 1895	—	—
Parmacellidae Gray, 1860	Dolichonephra	Zonitoidea
Limacidae Rafinesque, 1815	Dolichonephra	Zonitoidea
Milacidae Germain, 1930	Dolichonephra	Zonitoidea
Trigonochlamydidae Hesse, 1882	Dolichonephra	Zonitoidea
Testacellidae Gray, 1840	Dolichonephra	Achatinoidea ²⁰
Polygyridae (= Mesodontidae) Pilsbry, 1894	Dolichonephra	Helicoidea
Sagdidae Pilsbry, 1895	Dolichonephra	Helicoidea
Corillidae (= Plectopylidae) Pilsbry, 1905	Brachynephra	Acavoidea
Oleacinidae Adams, 1855	Dolichonephra	Achatinoidea
Camaenidae Pilsbry, 1894	Dolichonephra	Helicoidea
Ammonitellidae Pilsbry, 1930	Brachynephra	Acavoidea ²¹

APPENDIX. (Continued)

Family	Solem, 1978		
	Order	Suborder	Superfamily
Oreohelicidae			
Pilsbry, 1939	Sigmurethra	Holopoda	Camaenacea
Bradybaenidae			
Pilsbry, 1939	Sigmurethra	Holopoda	Helicacea
Helminthoglyptidae (= Xanthonychidae)			
Pilsbry, 1939	Sigmurethra	Holopoda	Helicacea
Helicidae			
Rafinesque, 1815	Sigmurethra	Holopoda	Helicacea
Megalobulimidae			
(in Strophocheilidae)			
Leme, 1973	—	—	—
Anadromidae			
Zilch, 1959 (fossil)	—	—	—
Stenogyridae			
(in Subulinidae?)			
Wenz, 1923 (fossil)	—	—	—
Filholiidae			
Wenz, 1923	—	—	—
Dendropupidae			
Wenz, 1938	—	—	—
Thysanophoridae			
(in Polygyridae?)			
Pilsbry, 1926	—	—	—
Gastrodontidae			
(in Zonitidae)			
Tryon, 1866	—	—	—
Chlamydephoridae (= Aperidae)			
Cockerell, 1935	—	—	—
Sphincterochilidae			
(in Helicidae)			
Zilch, 1959	—	—	—
Helicodontidae (in Helicidae)			
Hesse, 1918	—	—	—
Humboldianidae			
(in Helminthoglyptidae)			
Pilsbry, 1939	—	—	—
Hygromiidae (in Helicidae)			
Tryon, 1866	—	—	—
Daudebardiidae (in Zonitidae)			
Pilsbry, 1908	—	—	—
Boetgerillidae			
(in Parmacellidae)			
Van Goethem, 1972	—	—	—
Agriolimacidae (in Limacidae)			
Wagner, 1935	—	—	—
Helicellidae (in Helicidae)			
Wenz, 1923	—	—	—
Cerastuidae (in Enidae)			
Wenz, 1923	—	—	—
Coelioxidae (in Subulinidae)			
Pilsbry, 1907	—	—	—
Megomphicidae			
(in Ammonitellidae)			
H.B. Baker, 1930	—	—	—
Sculptariidae (in Corillidae)			
Nordsieck, 1986?	—	—	—
Oopeltidae (in Arionidae)			
H.B. Baker, 1930	—	—	—
Cystopeltidae			
(in Ariophantidae)			
Cockerell, 1891	—	—	—
Solaropsidae (in Camaenidae)			
Nordsieck, 1986	—	—	—

(continued)

APPENDIX. (Continued)

Family	Schileyko, 1979			
	Order	Suborder	Infraorder	Superfamily
Oreohelicidae Pilsbry, 1939	Geophila	Helixina	Helixinia	Helicoidea
Bradybaenidae Pilsbry, 1939	Geophila	Helixina	Helixinia	Helicoidea
Helminthoglyptidae (= Xanthonychidae) Pilsbry, 1939	Geophila	Helixina	Helixinia	Helicoidea
Helicidae Rafinesque, 1815	Geophila	Helixina	Helixinia	Helicoidea
Megalobulimidae (in Strophocheilidae) Leme, 1973	Geophila Ferussac, 1812	Achatinina Schileyko, 1979	—	Achatinoidea
Anadromidae Zilch, 1959 (fossil)	Geophila	Achatinina	—	Achatinoidea
Stenogyridae (in Subulinidae?) Wenz, 1923 (fossil)	Geophila	Achatinina	—	Subulinoidea
Filholiidae Wenz, 1923	Geophila	Achatinina	—	Clausilioidea
Dendropupidae Wenz, 1938	Geophila	Pupillina	—	Achatinelloidea
Thysanophoridae (in Polygyridae?) Pilsbry, 1926	Geophila	Pupillina	—	Sagdoidea
Gastrodontidae (in Zonitidae) Tryon, 1866	Geophila	Helixina	Helixinia	Gastrodontoidea
Chlamydephoridae (= Aperidae) Cockerell, 1935	Geophila	Helixina	Helixinia	Rhytidoidea
Sphincterochilidae (in Helicidae) Zilch, 1959	Geophila	Helixinia	Helixinia	Sphincterochiloidea
Helicodontidae (in Helicidae) Hesse, 1918	Geophila	Helixina	Helixinia	Helicodontoidea
Humboldtianidae (in Helminthoglyptidae) Pilsbry, 1939	Geophila	Helixina	Helixinia	Helicoidea
Hygromiidae (in Helicidae) Tryon, 1866	Geophila	Helixina	Helixinia	Hygromioidea
Daudebardiidae (in Zonitidae) Pilsbry, 1908	Geophila	Helixina	Zonitina	Zonitoidea
Boetgerillidae (in Parmacellidae) Van Goethem, 1972	Geophila	Limaxina	Limaxinia Schileyko, 1979	Limacoidea
Agriolimacidae (in Limacidae) Wagner, 1935	Geophila	Limaxina	Limaxinia	Limacoidea
Helicellidae (in Helicidae) Wenz, 1923	—	—	—	—
Cerastuidae (in Enidae) Wenz, 1923	—	—	—	—
Coeliacidae (in Subulinidae) Pilsbry, 1907	—	—	—	—
Megomphicidae (in Ammonitellidae) H.B. Baker, 1930	—	—	—	—
Sculptariidae (in Corillidae) Nordsieck, 1986?	—	—	—	—
Oopeltidae (in Arionidae) H.B. Baker, 1930	—	—	—	—
Cystopeltidae (in Ariophantidae) Cockerell, 1891	—	—	—	—
Solaropsidae (in Camaenidae) Nordsieck, 1986	—	—	—	—

APPENDIX. (Continued)

Family	Boss, 1982			Nordsieck, 1985, 1986		
	Suborder	Infrorder	Superfamily	Order	Suborder	Superfamily
Oreochelonicidae						
Pilsbry, 1939	Sigmurethra	Holopoda	Helicea	Sigmurethra	Achatinida	Punctoidea
Bradybaenidae						
Pilsbry, 1939	Sigmurethra	Holopoda	Helicea	Sigmurethra	Helicida	Helicoidea
Helminthoglyptidae (= Xanthonychidae)						
Pilsbry, 1939	Sigmurethra	Holopoda	Helicea	Sigmurethra	Helicida	Helicoidea
Helicidae						
Rafinesque, 1815	Sigmurethra	Holopoda	Helicea	Sigmurethra	Helicida	Helicoidea
Megalobulimidae						
(in Strophocheilidae)						
Leme, 1973	—	—	—	—	—	—
Anadromidae						
Zilch, 1959 (fossil)	—	—	—	—	—	—
Stenogyridae						
(in Subulinidae?)						
Wenz, 1923 (fossil)	—	—	—	—	—	—
Filholiidae						
Wenz, 1923	—	—	—	—	—	—
Dendropupidae						
Wenz, 1938	—	—	—	—	—	—
Thysanophoridae						
(in Polygyridae?)						
Pilsbry, 1926	Sigmurethra	Holopoda	Polygyracea	Sigmurethra	Helicida	Mesodontoidea
Gastrodontidae						
(in Zonitidae)						
Tryon, 1866	—	—	—	Sigmurethra	Helicida	Gastrodontoidea
Chlamydephoridae (= Aperidae)						
Cockerell, 1935	—	—	—	Sigmurethra	Achatinida	Rhytidoidea
Sphincterochilidae						
(in Helicidae)						
Zilch, 1959	—	—	—	Sigmurethra	Helicida	Helicoidea
Helicodontidae (in Helicidae)						
Hesse, 1918	—	—	—	—	—	—
Humboldianidae						
(in Helminthoglyptidae)						
Pilsbry, 1939	—	—	—	—	—	—
Hygromiidae (in Helicidae)						
Tryon, 1866	—	—	—	Sigmurethra	Helicida	Helicoidea
Daudebardidae (in Zonitidae)						
Pilsbry, 1908	Sigmurethra	Aulacopoda	Limacacea ¹²	Sigmurethra	Helicida	Vitrinoidea
Boetgerillidae						
(in Parmacellidae)						
Van Goethem, 1972	—	—	—	Sigmurethra	Helicida	Limacoidea
Agriolimacidae (in Limacidae)						
Wagner, 1935	—	—	—	Sigmurethra	Helicida	Limacoidea
Helicellidae (in Helicidae)						
Wenz, 1923	Sigmurethra	Aulacopoda	Helicea	—	—	—
Cerastuidae (in Enidae)						
Wenz, 1923	—	—	—	Orthurethra	—	Buliminoidea
Coeliaxidae (in Subulinidae)						
Pilsbry, 1907	—	—	—	Sigmurethra	Achatinida	Achatinoidea
Megomphicidae						
(in Ammonitellidae)						
H.B. Baker, 1930	—	—	—	Sigmurethra	Achatinida	Acavoidea
Sculptariidae (in Corillidae)						
Nordsieck, 1986?	—	—	—	Sigmurethra	Achatinida	Plectopyloidea
Oopeltidae (in Arionidae)						
H.B. Baker, 1930	—	—	—	Sigmurethra	Achatinida	Punctoidea
Cystopeltidae						
(in Ariophantidae)						
Cockerell, 1891	—	—	—	Sigmurethra	Helicida	Helixarionoidea
Solaropsidae (in Camaenidae)						
Nordsieck, 1986	—	—	—	Sigmurethra	Helicida	Camaenoidea

(continued)

APPENDIX. (Continued)

Family	Tillier, 1989	
	Suborder	Superfamily
Oreohelicidae		
Pilsbry, 1939	Brachynephra	Acavoidea
Bradybaenidae		
Pilsbry, 1939	Dolichonephra	Helicoidea
Helminthoglyptidae (= Xanthonychidae)		
Pilsbry, 1939	Dolichonephra	Helicoidea
Helicidae		
Rafinesque, 1815	Dolichonephra	Helicoidea
Megalobulimidae		
(in Strophocheilidae)		
Leme, 1973	—	—
Anadromidae		
Zilch, 1959 (fossil)	—	—
Stenogyridae		
(in Subulinidae?) (fossil)		
Wenz, 1923	—	—
Filholidae		
Wenz, 1923	—	—
Dendropupidae		
Wenz, 1923	—	—
Thysanophoridae		
(in Polygridae?)		
Pilsbry, 1926	—	—
Gastrodontiidae		
(in Zonitidae)		
Tryon, 1866	—	—
Chlamydephoridae (= Aperidae)		
Cockerell, 1935	Brachynephra	Acavoidea ²²
Sphinterochilidae		
(in Helicidae)		
Zilch, 1959	—	—
Helicodontidae (in Helicidae)		
Hesse, 1918	—	—
Humboldianidae		
(in Helminthoglyptidae)		
Pilsbry, 1939	—	—
Hygromiidae (in Helicidae)		
Tryon, 1866	—	—
Daudebardiiidae (in Zonitidae)		
Pilsbry, 1908	—	—
Boetgerillidae		
(in Parmacellidae)		
Van Goethem, 1972	—	—
Agriolimacidae (in Limacidae)		
Wagner, 1935	—	—
Helicellidae (in Helicidae)		
Wenz, 1923	—	—
Cerastuidae (in Enidae)		
Wenz, 1923	—	—
Coeliaxidae (in Subulinidae)		
Pilsbry, 1907	—	—
Megomphicidae		
(in Ammonitellidae)		
H.B. Baker, 1930	—	—
Sculptariidae (in Corillidae)		
Nordsieck, 1986?	—	—
Oopeltidae (in Arionidae)		
H.B. Baker, 1930	—	—
Cystopeltidae		
(in Ariophantidae)		
Cockerell, 1891	—	—
Solaropsidae (in Camaenidae)		
Nordsieck, 1986	—	—

¹Synonymized under Achatinellidae.; ²Synonymized under Pupillidae.; ³Synonymized under Pleurodiscidae.; ⁴Synonymized under Acavidae.; ⁵Synonymized under Bulimulidae.; ⁶Synonymized under Charopidae.; ⁷Synonymized under Helicarionidae.; ⁸Synonymized under Zonitidae.; ⁹Synonymized under Limacidae.; ¹⁰Synonymized under Endodontidae.; ¹¹Synonymized under Helicarionidae.; ¹²Synonymized under Zonitidae.; ¹³Occupies an isolated position in the order, so may be a separate suborder.; ¹⁴Synonymized under Orthalicidae.; ¹⁵Synonymized under Caryodidae.; ¹⁶Synonymized under Megomphicidae.; ¹⁷Synonymized under Punctidae.; ¹⁸Synonymized under Valloniidae.; ¹⁹Synonymized under Arionidae.; ²⁰Synonymized under Oleacinidae.; ²¹Synonymized under Oreohelicidae.; ²²Synonymized under Rhytididae.

