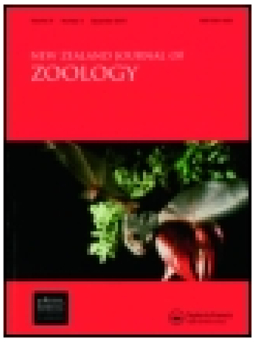

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Description and affinities of the subterranean molluscan fauna of New Zealand

F. M. Climo
National Museum, Wellington, New Zealand

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The New Zealand subterranean molluscan fauna is described, and its systematic relationships with surface-dwelling species in the Australasian region is superficially investigated. The subterranean elements are related to surface-dwelling taxa in New Zealand, with one exception which shows relationships with a Dalmatian snail, and these New Zealand taxa have relatives confined to restricted areas of the south-west Pacific. The Australasian members of Hydrobiidae (Prosobranchia: Rissoacea) examined in this study are attributed to subfamily Hydrobiinae, and are grouped in three nomenclatively informal tribes.

Literature relating to phreatic and cavernicolous Mollusca from other parts of the world is briefly reviewed. It is concluded that phyletic links between taxa in New Zealand and the Northern Hemisphere rarely exist below subfamily level, and that morphological similarities are matters of convergence or parallelism; the southern genera are regarded, for purposes of this treatment, as endemic.

A new phreatic stylommatophoran pulmonate genus, *Hydrophrea*, is erected for *Laoma (Phrixgnathus) academia* Climo, 1970. This is the first record of an aquatic subterranean stylommatophoran pulmonate. The following new taxa are described within Hydrobiinae: *Potamopyrgus cresswelli* n. sp.; *P. manneringi* n. sp.; *P. gardneri* n. sp.; *Hadopyrgus anops* n. gen. & n. sp.; *H. brevis* n. sp.; *Kuschelita mica* n. gen. & n. sp.; *K. inflata* n. sp.; *Catapyrgus spelaeus* n. gen. & n. sp.; *Opacuincola troglodytes* n. sp.; *O. kuscheli* n. sp. *Potamopyrgus subterraneus* Suter, 1905 is reconstituted as a valid species.

INTRODUCTION

The discovery on Mr O. Livingston's farm of a new subterranean dytiscid beetle (Hydroporinae: Dytiscidae) in water pumped from a well sunk in the alluvial gravels of the Waiiti River ("Livingston's well"), near Brightwater, Nelson, prompted Dr G. Kuschel and other staff members of the Entomology Division of the Department of Scientific and Industrial Research to collect more extensively. The initial discoveries were made in the flood-plain gravels of the Waiiti (a tributary of the Waimea) and Maitai Rivers, Nelson, but later sampling revealed that a subterranean phreatic molluscan fauna, varying in diversity from area to area, occurs in many parts of New Zealand. These areas, which are not enumerated in detail here, are shown in Fig. 1, and are also discussed where relevant in the systematics section of this paper.

Specimens were collected in the following ways.

(a) From wells and bores. A pump was used with a filter and a large container interposed between the suction pipe and the pump itself.

(b) From river gravels. A pipe was driven into the sediment, and water was sampled as in (a). A shallow hole dug by hand produced specimens in the Lee Valley, Nelson.

(c) From caves. Fine dip-nets were used to sample detritus stirred off the bottom of streams or ponded water bodies. The detritus was sorted under a binocular microscope.

All molluscan material was preserved in 75% ethanol. Transparent animal material was stained a light blue by brief immersion in Chlorazol Black E. Radulae were mounted in polyvinyl alcohol lactophenol and stained with Lignin Pink incorporated in the mountant, which was hardened by drying at 37°C for 2 days.

The term 'phreatic' refers to snails taken from water in the interstices of gravels, and 'cavernicolous' to those collected from streams or seepages in caves. Dimensions of shells mentioned in the text are shell height, unless otherwise specified. I have used Berry's (1943) method of writing the radula formulae of the hydrobiid species described. By this method the number of cusps on the lateral wings of the central tooth are indicated below the horizontal line, and those in the normal position on the crest of the tooth, above the line. The cusp formulae of the lateral tooth and two marginal teeth are then expressed to the right of that of the central tooth. Map grid co-ordinates are taken from the current NZMS 1 (1: 63 360) series, and the sheet number is indicated before the six-figure co-ordinate. The following acronyms are used: AKM, Auckland Institute and Museum; AM, Australian Museum, Sydney; DSIR, Entomology Division, DSIR, Auckland; NM, National Museum, Wellington. Note also that Figs 5–15 are set *en bloc* at the end of this paper.

WORLD OCCURRENCE OF SUBTERRANEAN SNAILS

The major component of the fauna of aquatic subterranean snails is the prosobranch rissoacean family Hydrobiidae, although Micromelaniidae and the valvatacean family Valvatidae are further components, e.g., *Valvata klemmi* Schütt and *Dianella schlickumi* Schütt from the Balkan Peninsula (Schütt 1962). A stylommatophoran pulmonate of superfamily Arionacea, described below from New Zealand, adds another molluscan group to the aquatic subterranean environment.