ASPECTS OF THE LIFE CYCLE, POPULATION DYNAMICS, GROWTH AND
SECONDARY PRODUCTION OF THE SNAIL *MONACHA CARTUSIANA*
(MÜLLER, 1774) (GASTROPODA PULMONATA) IN GREECE

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ABSTRACT

The life cycle, population dynamics, growth and secondary production of the land snail *Monacha cartusiana* were studied in northern Greece. Demographic analysis of the populations of *M. cartusiana* revealed that (a) two to three cohorts existed in the field throughout the year, (b) the reproductive period started in the beginning, middle or end of autumn, depending on the weather conditions, and (c) growth of newly hatched individuals was also influenced by weather conditions. Net reproductive rate (R_0) was equal to 2.07, and the finite capacity for increase (r_c) was equal to 1. Estimated annual secondary production with the Hynes' size frequency method revealed a mean standing crop (B) of 0.147 g/m²/year and a production (P) of 0.31 ± 0.02 g/m²/year. Annual turnover ratio (P/B) was equal to 2.11.

INTRODUCTION

Several species of the helioid snail *Monacha* are known to exist in Greece. Pinter (1978) described the systematics and distribution of three Greek *Monacha* species: *M. messenica*, *M. dirphica* and *M. beieri*.

Although *Monacha cartusiana* is widespread in Europe (Germain, 1930), little is known about its life history (Taylor, 1921; Germain, 1930; Chatfield, 1968).

M. cartusiana was studied in a natural habitat, where it coexists with three other helioid species, namely *Helix lucorum*, *Bradybaena fruticum* and *Cepaea vindobonensis*, the ecology of which has also been studied (Staikou et al., 1988; Staikou & Lazaridou-Dimitriadou, in press). The relationships of these coexisting species are important for two reasons: in culturing *H. lucorum*, the most important of the edible Greek species, in open enclosures, and in order to study their possible competitive strategies. So in this paper the biology, ecology, relative growth and the annual secondary production of *M. cartusiana* are studied.

Study Area

The habitat of *M. cartusiana* was situated in the Logos region of Edessa (N. Greece), which lies 100 km from Thessaloniki. The

study on the ecology and biology of the edible snail *Helix lucorum*, which was carried out in the same region, had made it necessary to fence off the study area to prevent local people collecting *Helix lucorum*. A full description of the study area and the main characteristics of the coexisting snail species have been given in a previous paper (Staikou et al., 1988). The vegetation was not uniform but had patches where different plant species dominated. The climate of the region is of the humid mediterranean type, characterised by prolonged rainy periods in mid-summer (Staikou et al., 1988).

METHODS AND MATERIALS

The study of *M. cartusiana* started in June 1982 and lasted four years. Data from May 1983 to December 1985 were used for the demographic analysis of the populations.

Samples were taken randomly every 15 days throughout the year. The quadrat sample-size used (50 × 50 cm²) was determined by Healy's method (Cancela da Fonseca, 1965). Elliot's method (1971) was used to determine the necessary total number of sampling units for a sampling error less than 20%. Sampling was carried out during morning hours in the absence of rain. All snails found in a quadrat were collected, measured and

then returned to their initial places. The largest diameter of the shell (D) and the peristome diameter (d) were measured.

Spatial distribution of the snails in the habitat was examined by using Taylor's power law (1961). The parameter b from Taylor's equation $s^2 = a\bar{x}^b$ (where a = constant, s^2 = variance, \bar{x} = mean number of snails found in a sample unit) was used as an index of dispersion. Parameter b is fairly constant and characterizes a species (Southwood, 1966); it is independent of the total number of samples and the total number of animals in the samples; it depends only on the quadrat size (Elliott, 1971).

The class interval of the monthly size frequency histograms was 1 mm (Fig. 1) and was determined by Goulden's method (Cancela da Fonseca, 1965). The largest diameter of the shell (D) was used for the construction of the histograms because it is generally accepted as the most reliable morphometric parameter (Lazaridou-Dimitriadou, 1978; Charrier & Daguzan, 1978; Daguzan, 1982).

The cohorts were discriminated using probability paper (Harding, 1949). This method was valid because the modes of the age classes were separated by at least 2.5 standard deviations (Grant, 1989), except in October and November 1983 and September and November 1984. Although many age classes had less than 50 individuals, the modal values are consistent from month to month (Fig. 2), which confirms that the modes are real and not the result of sampling variation. This method has been used for demographic analyses of the populations of other molluscs (Hugues, 1970; Levêque, 1972; Daguzan, 1975; Lazaridou-Dimitriadou, 1978, 1981; Lazaridou-Dimitriadou & Kattoulas, 1985; Staikou et al., 1988).

An age-specific life table was constructed based on the fate of a real cohort that entered the population in 1983 (Fig. 2). The methodology for the construction of the life table is described in detail by Staikou et al. (1988). To determine the total number of snails hatched in 1983, the method of Richards and Waloff (Southwood, 1966) was used. The number of snails of the 1983 cohort in the following years was extrapolated from the results of the demographic analyses of the populations of *M. cartusiana*.

Mayrat's method (1965a,b) was used to distinguish between juveniles and adults by comparing the growth of the largest shell diameter (D) relative to the dry weight of

the snail (W) and to the peristome diameter (d).

To determine annual production, the snails were grouped into 15 size classes. The mean number of snails (\bar{n}) in each size class was determined using data from the population dynamics. To determine dry body and shell weight, 63 snails representing all size classes were used following the methodology described in detail in Staikou et al. (1988). Annual production in 1984 was calculated by the Hyne's size frequency method modified according to Benke (1979) and Krueger & Martin (1980). This has the advantage that single cohorts within the data need not be identified to calculate production, although it may produce an overestimate (Waters & Crawford, 1973). The formulae used were given by Staikou et al. (1988).

RESULTS

A. Aspects of the Biology

Individuals were sexually mature when the largest shell diameter (D) exceeds 7 mm. Sexual maturity is indicated externally by the presence of a characteristic reddish strip near the edge of the aperture and the formation of an internal lip. During the breeding season, all snails with $D > 9$ mm showed these external characteristics. Examination of the external features of the shell and the genitalia of 48 snails ($7.15 \text{ mm} < D < 14.25 \text{ mm}$) showed that genitalia were fully formed only when the red ribbon appeared around the aperture. Gonad maturation was histologically checked in 36 snails collected in June with $3.5 \text{ mm} < D < 14 \text{ mm}$. It was found that differentiation of oocytes started when D reached 5 mm, but grown oocytes were present in the gonad when D exceeded 7 mm. Spermatocytes turned to spermatids when $D > 9$ mm.

Sexual maturity was normally attained two years after hatching. However, about 14% reached maturity one year after hatching; these snails laid eggs one year after hatching and died immediately after (Fig. 2). The reproductive period started at the beginning or in the middle of autumn, and it was often prolonged until the start of winter (December or January). In 1984, some snails laid eggs in late August as well as in late October. The snails were active during winter. They aestivated in summer under dry, creeping vegetation or in the ground at surface level, forming

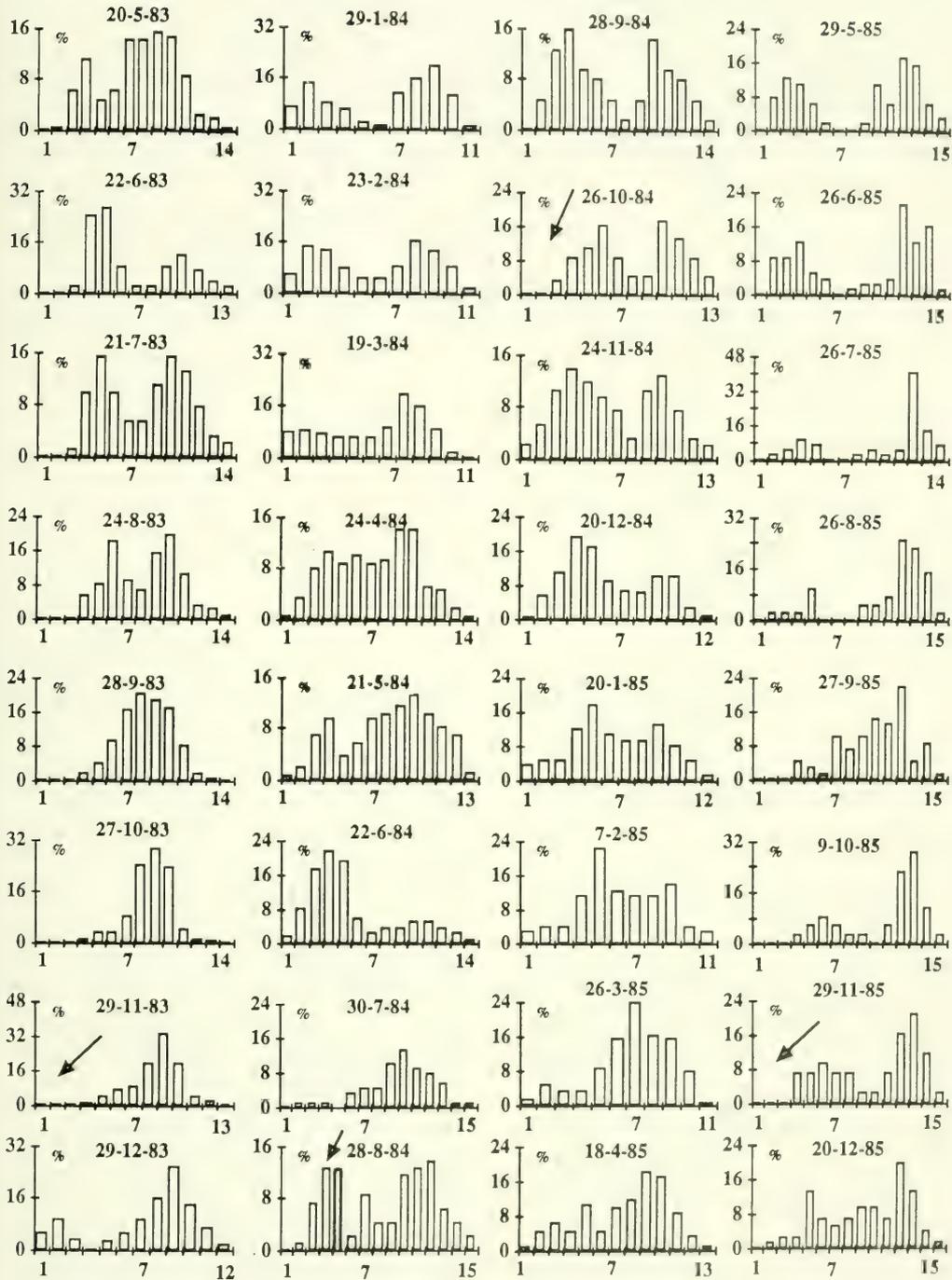


FIG. 1. Size frequency histograms of the populations of *Monacha cartusiana* at Edessa (N. Greece) from May 1983 to December 1985 (arrows represent the beginning of the reproductive period).

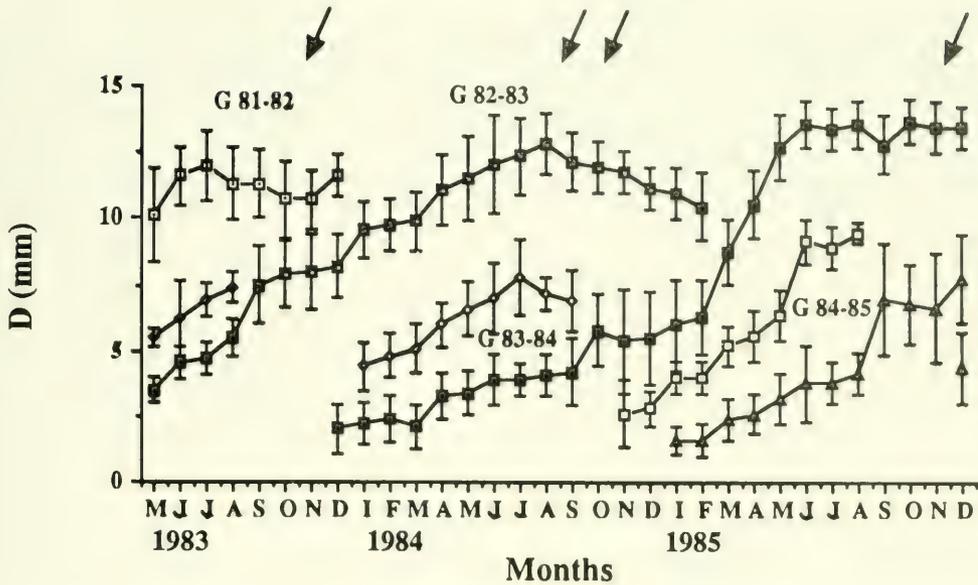


FIG. 2. Modal distributions of *Monacha cartusiana* populations at Edessa (N. Greece) from May 1983 to December 1985 (arrows represent the beginning of the reproductive period).

rity in their second year, at a greater adult size than the faster growing snails and some months before reproduction occurs.

(d) Therefore, there are three cohorts present in most months; the fast-growing snails, the slow-growing snails less than one year old, and the slow-growing snails in their second year.

E. Life and Fertility Table (Table 2)

From observations and calculations of marked snails in the field it was found that (a) the fastest growing snails laid eggs one year after hatching and died immediately after, while the majority of the population reached maturity and laid eggs two years after hatching; (b) all the adult snails died after the reproductive period, none of the 200 marked adults surviving to lay eggs for a second year; (c) the mean number of eggs laid per snail was 32.67 ± 10.82 ($N = 9$), and 24.5% of the eggs did not hatch because of desiccation or other reasons; and (d) there was 30% mortality just after hatching (75 isolated hatchlings were marked and followed).

The cohort G83-84 (Fig. 2) studied in the life table was followed until the maturation and subsequent death of all adults.

From the life table, the following conclusions may be drawn:

- Mortality rate (k_x) is low during the first year and increases after the attainment of sexual maturity.
- Life expectancy (e_x) decreases with increasing age.
- The value of net reproductive rate (R_0) is greater than one.
- The finite capacity for increase (r_c) is low.

F. Relative Growth

The study of relative growth (D relative to W or to d for the whole population of *M. cartusiana*) (Fig. 3) showed that there is a positive correlation between D and W and d ($r^2 = 0.859$ $N = 145$, and $r^2 = 0.938$ $N = 1303$ respectively). There was no statistical difference between juvenile and adult snails in the growth rate of D relative to d. However, growth rate of D in relation to W was faster in juveniles ($D < 7\text{mm}$) than in adults (adults: $\log W = 2.78 \log D - 3.44$ $r^2 = 0.967$ $N = 80$; juveniles: $\log W = 3.24 \log D - 3.76$ $r^2 = 0.726$ $N = 65$). The intersection point between these two subpopulations occurs at $D = 5$ mm, which is the diameter at which oocytes start differentiating according to histological examination of gonads.

TABLE 2. Life and fertility table of a cohort of *Monacha cartusiana* starting in 1983 [x, age in months; a_x = numbers of animals surviving at the beginning of age class x; l_x = number of animals surviving at the beginning of age class x if a thousand were originally hatched; d_x = number of animals dying during age interval x; q_x = d_x/l_x mortality rate during age interval x; K_x = $\log_{10}ax - \log_{10}ax + 1$ intensity or rate of mortality; $L_x = l_x + l_x + 1/2$ number of animals alive between age x and x + 1; $T_x = L_x + L_x + 1 \dots L_w$ = total number of animal x age units beyond the age x; $e_x = T_x/l_x$ expectation of life; l'_x = number of animals alive during age interval x as a fraction of an initial population of one (in parenthesis is noted the number of animals that laid eggs); m_x = number of living animals hatched per adult animal; V_x = total number of hatchings in each age interval; R_0 = net reproductive rate; r_c = per capita rate of increase; T_c = generation time].

Age	a_x	l_x	d_x	q_x	$\log_{10}ax$	K_x	L_x	T_x	e_x	l'_x	m_x^{**}	V_x
0	2344	1000	357	0.36	3.37	0.19	822	2090	2.09	1	—	—
6	1507	643	233	0.36	3.18	0.20	527	1268	1.97	0.64	—	—
12	960	410	2	0.005	2.98	0.00	409	741	1.80	0.49	(0.05)*	17.26
18	956	408	281	0.69	2.98	0.51	268	332	0.81	0.33	—	—
24	297	127	127	1.00	2.47	—	64	64	0.50	0.07	(0.07)	17.26
30	0	0	—	—	—	—	0	0	0	0	—	—

$R_0 = \sum V_x = \sum l'_x m_x = 2.07$
 $r_c = \ln R_0 / T_c = 0.001$
 $\text{antilog}_e r_c = 1$

**The numbers of the m_x column have been calculated on the hypothesis that 24.5% of the eggs do not hatch and there is a 30% mortality just after hatching.

*This number represents the individuals which become mature one year after hatching.

G. Secondary Production

The computed estimates of annual production according to the Hynes' size frequency method are listed in Table III. The mean biomass of each size class is expressed in dry weight on the basis of the following relationship between dry body weight (Wb ;) and D and dry shell weight (Ws ;) and D :

$$\text{Log } Wb = 2.77 \text{Log } D - 4.29 (r^2 = 0.992; N = 48)$$

$$\text{Log } Ws = 3.27 \text{Log } D - 4.73 (r^2 = 0.988; N = 48)$$

The shell organic matter of mature snails was 7.43% ($N = 28$ snails), and that of immature snails was 7.38% ($N = 20$ snails). These values do not differ statistically, therefore a common mean value of $7.57 \pm 0.29\%$ ($N = 48$) was used to determine the organic matter of the shell of all the snails used (Table 3).

Applying Benke's correction, values of n (mean annual density), B (mean annual crop) and P (annual production) were calculated to be 7.20 individuals / m^2 , 0.147 g / mg^2 / year and 0.31 ± 0.02 g / m^2 / year respectively. The annual turnover ratio P/B was 2.11.

DISCUSSION

The life history of *M. cartusiana* in the locality studied in northern Greece was similar

to that reported for the same species in France (Chatfield, 1968). The size range of the largest shell diameter (D) of adult snails is similar in the Greek and French populations (Chatfield, 1968). The internal lip in *M. cartusiana* from France formed with $D \geq 8.0$ mm, while in Greece it was formed in specimens whose $D \geq 7.00$ mm. The lip formation occurred in mid-summer in France and in late spring or early summer (May-June) in Greece. Aestivation, which took place in mid-summer, may reduce competition with coexisting species of snails in the same biotope, which did not aestivate in summer but hibernated during winter. Weather conditions seemed to influence the onset of the reproductive period because in the wet August 1984 (fig. 1 in Staikou et al., 1988), reproduction started earlier than in 1983 and 1985. The same dependance of the onset of reproductive period on weather conditions was also noticed in the other coexisting snails studied, namely *H. lucorum* and *B. fruticum* (Staikou et al., 1988; Staikou & Lazaridou-Dimitriadou, in press).

The recruitment of newly hatched snails in the population during the breeding season was the main reason for the rise in population density in September and October 1983 and in December 1984 and 1985. The low estimates of population density, which coincided with a high sampling error (Table 1), were

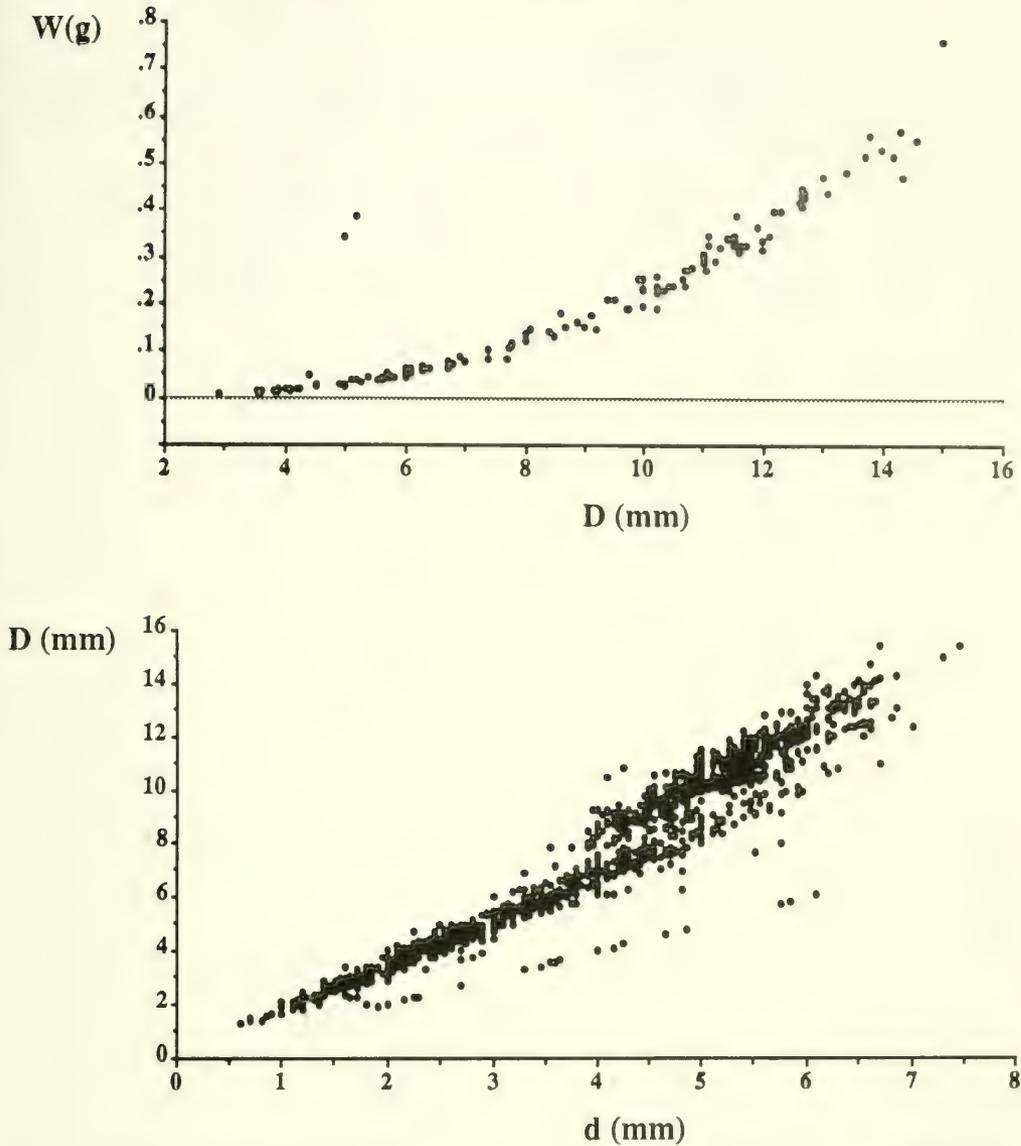


FIG. 3. Relative growth of the largest shell diameter (D mm), in relation to snail dry weight (Wg), or to peristome diameter (d mm), in *Monacha cartusiana*.

probably caused by unusually dry conditions (fig 1 in Staikou et al., 1988) that might have caused aestivation.

The populations of *B. fruticum* in the same area also showed contagious spatial distribution, while the spatial distribution of *H. luco-rum* was random (Staikou et al., 1988). In Greece, contagious distribution has been reported mainly for such xerothermophilic species as *Euparypha pisana*, *Xeropicta arenosa*

and *Cerņuella virgata* (Lazaridou-Dimitriadou, 1981). However, *M. cartusiana* can not be considered a xerothermophilic species, so this kind of distribution may be provoked by some other cause, which needs to be studied.

Seasonal variations in growth rate related to weather conditions have been reported for other snails in Greece, namely *X. arenosa*, *C. virgata* and *E. vermiculata* (Lazaridou-Dimitri-

TABLE 3. Calculation of production of *Monacha cartusiana* by the size-frequency method. Annual production based on 12 sets of samples from January 84 to December 84 (where n_j = mean number of snails at the size class j ; U = variance of n_j ; W = mean individual dry body weight + mean dry shell organic matter; G = geometric mean; B = Mean standing crop or population biomass; P = annual production; P/B = annual turnover ratio; a = number of size classes; CPI = cohort production interval).

Size class			$\bar{n}_j - \bar{n}_j + 1$ /m ²	\bar{w}_j (mg)	G _j ($\bar{w}_j \cdot \bar{w}_j$) ^{0.5}	$\langle \bar{B} \rangle$ [$\bar{n}_j/m^2 \cdot \bar{w}_j$ (mg)] (mg·m ⁻²)	P· ($\bar{n}_j - \bar{n}_j + 1$)(G _j) [mg·m ⁻²]
	\bar{n}_j/m^2	$U\bar{n}_j$					
1-2	0.13	0.00056	-0.235	0.2	0.34	0.027	-0.0881
2-3	0.37	0.00388	-0.333	0.7	1.12	0.259	-0.373
3-4	0.70	0.00476	-0.203	1.8	2.51	1.265	-0.511
4-5	0.91	0.01190	0.136	3.5	4.58	3.171	0.625
5-6	0.77	0.00725	0.274	6.0	7.75	4.619	2.121
6-7	0.50	0.00466	0.019	10.0	11.83	4.959	0.225
7-8	0.48	0.00302	-0.159	14.0	16.73	6.677	-2.664
8-9	0.64	0.00276	-0.143	20.0	23.24	12.721	-3.312
9-10	0.78	0.00578	0.003	27.0	30.74	21.022	0.1021
10-11	0.78	0.00731	0.255	35.0	39.69	27.135	10.129
11-12	0.52	0.00174	0.174	45.0	50.65	23.402	8.824
12-13	0.35	0.00089	0.158	57.0	63.17	19.712	9.973
13-14	0.19	0.00030	0.102	70.0	77.14	13.156	7.879
14-15	0.09	0.00011	0.069	85.0	93.11	7.295	6.468
15-16	0.02	0.00002	0.016	102.0	102.00	1.666	1.667
	7.20					147.1	41.06

$$P = a \cdot P' \cdot 365 / CPI = 15 \cdot 41.06 \cdot 365 / 730 = 308.25 \text{ (mg/m}^2\text{)} = 0.31 \text{ (g/m}^2\text{)}$$

$$U(P) = U\bar{n}_j(G_j - G(j-1))^2 \cdot 2^2 \cdot (365/CPI)^2 = (3.93 \cdot 10^{-4}) \cdot (365 / 730)^2 = 0.000098$$

$$\text{Confidence interval of } P = P \pm 2[U(P)^{0.5}] = 0.31 \pm 0.02$$

$$P/B = 0.31 / 0.1471 = 2.11$$

adou, 1981; Lazaridou-Dimitriadou & Kattoulas, 1985). In the same biotope *B. fruticum* showed increased growth rate in spring and in autumn, while *H. lucorum* like *M. cartusiana* increased growth rate only in spring (Staikou et al., 1988).

High mortality after the reproductive period is common among those helicid snails which are also r-strategists. R_0 is greater than unity, showing the tendency of the population to increase. The reproductive success of *M. cartusiana* may be related to its lifespan, which is much shorter than that of such species as *H. pomatia* (Pollard & Welch, 1980; Lomnicki, 1971) and *H. lucorum* (Staikou et al., 1988). However, it must be noted that *B. fruticum* in the same biotope (Staikou & Lazaridou-Dimitriadou, 1990) and *E. vermiculata* in similar biotopes (Lazaridou-Dimitriadou & Kattoulas, submitted), have a higher reproductive successes ($R_0 = 3.15$ and 3.43 respectively) although they have a longer life span than *M. cartusiana*. The value of the annual turnover ratio P/B , which seems to be related to the life span of the species (Russell-Hunter & Buckley, 1983; Lamotte & Stern, 1987), was similar to that found for *E. vermiculata* ($P/B = 2.00$) (Lazaridou-Dimitriadou & Kattoulas,

submitted), which has the same CPI but a longer life span. *M. cartusiana* has a lower P/B than *B. fruticum* ($P/B = 2.37$) from the same biotope, the same CPI , but a longer life span (Staikou & Lazaridou-Dimitriadou, 1990).

Finally, the fact that internal changes in genitalia and maturation of the gonad of this species correspond to external morphometric changes of the shell is in agreement with the results reported for such other helicids as *E. vermiculata*, *H. aspersa* (Lazaridou-Dimitriadou & Kattoulas, 1981), *Cerņuella virgata* and *Xeropicta arenosa* (Lazaridou-Dimitriadou, 1986) and *H. lucorum* (Staikou et al., 1988) in Greece and elsewhere as in *H. aspersa* (Charrier & Daguzan, 1978) and other Helicidae (Yom-Tov, 1971; Bonavita, 1972; Williamson, 1976).

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CALYPTOGENA (CALYPTOGENA) BIRMANI, A NEW SPECIES OF
VESICOMYIDAE (MOLLUSCA-BIVALVIA) FROM BRAZIL

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ABSTRACT

Calyptogena (Calyptogena) birmani, a new species of a rare deep-sea family, Vesicomidae, is described from material collected at a depth of 400 m off the State of Paraná, southwest Atlantic Ocean, Brazilian coast, by the R/V W. BESNARD. No living specimens were obtained, and only the shell characters were compared with the known *Calyptogena* species from the Atlantic and with the most closely related species from the Pacific.

Key words: bivalve, Vesicomidae, *Calyptogena*, systematics, Brazil.

INTRODUCTION

During the 2–4 October 1978, the R/V W. BESNARD, of the Instituto Oceanográfico, Universidade de São Paulo, collected off the coast of São Paulo and Paraná states, Brazil, in the southwest Atlantic Ocean, a number of shallow to deep-water samples, using a Campbell Photo-Grab. At station 2 in a depth of 400 m, 14 empty shells (entire specimens with both valves), 87 left valves and 93 right valves were obtained of an unusually small veneroid-shaped bivalve. Based on careful examination and comparison of this material with the published literature, the specimens were found to be a new species referable to Vesicomidae Dall & Simpson, 1901. The Vesicomidae were not known from Brazil until 1975 (Lange de Morretes, 1949, 1954; Rios, 1970, 1975). In a preliminary study, Birman & Lopes (1985) suggested that the R/V W. BESNARD material belonged to *Calyptogena* Dall, 1891, and considered it the first occurrence of the Vesicomidae along the Brazilian coast. On this basis, Rios (1985) updated his catalogue. A more accurate review of the papers related to Vesicomidae revealed that Dall (1889) had already described *Callocardia albida* from off Rio de Janeiro, at a depth of 108 m, and had placed it in the Isocardiidae; later, Keen (1969) allocated it to the Vesicomidae.

The taxa grouped under Vesicomidae have had a confused history as discussed by Boss (1968, 1969, 1970), Boss & Turner (1980) and Turner (1985). The lack of a sat-

isfactory diagnosis that would exclude them from all other related heterodonts has led various authors to assign these taxa to such families as the Arcticidae (= Cyprinidae), Carditidae, Kelliellidae and Veneridae (Boss & Turner, 1980). It is beyond the scope of this paper to discuss the systematics of the group. Most authors, following Keen (1969) and Boss & Turner (1980), have considered *Calyptogena* to belong to the Vesicomidae.

Vesicomidae is a rare deep-sea family whose living species examined to date come from sulfide-rich substrates (Turner, 1985).

The discovery of deep-sea hydrothermal vents on the eastern Pacific sea floor and deep sulfide seeps in the Gulf of Mexico has attracted the attention of zoologists to their abundant macrofauna of which Vesicomidae was found to be one of the major components (Turner, 1985). Besides bacterial chemosynthetic activity, which provides the major bulk of the food supply for the vent and seep communities (Turner & Lutz, 1984), a symbiotic association of these bacteria with clams, mussels, tube worms, plays an important role in their nutrition and distribution (Cavanaugh, 1983), and in the food chain dynamics at the vents and seeps (Turner & Lutz, 1984). Vesicomidae are also known from reducing sediments not related to vents or seeps, as is the case of *Calyptogena (Ectenagena) australis* Stuardo & Valdovinos, 1988, from off the coast of central Chile (Stuardo & Valdovinos, 1988).

All living species of Vesicomidae known to date shelter chemoautotrophic symbiotic bac-

teria in their large and thick gills (Turner, 1985; Stuardo & Valdovinos, 1988). Based on this fact and on shell characters, Turner (1985) suggested the origin of the large species of Vesicomidae, found at the vents and seeps, from small, infaunal deep-sea kelliellid bivalves, by adopting the habit of harbouring symbiotic bacteria in the gills. On the other hand, Stuardo & Valdovinos (1988) speculated that vesicomids might have developed endosymbiosis as an adaptation to reducing sediments, becoming preadapted to invade the specialized habitat of the hydrothermal vents. The requirement of such a special environment makes the Vesicomidae good indicators of sulfide-rich sediments and/or vents or seeps.

The deep sea of the southern Atlantic is scarcely explored for these habitats, and the discovery of a new vesicomid from off the coast of Paraná (25°40'5''S; 44°59'0''W) contributes to the knowledge of the Vesicomidae distribution and opens new perspectives to carry on important research projects that may lead to the discovery of similar sulfide-rich or reducing habitats and associated communities in southern latitudes.

Calyptogena (Calyptogena) birmani,
Domaneschi & Lopes, sp. n.
Figs. 1–14

Holotype: Museu de Zoologia, Universidade de São Paulo (MZUSP) 26691 (Figs. 1–4, 5, 8).

Measurements: length: 12.7 mm; height: 8.3 mm; width: 5.2 mm.

Paratypes: Museu de Zoologia, Universidade de São Paulo 26692 to 26699 (complete shells), 26700 to 26705 (odd valves); Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo (DZ-IBUSP), without registration numbers, only odd valves (80 right, 74 left); Academy of Natural Sciences of Philadelphia (ANSP) (two complete shells and ten odd valves: five right, five left); United States Natural Museum (USNM) (two complete shells and ten odd valves: five right, five left).

Type-locality: R/V W. BESNARD station 2, 25°40'5''S; 44°59'0''W, off the Paraná coast, Brazil, at a depth of 400 m; sand-clay bottom sediment containing 39.92% calcareous and 1.76% organic matter; water temperature and salinity 2 m above bottom surface respectively 15.15°C and 35.55‰.

Description: Shell to 21.6 mm in length and 15.3 mm in height (largest known specimen—Fig. 14), subtrigonal to elongate ovate (Figs. 11–13), inequilateral, equivalve, rather solid, moderately inflated, with both valves of equal convexity, not gaping (Fig. 1–4). Umbones anterior (1/3 of shell length behind anterior end), small, pointed, weakly involute, prosocline; umbonal cavity shallow. Anterior margin rather short, convex and uniformly rounded; ventral margin smooth, moderately to broadly convex and rising gently posteriorly; posterior margin at the lower half of the shell height, short and narrowly rounded, forming pointed angular outline; anterodorsal margin short, slightly convex and gently descending, with a weak concavity near the umbones; posterodorsal margin long, convex to nearly straight, moderately to rather steeply descending. Concentric sculpture consisting of growth lines and weak lirations, best preserved on the anterior and posterior slopes; radial sculpture lacking. Radial posterior ridges proceeding from the umbones form the posterior dorsal margin and border a lanceolate, long and deep escutcheon, steeper walled near the umbones. Ligament opisthodontic, light brown, elongate (2/3 of escutcheon length), deeply inset and subtended by thickened, elongate and somewhat protuberant nymphal callosities (ligament lost in most specimens examined or with the periostracal portion present, sometimes associated with residues of the calcareous portion). No lunule; lunular area circumscribed by weakly elevated lines. Left valve with moderately thickened, elongated, shelf-like posterodorsal cardinal tooth and subumbonal cardinal tooth consisting of two portions, the anterior longer, shelf-like and the posterior massive, protuberant; excavated U-shaped socket between them (Figs. 5–7). Right valve with dorsal arched cardinal tooth consisting of a narrow, shelf-like anterior extension which advances forward a short distance from the umbo and a broad, thickened posterior portion; ventral cardinal tooth somewhat pointed, elongated, arcuate and extending anteriorly; posterior cardinal tooth lacking (Figs. 8–10, 14). True internal radial rib lacking, but rib-like thickening radiating posteriorly, often present inside umbonal cavity. Anterior adductor muscle scar dorsoventrally elongate, ovate, strongly impressed especially on the posterior margin; posterior adductor muscle scar irregularly rounded, but more weakly impressed. Anterior pedal retractor scar deeply impressed, slightly sepa-

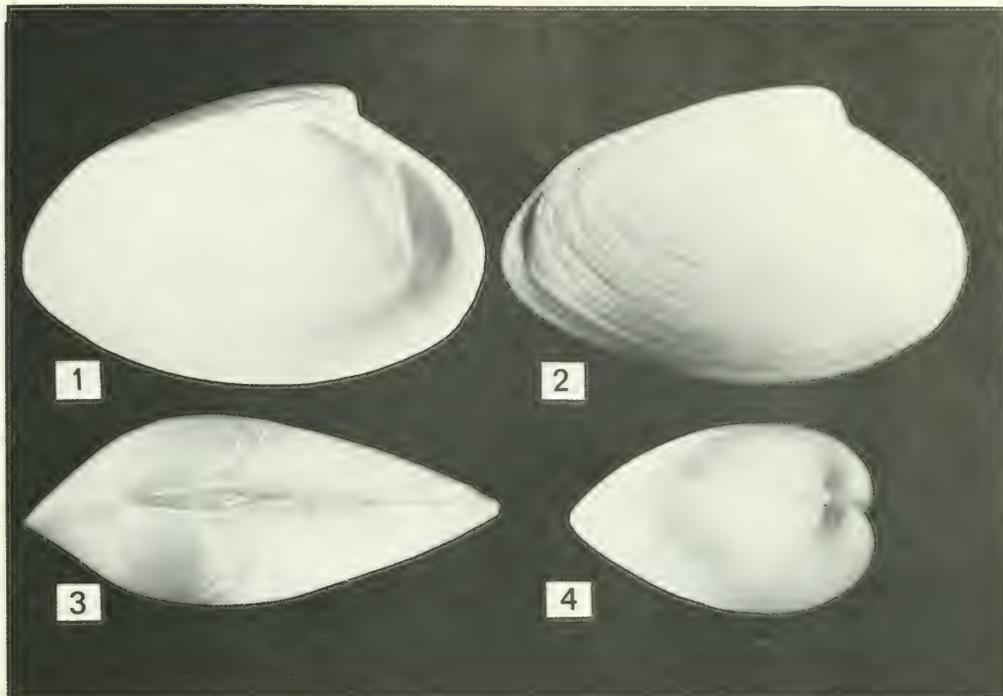


FIG. 1-4. The holotype of *Calyptogena birmani*, MZUSP 26691 (length = 12.7 mm): 1, internal view of the left valve showing muscle scars; 2, external view of the right valve; 3, dorsal view of complete specimen showing ligamental area, escutcheon; 4, anterodorsal view of complete specimen to show faintly circumscribed lunular area.

rated from the dorsal end of adductor scar; posterior pedal retractor scar fused with the adductor. Pallial line smooth and convex; pallial sinus extremely shallow, broad and rounded (Figs. 11-13). Shell chalky, dirty white, shining; interior white with a central russet stain. Inner margin of the valves incised by parallel oblique lines.

Measurements (mm) (material deposited in the MZUSP):

Specimens with both valves

length	height	width	
20.7	12.8	8.7	Paratype (MZUSP 26692)
19.3	13.9	9.9	Paratype (MZUSP 26693)
15.7	10.6	7.1	Paratype (MZUSP 26694)
15.4	9.7	6.2	Paratype (MZUSP 26695)
14.8	11.4	7.7	Paratype (MZUSP 26696)
14.1	8.6	5.6	Paratype (MZUSP 26697)
12.8	8.3	5.2	Paratype (MZUSP 26698)
12.7	8.3	5.2	Holotype (MZUSP 26691)
11.2	7.7	4.7	Paratype (MZUSP 26699)

Single valves

		hemidiameter	
21.6	15.3	5.0 (right valve)	Paratype (MZUSP 26700)

16.1	10.7	3.4 (left valve)	Paratype (MZUSP 26701)
14.2	9.0	2.9 (right valve)	Paratype (MZUSP 26702)
12.2	8.1	2.8 (left valve)	Paratype (MZUSP 26703)
10.7	7.3	2.3 (right valve)	Paratype (MZUSP 26704)
7.8	5.5	1.8 (left valve)	Paratype (MZUSP 26705)

Remarks: This species is placed in the genus *Calyptogena* Dall, 1891 (type-species, by monotypy, *Calyptogena pacifica* Dall, 1891: 190), based on the original description of the genus, the figures given by Boss (1968: 740-741, figs. 16-17, 19-20) and Keen (1969: N663, fig. E138-11a,b), and the redescription given by Boss & Turner (1980: 162-164). The presence of an escutcheon and the close resemblance of its hinge plate elements to that of *C. pacifica* allow the inclusion of this species in the subgenus *Calyptogena* s.s. as established by Keen (1969), followed and modified by Boss & Turner (1980: fig. 10).

Callocardia [= *Vesicomya*] *albida* Dall, 1889: 268, from ALBATROSS station 2762, Rio de Janeiro coast, Brazil, at a depth of 108 m, was the first member of the Vesicomyiidae



FIG. 5–7. The dentition of the left valve of *Calyptogena birmani*: 5, holotype (length = 12.7 mm, area shown = 7.6 mm); 6–7, paratypes (DZ-IBUSP, single valves without registration number) (6, length = 12.5 mm, area shown = 7.5 mm; 7, length = 11.7 mm, area shown = 7.1 mm). Note differences in dental elements.

reported from the southwest Atlantic. It is easily distinguished from *Calyptogena birmani* by its rounded, inflated shell (Dall's measurements from a single left valve, the only specimen known to date: "altitude of shell 8; longitude 9; diameter 7 mm").

Fourteen living species are currently referable to *Calyptogena*, three of which are from the Atlantic (Boss & Turner, 1980; Okutani & Métivier, 1986; Métivier, Okutani & Ohta, 1986; Stuardo & Valdovinos, 1988). The Atlantic species most closely related to *C. birmani* is *C. (C.) valdiviae* (Thiele & Jaekel, 1931: 229, pl. 9 (4), fig. 101), from VALDIVIA station 33 (24°35.3'N; 17°4.7'W), about 225 km off Morro Garnet, Rio de Oro, West Africa, at a depth of 2,500 m, and station 103 (35°10.5'S; 23°2'E), about 116 km south of Knysna, Republic of South Africa, at a depth of 500 m. *Calyptogena birmani* is distinguished from *C. valdiviae* by being much smaller, less inflated, having a pointed, angular posterior margin, giving a veneroid outline to most specimens. The anterodorsal margin

in *C. birmani* is convex; that in *C. valdiviae* is slightly concave, as can be seen in Boss' (1970) figures 3 and 4, selected by him as lectotype for *C. valdiviae*, though he described it as convex. In addition, the posterior ramus of the subumbonal cardinal tooth of the left valve is stronger and more elevated than that of *C. valdiviae*.

Calyptogena (C.) ponderosa Boss, 1968: 737–742, figs. 9, 11–15, 18, type-locality M/V Oregon I station 1426 (29°7'N; 87°54'W), about 124 km south of Mobile Bay, Gulf of Mexico, at a depth of 1,097 m, is similar to *C. birmani* in outline, configuration of the pallial sinus, and internal russet stain, but greatly differs in its much larger size, heavier and thicker shell, more anteriorly placed umbos, rounded adductor muscle scars and distinctly cardinal dentition of both valves.

Calyptogena (Ectenagena) modioliforma (Boss, 1968: 742–746, figs. 10, 21–24, 26–27), type-locality R/V Pillsbury station 394 (9°28.6'N; 76°26.3'W), Golf del Darien, 106 km NNE of Punta Caribana, Colombia, at the



FIG. 8–10. The dentition of the right valve of *Calyptogena birmani*: 8, holotype (length = 12.7 mm, area shown = 7.6 mm); 9–10, paratypes (DZ-IBUSP, single valves without registration number) (9, length = 13.2 mm, area shown = 7.8 mm; 10, length = 11.3 mm, area shown = 7.9 mm). Note differences in dental elements. Figures 9–10 are not from the same specimens shown in Figures 6–7.

depth of 421–641 m, is the third *Calyptogena* previously known from Atlantic waters. The frangible, nearly modioliform shell and larger size of this species readily separate it from *C. birmani*. More importantly, the presence of a large ligament, lack of an escutcheon and of an anterodorsal cardinal element, traits used by Boss & Turner (1980) to define its subgeneric position in *Ectenagena* Woodring, 1938: 51 (type-species, by original designation, *Calyptogena elongata* Dall, 1916: 408), are striking features separating *C. modioliforma* from *C. birmani*.

The Pacific *Calyptogena* species most closely related to *C. birmani* are *C. pacifica* and *C. (Archivesica) kilmeri* Bernard, 1974: 17–18, text-figs. 1B, 2B, 3B, 4B and 4E, type-locality FRB station 67–50 (53°1'N; 132°56'W) off west coast of Moresby Island, Queen Charlotte Islands, British Columbia, Canada, in 1,170 m.

Calyptogena birmani differs from *C. pacifica* and *C. kilmeri* in its smaller size (less than

a half of the shell length attained by *C. pacifica* and *C. kilmeri*), longer ligament (2/3 of the escutcheon length in *C. birmani*, approximately 1/2 in *C. pacifica* and about 1/3 in *C. kilmeri*), more convex ventral margin and more angular posterior margin. *Calyptogena birmani* also differs from *C. pacifica* by the presence of a distinct pallial sinus and by the hinge traits of its right valve: it has a shorter anterior extension of the dorsal cardinal tooth and absence of any trace of posterior cardinal tooth. The presence of a distinct pallial sinus and absence of any trace of posterior cardinal tooth are traits shared by *C. birmani* and *C. kilmeri*.

As noted in Boss (1968) and Boss & Turner (1980), there is in *Calyptogena* a great intraspecific variation in outline and all dental elements. Figures 5–14 of *Calyptogena birmani* confirm those authors' observations.

Considering the size attained (200 mm or more in length) by specimens of the species of *Calyptogena*, the examined shells of *C. bir-*

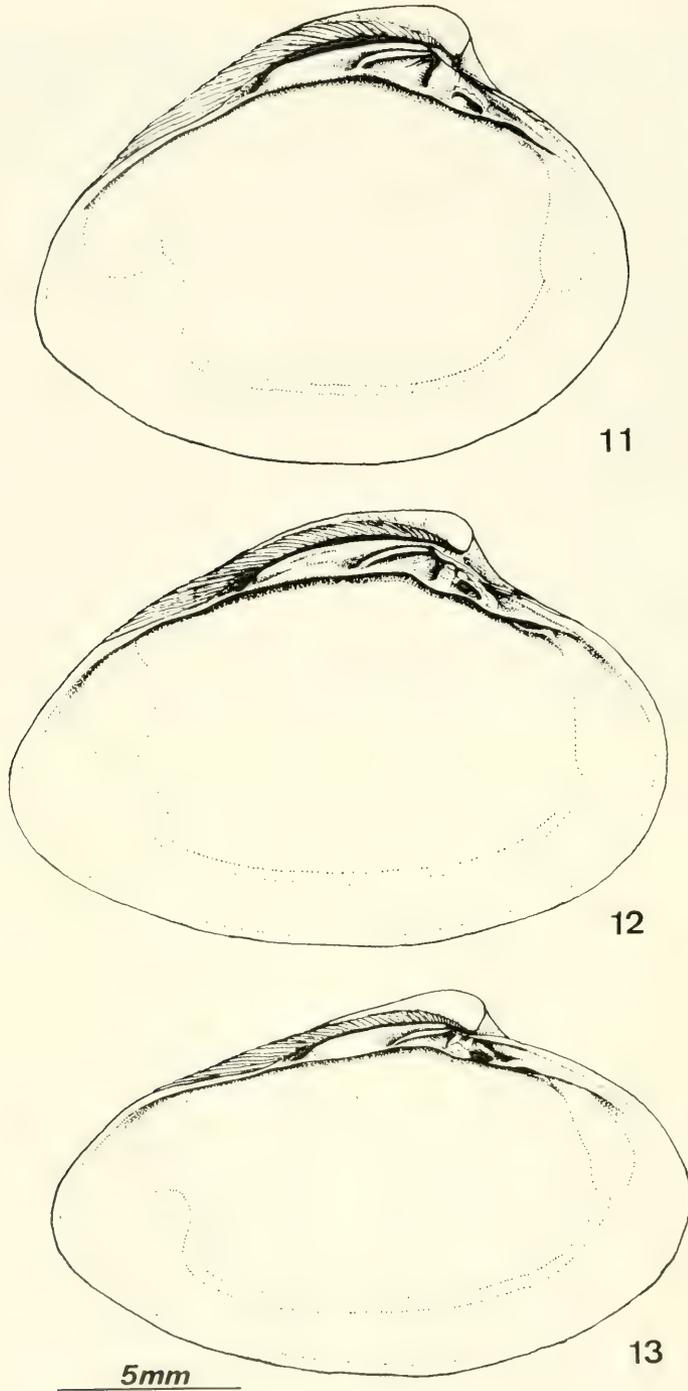


FIG. 11–13. Camera lucida drawing of left valves showing shell outlines, hinge and muscle scars of *Calypptogena birmani*. 11, a conspicuous subtrigonal, veneroid-type; 12, an intermediate form between 11 and 13; 13, a characteristic oval-elongate type. Note variations in the hinge height, subumbonal cardinal tooth and convexity of the posterior dorsal margin. 11, paratype MZUSP 26696; 12 and 13, paratypes DZ-IBUSP, without registration number.

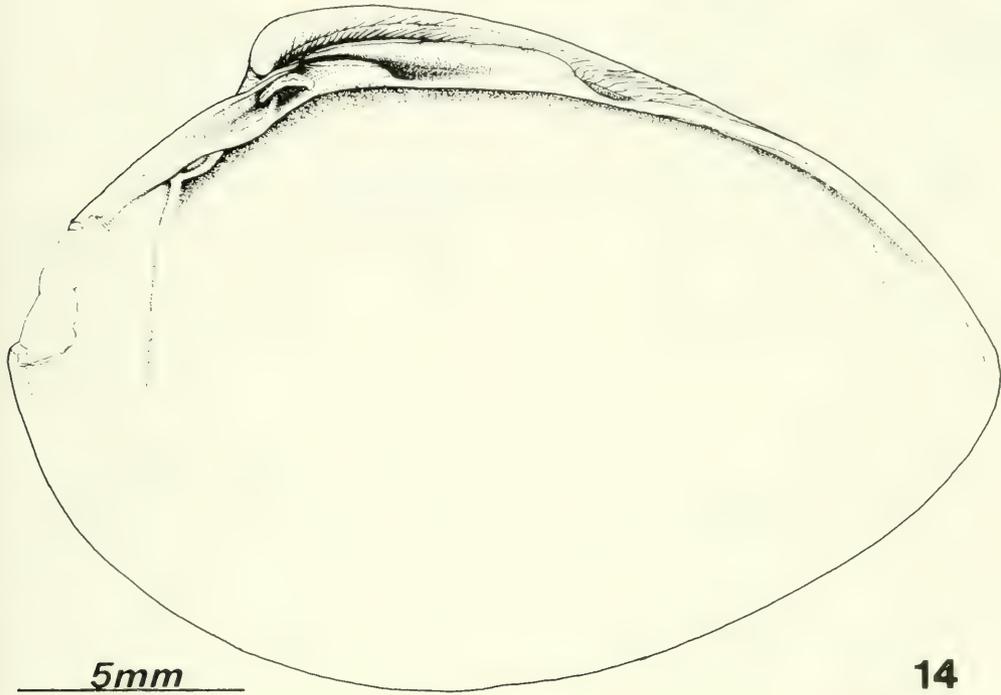


FIG. 14. Camera lucida drawing of the largest specimen of *Calyptogena birmani* (paratype MZUSP 26700). Internal view of the single right valve showing details of the hinge plate and well-impressed anterior muscle scars (adductor and pedal retractor). Valve damaged at the anterior slope; pallial and posterior adductor muscle scars partially vanished by erosion.

mani, ranging from 7.8 to 21.6 mm in length, may represent a collection of young of a much larger species. Further collecting in the area where these specimens come from may produce additional material to confirm this premise.

Etymology: This species is named for Adolpho Birman, a physician interested in molluscan studies and collections, who generously donated the specimens analysed in this paper.

Observations: The holotype is the best preserved specimen among all complete ones. Nevertheless, the right valve has the shelf-like anterior extension of the dorsal cardinal tooth slightly broken and the left valve was unfortunately broken during handling for photos, but it was reconstructed later.

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LETTERS TO THE EDITOR

HASZPRUNAR'S "CLADO-EVOLUTIONARY" CLASSIFICATION OF THE GASTROPODA—A CRITIQUE

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ABSTRACT

A recent classification of the Gastropoda (Haszprunar, 1988b), based on a "clado-evolutionary" methodology (Haszprunar, 1986), is analyzed and criticized. Although his publication (1988b) provides a wealth of new anatomical information and a valuable summary of recent research efforts in gastropod systematics, the methodology employed by Haszprunar, combining elements of cladistic data analysis and intuitive evolutionary taxonomy, is considered to be inferior to standard cladistic approaches.

The presentation of the data is incomplete and inconsistent. The analysis is not repeatable, Haszprunar's hypothesis of phylogenetic relationships therefore not testable. So-called "cladistic" or "sequential" classifications as provided for comparative purposes are improperly or inconsistently derived. Rather than preserving traditional nomenclature as claimed, his "clado-evolutionary" approach leads to the unnecessary naming of monophyletic **and** paraphyletic groupings.

Key words: Gastropoda, systematics, classification, phylogeny, methodology, cladistics, critique.

INTRODUCTION

Whatever the scientific question, it is an integral part of any study to present the data unambiguously, to employ reproducible methods, and to offer testable hypotheses. The current method of choice among many systematists involved in phylogenetic studies is based on Hennig (1950, 1966), which is a cladistic analysis that defines monophyletic groups based on interestested sets of synapomorphies (shared derived characters). Published cladistic studies should provide a character analysis, a listing of taxa and their character states, the means leading to the decision of which character state is thought to be primitive or derived (polarity; often by out-group comparison), and at least one graphic representation illustrating the most parsimonious or preferred reconstruction of phylogeny based on the given data set (i.e. a cladogram). Often the next step in such a study is the transformation of the information contained in the cladogram into a classification.

The above procedures force workers to clearly present the data on which the cladogram was based. The graphic representation in combination with the data matrix makes it easy to determine how well supported any particular "branch" is; moreover, it also allows one to retrace the transformation into a classification. Other workers are thus able to use, update or falsify the hypotheses presented.

In a series of papers, Haszprunar (1985a, b, c, 1988a, b) and Salvini-Plawen & Haszprunar (1987) have presented hypotheses of gastropod phylogeny as well as associated classifications. These papers summarized many of the recent findings in the field and presented a wealth of new information and original research data, culminating in an extensive publication by Haszprunar (1988b) providing a valuable summary of the field of gastropod systematics. The reader, however, is faced with several difficulties: the papers were published in rapid sequence with various modifications of the same theme, referring exten-

sively to each other and to works in preparation; they contained a plethora of new names for "higher" taxa; and most importantly, the hypotheses of phylogenetic relationships cannot be tested because data matrices were not presented or were incompletely presented, and the methods, in addition to being inconsistently applied, were not well documented. Haszprunar employed a non-standard, "clado-evolutionary" method of classification. This method, introduced by Haszprunar (1986) in a German-language paper, is described as combining "the advantages of the phylogenetic (clear retransformation into the phylogram) and of the evolutionary method (use of Linnaean categories to express order and divergence of groups)" (Haszprunar, 1986: 89). More controversially, it combines the use of clades (monophyletic groups) and grades (paraphyletic groups) in the same classification. (The term "grade" has been used variously in phylogenetic analyses and classifications in the past. Haszprunar uses it for paraphyletic taxa (stage groups), the third possibility in Hickman's (1988: 25) discussion of this term.)

It is not the aim of this paper to review the individual data employed in Haszprunar's papers, although I am aware of some errors of fact and interpretation¹, but rather to document methodological and technical problems with his approach. I will mainly concentrate on Haszprunar's (1988b) latest, most extensive treatment. His stated goal of "synthesis between cladistics and evolutionary classification" is "to arrive at a classification which on the one hand can be unequivocally retransformed into the basic phylogram, but on the other hand is maximally stable and compatible with traditional systems, is maximally practicable, and can be also used by paleontologists" (Haszprunar 1988b: 426).

There is no question about Haszprunar's acceptance of Hennig's method (cladistics) *per se*. Haszprunar (1988b: 369) stated "[i]t has become essential in phylogenetics to distinguish between synapomorphic (shared derived) and symplesiomorphic (shared primitive) homologies." And although Haszprunar uses a form of cladistic methodology to derive a cladogram and then applies his "clado-evolutionary" approach to produce a classification, the confusion stems from how the cladistic analysis is done and documented, and how the classification is derived from his analysis.

I discuss below (a) Haszprunar's (1988b)

presentation of the data set, (b) his cladistic analysis leading to a phylogram (1988b: fig. 5), (c) the so-called cladistic, sequential and "clado-evolutionary" classifications derived from this phylogram (1988b: table 5), and (d) Haszprunar's claim that his approach leads to a preservation of traditional names.

(a) Presentation of Data

Haszprunar does not share his knowledge of character-state distributions with the reader by presenting a complete data matrix. He frequently avoids clear statements about the distribution of a character state in the entire group. Is it not present in the other groups; is it not applicable because the character itself is not present; or are the data not yet available? The reader cannot reach a decision based on the presentation. My initial attempt to test a possible interpretation of the data set and the resulting phylogram using available phylogenetic analysis computer programs PAUP (Swofford, 1985) and HENNIG86 (Farris, 1988) was abandoned because I was unable to unequivocally recreate the data matrix from the information contained in the publication (1988b).

Haszprunar gives two text listings describing the characters used: table 2, p. 400 ("Review of the character analysis"), and the caption to figure 5 (p. 425). In these listings, he does not distinguish between raw data and interpretation. The numbering system (e.g. 1988b: 425, nos. 1–49) refers to branching points in the phylogram, not to individual characters. The reader is forced to search for the information backing a particular branching point in two places in the paper. The listing in Haszprunar's table 2, covering most but not all of the branching points, merely gives the character and its assumed plesiomorphic and apomorphic states, as well as the "number of changes," the latter frequently given as "many," without further reference to the type of change. In other cases, the reader is referred to the phylogram (1988b: fig. 5), and the numbers in parentheses are said to correspond to that phylogram, e.g. "number of changes . . . several (9p, 31pp, 37)," thus apparently implying multiple occurrences of a change from the plesiomorphic to the apomorphic state for the same character. The abbreviation "p" is explained as meaning "in part," while the frequently used abbreviation "pp" is left unexplained in the publication. According to Haszprunar (*in litt.*), a single "p"

refers to a single change within a clade, while "pp" denotes that this change occurs several times convergently ("mehrfach parallel, konvergent") within a clade. The second source of information, the caption explaining the phylogram (1988b: fig. 5) matches Haszprunar's table 2 in some cases (e.g. branch 14, presence of ctenidial rods); in other cases, it is apparently meant to supply additional information. It appears to be a somewhat expanded version of an earlier listing (Haszprunar, 1988a: fig. 1) that has not been reworked to accommodate the data of table 2 (1988b). For instance step 35 (leading to Campaniloidea and Heterobranchia in the phylogram) is backed by a single change in table 2, from pedal cords to pedal ganglia (with convergences in branches 8, 9 and 30). The description of the phylogram, however, tells us that hypothetical evolutionary step 35 means "chalazae; genital apparatus with special spermatheca; change of fine-structure of paraspermatozoa." In the caption of figure 5, no direction of change or the possibility of multiple occurrence is indicated, and the reader can only guess whether the characters described and statements given in the caption of figure 5 are meant to be descriptions of apomorphic character states (e.g. statement to branch 10, "primarily coiled forms (?).")

Some confusion can be resolved and some additional data are found in the extensive text. But in some cases the text does not match either the phylogram or the character table and thus adds to the confusion: for example, Haszprunar (1988b: 389) states that chalazae are found in "*Campanile* . . . , in the Valvatidae, in the Architectonicidae and Pyramidellidae, and are generally known in primitive euthyneurans," but his "review of the character analysis" (p. 400, table 2) places the character state "connected by chalazae" in branch 39 of the phylogram, thus excluding Campanilidae and Valvatidae. Some of this might be due to sloppiness (as is, for instance, the reversal of branch labels 41 and 42 in the phylogram, figure 5), but many decisions of groupings seem to be based on the author's intuition or knowledge **not** shared with the reader.

(b) Phylogenetic Analysis

Haszprunar employs cladistic methodology for the character analysis and the construction of a "phylogram." As no other information was given, it is assumed that the analysis was

done with paper and pencil; i.e. the phylogram was derived manually. Today most phylogenetic analyses of large data sets are handled with the aid of computer programs, allowing a thorough testing of potential branching patterns present in the data set (e.g. analyses by Davis et al., 1984; Houbrick, 1988; Lindberg, 1988; Bieler, 1988), although excellent analyses of small data sets have been produced manually (e.g. Waller, 1978; Davis & Greer, 1980; Meier-Brook, 1983). Haszprunar, however, did not employ a cladistic method in standard fashion, but used a "new" approach.

Comments on methodology are scattered throughout Haszprunar's paper (1988b: p. 370; table 4, p. 405; p. 426). These comments reveal that the cladistic method is partly misrepresented. Haszprunar (p. 370) states: "Again it is often argued that phylogenetics must be solely based on apomorphies, and again this is simply not true." He continues by stressing the importance of **both** plesiomorphies and apomorphies. The essence of phylogenetic systematics **is** the distinction between the two; phylogenetics is not based solely on apomorphies, but **phylogenies** are. Retained ancestral characters are uninformative about phylogenetic relationships. Haszprunar does not use the term "monophyly" in the conventional cladistic sense (Hennig, 1966; Farris, 1974; Wiley, 1981; Ax, 1984), but modifies it from Ashlock's (1971, 1973, 1979) concept ["*Monophyletic taxon*: Taxon which represents a continuous lineage (respectively a continuum of generations). *Holophyletic taxon* (= monophyletic *sensu* Hennig): A monophyletic (*sensu lato*) taxon which includes all descendants of the last common ancestor" (Haszprunar, 1988b: 405, table 4)]. Haszprunar's conception of "parsimony" also diverges from current usage. He (1988b: 426) claims that his phylogram is the "most parsimonious." While in "conventional" cladistic analyses the shortest possible cladogram (and thus the one involving the fewest number of "*ad hoc* hypotheses" of homoplasy) is viewed as the most parsimonious, Haszprunar provides the reader with a vague statement: "The concept of parsimony has been much debated, but the term 'most parsimonious' is used here in the sense of 'most probable'." It remains unclear whether his phylogram is a result of an attempt to find the shortest possible, based on the data available to Haszprunar, or just an *ad hoc* one. And, as outlined above, the data are not presented in

a fashion that would allow a test of parsimony by other workers.

In his character analysis, all characters are treated as binary ones (1988b: table 2), the concept of multistate characters or any form of complex transformation series is not addressed by the author (although several of the binary characters could be recoded as multistate, for example stereoglossate/flexoglossate and rhipidoglossate/taenioglossate as docoglossate/rhipidoglossate/taenioglossate). The possibility of reversals, the hypothetical return to the "primitive" condition, easily construed by loss in case of presence/absence character states, is not discussed by Haszprunar.

Haszprunar's concept of almost linear "progressive" evolution in the gastropods with "offshoots" from a rhizome-like evolutionary path leading to the Pulmonata seems discomfitingly teleological. According to Haszprunar (1988b: 367) the Allogastropoda, "a grade, . . . represent a step by step evolution towards the euthyneuran level of organization," while the "Pulmonata . . . [are] the crown group of Gastropoda." Almost casual remarks about groups shooting off the path distract from the hypotheses of phylogenetic relationship implied: by viewing the Pyramidelloidea as the last offshoot before "the euthyneuran level of organization," Haszprunar states that this superfamily is the sister group of the Euthyneura (comprising Opisthobranchia and Pulmonata), a significant statement that deserved not to be buried.

(c) Classifications

Haszprunar's nomenclature of classification methods regains special mention. To understand his discussions of "clado-evolutionary" versus "sequential" and "cladistic" classifications (1986, 1988b) the reader must be aware of Haszprunar's unique conception of these methods. Because Haszprunar uses modified cladistic terminology, it could easily be overlooked that he is **not** using conventional cladistic methodology. For comparison with his two "clado-evolutionary" classifications, Haszprunar presents (1) a "cladistic" classification and (2) a "sequential" classification.

(1) Haszprunar (1988b: 428, 430, tab. 5) gives a "Cladistic [classification], according to the rules of Hennig (1966)" in the format of an indented listing. Apparently under the impres-

sion that a cladistic approach demands naming of all branches or clades (see also Haszprunar, 1986: 90), he names all but one branching point. The naming is done by using quotation marks, without citing authorship for named taxa (most of them are apparently new)². The method of indenting the taxa according to their sister group relations is either incorrectly applied, or secondarily brought out of order due to a printer's error (see Docoglossa to "Helicoidea" in table 5(d)). In contrast to the other classifications offered, Haszprunar uses an unranked order in the "cladistic classification."

In an attempt to distinguish his "clado-evolutionary" method from other, more-or-less differing approaches, Haszprunar narrowed the concept of "cladistic classification" by defining it as something that Wiley (1979: 317; 1981: 203) called "subordination by pure indentation," a method rarely used in today's phylogenetic classifications of mollusks. (Haszprunar derives most of his examples (1986) from work on Platyhelminthes by Ax and Ehlers; e.g. in Ax, 1984.) This approach can be very useful for a scheme containing a small number of ranked and unranked taxa and is ideal for preliminary groupings since it avoids preliminary names (see also Gauthier et al. (1988)).

(2) The second non-"clado-evolutionary" classification presented by Haszprunar (1988b: 428, 430, "(c)") is labeled as "sequential, according to the rules of Wiley (1979, 1981)." The "rules of Wiley"³ are not specific to sequential classifications but are intrinsic to any phylogenetic classification (Wiley, 1981: 199). Sequencing was addressed by Wiley in "convention 3" (1979: 319, 321; 1981: 209), based on the phyletic sequencing convention of Nelson (1972, 1974). Neither Wiley (1981) nor Haszprunar considered these as part of the "rules"; Haszprunar, without making a clear statement, applies most of Wiley's (1981) conventions for annotated Linnaean classifications, while partly ignoring others (see below).

Haszprunar's example of "sequential classification" (1988b: table 5 (c)) is difficult to interpret. This is partly due to confusing technicalities such as the introduction of names not present in the phylogram ("Flexoglossata," "Taenioglossa"), the absence of groups that were in the phylogram (e.g. Omalogyridae), and the inconsistent use (and interpretation in Haszprunar's classifications) of symbols coding for tentative placement

(dotted line, dashed line, question mark, box). Haszprunar applies the same sequencing convention⁴ in classification "(c)" and in his "clado-evolutionary" classifications. The puzzling part is that he uses the convention in very different ways in the two approaches: in "(c)," meant to be an example for a "sequential classification," he changes without explanation to subordination after the first three taxa.

Because this classification "(c)" differs greatly from the others, I attempted to retrace the transformation of Haszprunar's phylogram (1988b: fig. 5) into a strict "sequential" classification. For this, I used the following approach. To avoid naming and categorizing every branching point, Nelson's phyletic sequencing convention was utilized. Names in brackets are other names used by Haszprunar (1988b) as redundant categories for monotypic taxa, with some of the more confusing misspellings (or unmarked new names?) in single quotes.

As in Haszprunar's classifications, Wiley's (1979) *sedis mutabilis* label is used, indicating taxa of interchangeable position at that level. This classification allows for unequivocal retransformation of the clades. The Cerithioidea (Cerithiimorpha) nebulously addressed as the "basic stock" and placed within a branch of his phylogram (Haszprunar, 1988b: 415 and fig. 5) could not be interpreted. The resulting classification derived from Haszprunar's phylogram is here given in Table 1.

The classification (Table 1), derived with established cladistic procedures should be largely congruent with Haszprunar's classification "(c)", but it is not. Instead the classification in Table 1 differs little from Haszprunar's "clado-evolutionary" classifications (compare Table 1 with Haszprunar's 1988b: 428, table 5(a), here reproduced in Table 2). If, for instance, all taxa (except Euthyneura) of the first level of indentation in Table 1 were categorized as suborders, only two differences are found: (1) Haszprunar interprets *Melanodrymia* and Neomphaloidea as belonging to Neritimorpha (thus diverging from his own phylogram, claimed to be the "most probable reconstruction of gastropod phylogeny"; 1988b: 426), and (2) he places the groups Omalogyridae to Pyramidelloidae in a paraphyletic taxon *Allogastropoda*.

What then is Haszprunar's new approach? His "clado-evolutionary classification" claims to be a "new synthesizing methodology," combining "the advantages of the phyloge-

TABLE 1. Cladistic classification derived from Haszprunar's phylogram (1988b: 424, figure 5), employing Nelson's phyletic sequencing method. Haszprunar's dashed and stippled lines were interpreted as tentative placements and are here indicated by question marks "(?)". His question marks were interpreted as unresolved polychotomies, the taxa involved marked with Wiley's *sedis mutabilis* "(s.m.)" label. The position of Cerithiimorpha could not be interpreted, and the group is here omitted. The grade comprising the paraphyletic group Allogastropoda is marked separately.

<hr/>	
Docoglossa	
Patelloidea	
Nacelloidea	
"Hot-Vent-C" (?)	
Cocculiniformia	
Cocculinoidea	
Lepetelloidea	
Neritimorpha (4 superfamilies)	
<i>Melanodrymia</i> (?) ["Hot-Vent-A"]	
<i>Neomphalus</i> (?) [Neomphaloidea, 'Neomphalida']	
Vetigastropoda (?)	
Lepetodriloidae (s.m.)	
Fissurelloidea (s.m.)	
Scissurelloidea (s.m.)	
Haliotoidea (s.m.)	
n.n. (s.m.)	
Pleurotomarioidea	
Trochoidea	
Seguenzioidea [Seguenziina, 'Seguenziida']	
Architaenioglossa (?)	
Cyclophoroidea (s.m.)	
Ampullarioidea (s.m.) [Viviparina]	
Caenogastropoda [excluding *Cerithiimorpha*,	
"Cerithimorpha"]	
Ctenoglossa (s.m.)	
"Neotaenioglossa" (part.) (s.m.)	
n.n. (s.m.)	
"Neotaenioglossa" (part.)	
Stenoglossa	
Campaniloidea [Campanilimorpha]	
Valvatoidea [Ectobranchia]	
n.n.	
Omalogyridae (?)	} "Allogastropoda"
Architectonicoidea	
Rissoelloidea	
Glacidorboidea	
Pyramidelloidea	
Euthyneura [= Pentaganglionata]	
<hr/>	

netic . . . and evolutionary method" (Haszprunar, 1986: 89). Haszprunar, who sees his technique of deriving a classification as a sequel to "Wiley's" sequential method (Haszprunar, 1986: 91), employs well-known approaches, such as the aforementioned phyletic sequencing convention of Nelson, and Wiley's *sedis mutabilis* label. He then ex-

TABLE 2. Reproduced from Haszprunar (1988b: 428, table 5(a)), entitled "Classification of the Recent streptoneuran Gastropoda. (a) Clado-evolutionary, primarily based on the nervous system (the preferred version)." (Author and date citations left out. Originally listed superfamilies of Ctenoglossa, *Neotaenioglossa* and Stenoglossa omitted, because they were not part of the phylogram.)

Class GASTROPODA
Subclass *Streptoneura*
Order * <i>Archaeogastropoda</i> *
Suborder DOCOGLOSSA
Superfamily Patelloidea
Superfamily Nacelloidea
?Suborder "HOT-VENT GROUP-C"
Suborder COCCULINIFORMIA
Superfamily Cocculinoidea
Superfamily Lepetelloidea
Suborder NERITIMORPHA
Superfamily *Neritoidea*
Superfamily Titiscanoidea (<i>s.m.</i>)
Superfamily Hydrocenoidea (<i>s.m.</i>)
Superfamily Helicinoidea (<i>s.m.</i>)
??Superfamily "Hot-vent group A"
(<i>Melanodrymia</i>)
??Superfamily Neomphaloidea
Suborder VETIGASTROPODA
Superfamily Lepetodriloida (<i>s.m.</i>)
Superfamily Fissurelloidea (<i>s.m.</i>)
Superfamily Scissurelloidea (<i>s.m.</i>)
Superfamily Haliotoidea (<i>s.m.</i>)
Superfamily Pleurotomarioidea
Superfamily Trochoidea
Suborder SEGUENZIINA
Superfamily Seguenzioida
Suborder *ARCHITAENIOGLOSSA*
Superfamily Cyclophoroidea (<i>s.m.</i>)
Superfamily Ampullarioidea (<i>s.m.</i>)
(= Viviparioidea)
Order * <i>Apogastropoda</i> *
Suborder CAENOGASTROPODA
Section * Cerithiimorpha *
Superfamily *Cerithioidea*
Section Ctenoglossa (<i>s.m.</i>)
Section * Neotaenioglossa * (<i>s.m.</i>)
Section Stenoglossa
Suborder CAMPALINIMORPHA
Superfamily Campanilloidea
Suborder ECTOBRANCHIA
Superfamily Valvatoidea
Suborder *ALLOGASTROPODA*
Superfamily Achitectonicoidea
?incl. Omalogyridae (= Prionoglossa)
Superfamily Rissoelloidea
Superfamily Glacidorboidea
Superfamily Pyramidelloidea
Subclass Euthyneura
(= Pentaganglionata)

pands on a topic discussed by earlier authors (e.g. Patterson & Rosen, 1977; Wiley, 1979,

1981); the utilization of especially marked paraphyletic assemblages in classifications. He is thus largely following Wiley's conventions for annotated Linnaean classifications (Wiley, 1981: 205–213), and up to this point Haszprunar has reinvented the wheel, considering that these are standard components of many modern phylogenetic analyses. (For a recent classification derived with this method and additional discussion see, for instance, Christoffersen (1987).)

Haszprunar uses three "new" approaches: (1) The splitting of paraphyly *sensu* Ashlock⁵ into paraphyly *s.l.* and orthophyly (a lineage system with only a single emerging line not included⁶), and the acceptance of only the latter in classifications. (2) The ranking of paraphyletic groupings (in contrast to Wiley's "convention 6"). (3) The replacement of a standardized or at least documented convention (e.g. Farris, 1976) to achieve categorization with the vague method inherent to "evolutionary taxonomy": instead of an objective and reproducible analysis of the data at hand he nebulously selects his "most suitable variation . . . by taking the anagenetic component into consideration," supplemented by "practicability and compatibility with traditional systems" (Haszprunar, 1986: 89). This allows him to select one or several "preferred versions" of classifications with only limited connections to the data base and phylogram generated earlier, and it explains why Haszprunar's "clado-evolutionary" classifications (1988b: 428–429, tab. 5 (a), (b)) cannot be reproduced from his phylogram.

The use of paraphyletic taxa thus allows Haszprunar to reach an agreeable (preconceived?) classification. As de Queiroz puts it: "Using phylogenetic definitions reveals the arbitrariness of paraphyletic taxa, for they must be defined as a common ancestor and only some of its descendants, and one group of descendants can be removed as well as any other" (1988: 254). With de Queiroz (1988), I view paraphyletic grades as hold-overs from "preevolutionary" taxonomies based on the *Scala Naturae*, or great chain of being. "The recognition of paraphyletic grades as taxa depends on emphasizing the derived traits of certain descendants (for example, birds) over those of others (for example, turtles) and, therefore, obscures the mosaic nature of evolution. The implication of paraphyletic grade taxa is that their various subgroups either did not evolve, which is simply incorrect, or that they did not evolve in an

important direction, which is a subjective judgment rather than a fact of nature" (de Queiroz, 1988: 252).

(d) Preservation of Traditional Names

One of the stated goals of Haszprunar's method is to arrive at a classification that is "maximally stable and **compatible with traditional systems**" [emphasis mine] (1986: 89). The formal recognition of non-monophyletic groupings is thus justified by the argument that considers "traditional components" (1986: 89) a primary property of a classification (see e.g. Michener, 1977, for additional example). Stability and convenience in classification are certainly desirable as long as analyses are not hampered and concepts not compromised. The goal of phylogenetic systematics is to estimate phylogeny, not to maintain stability (see also Kluge, 1989). Can a method which seeks to maintain stability of names and hierarchies established by essentialists, creationists and pheneticists be "evolutionary"?

In any case, Haszprunar's claim that one major advantage of the "clado-evolutionary method" of classification is the fact that it does not introduce unnecessary names, is not true. It always depends on the individual worker whether clades or grades in any given analysis are named. A review of many cladistic analyses in the recent malacological literature will show that very few authors find it necessary to name every branching point in a cladogram when transforming it into a classification. Several devices exist to avoid excessive naming, such as the application of the sequencing convention (Nelson, 1972, 1974), the suggested abandonment of Hennig's principle (1966: 155) that sister groups must have the same absolute rank (Farris, 1976), or the use of informal groupings such as "taxon A + taxon B + taxon C." Haszprunar rigorously adheres to Hennig's view and, against current convention (e.g. Wiley, 1979: 315; 1981: 205; Ax, 1984: 253), introduces redundant names (even for monotypic taxa) whenever he changes the rank of that taxon in a classification. There is no excuse for the introduction of new names in a classification considered as being preliminary or, as in the case of Haszprunar's classification "(c)" (1988b: 430), in one considered a less preferred example!

Haszprunar (1988a: 14) further claims that his "system is largely compatible with previous ones by using traditional taxa (any rigor-

ous cladistic classification would reject paraphyletic taxa such as the Archaeogastropoda or Streptoneura)." While some might see it useful to preserve names of taxa recognized as para- or polyphyletic (such as Archaeogastropoda⁷ and Mesogastropoda) by using them as names for stage groups or grades, it is interesting to note that most of Haszprunar's "to be protected" names are not "traditional." Of the eight higher category names flagged by Haszprunar (1988b: fig. 5) as representing "orthophyletic" groups (= paraphyletic, and thus not acceptable in a cladistic classification), five are not traditional at all: Allogastropoda Haszprunar, 1985; Apogastropoda Salvini-Plawen & Haszprunar, 1987; Cerithiimorpha Golikov & Starabogatov, 1975; and Architaenioglossa and Neotaenioglossa, both Haller, 1892, and recently revived by Haszprunar (1985a) to replace Thiele's Mesogastropoda.

If one of Haszprunar's main goals is the preservation of traditional names and thus nomenclatural stability, why did he replace Heterogastropoda Kosuge, 1966, by Heteroglossa Haszprunar, 1985 (1985a: *non* Heteroglossa Gray, 1857), and Euthyneura Spengel, 1881, by Pentaganglionata Haszprunar, 1985 (1985c), in the first place? Perhaps it is more than ironic that Haszprunar has not utilized Minichev & Starogobatov (1979) who subdivided the gastropods into eight subclasses, introducing a considerable number of new names for higher taxa which in part overlap with Haszprunar's groupings. I agree with Ponder (1988: 3) that "[i]f classification is to achieve a reasonable level of stability then higher groups should not receive new names simply because existing names were proposed to encompass wider or narrower groupings than the ones which a current analysis is identifying. . . . Likewise the argument that an existing higher group name is not suitable because it is based on characters that do not apply to all members of the group (e.g. not all Opisthobranchia have posterior gills), or to some groups (or parts of groups) outside it, is also certain to cause instability."

CONCLUSIONS

(a) The presentation of the data set in Haszprunar's publication (1988b) is incomplete and inconsistent. Raw data and interpretation are mixed.

(b) The analysis is not repeatable; Hasz-

prunar's hypothesis of phylogenetic relationships is not testable.

(c) Classifications labeled "cladistic" and "sequential," which were used by Haszprunar (1988b) in comparison with his "clado-evolutionary" classifications, are improperly or inconsistently derived. The procedures leading from the phylogram to the various classifications presented are not documented and can not be reconstructed from the published data.

(d) Rather than preserving traditional nomenclature, Haszprunar's approach leads to the unnecessary naming of monophyletic and paraphyletic groupings.

The question is whether the frequency of new-and-improved higher level classifications in the recent literature reflects major steps in the accumulation of knowledge of mere premature publications during an exciting time of data gathering in the field of malacology. Haszprunar's "clado-evolutionary method" attempts to legitimize an *ad hoc* scheme based on incomplete data. I do not criticize Haszprunar for the incompleteness of these data; on the contrary, his excellent anatomical work has closed many gaps in our knowledge and has forced us to re-analyze entrenched hypotheses of phylogenetic relationships. However, in his endeavor to combine the uncombinable in a "clado-evolutionary" potpourri, he has blurred the distinction between phylogenetic analysis based on "hard" data and the intuitive and authoritarian taxonomy of days past.

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APPENDIX: NOTES

1. Examples: Bieler & Mikkelsen (1988) did not describe a **bipectinate** gill in Vitrinellidae (used as a character by Haszprunar, 1988b: 381), but rather a **monopectinate** one; and Bieler (1988) found more than “only the shape of the osphradium and the radula” to distinguish Architectonicidae and Mathildidae (Haszprunar, 1988b: 420), e.g. the opercular morphology (with peg in Architectonicidae).

2. Haszprunar enclosed a disclaimer concerning these names (1988b: 428), stating that “[a] ‘Taxon’ has no nomenclatorial status.” These taxa are not to be confused with “orthophyletic” taxa [see note 6] originally demarcated by quotation marks (Haszprunar, 1986): Haszprunar (1988b: 426) now considers it “preferable to mark the orthophyletic taxa by stars (*) instead of quotation marks (‘).” These in turn should not be confused with the annotations proposed by Gauthier et al. (e.g. 1988: 16), with quotation marks denoting known paraphyletic groups and the asterisk (*) identifying so-called metataxa, i.e. “taxa for which there is no character evidence supporting **either** monophyly **or** paraphyly.”

3. "Rule 1. Taxa classified without qualification are monophyletic groups *sensu* Hennig (1966). Nonmonophyletic groups may be added if they are clearly qualified as such. Rule 2. The relationships of taxa within the classification must be expressed exactly" (Wiley, 1981: 200).

4. "Convention 3. Taxa forming an asymmetrical part of a phylogenetic tree may be placed at the same categorical rank . . . and sequenced in phylogenetic order of origin . . . with the first taxon listed being the sister group of all subsequent taxa . . ." (Wiley, 1981: 209).

5. Ashlock (1971: 69): "A *paraphyletic* group is a monophyletic group that does not contain all of the descendants of the most common ancestor of that group."

6. "*Orthophyletic taxon*: A paraphyletic taxon which represents a (usually branched)

lineage-system with only a single emerging line not included. This type is marked as "taxon" and can be used in a clado-evolutionary system." (Haszprunar, 1988b: 405).

7. Although I favor Hickman's (1988: 28) suggestion to use the taxon *Archaeogastropoda*, in a restricted sense, for a monophyletic group equivalent to (and thus replacing) *Vetigastropoda* Salvini-Plawen, 1980.

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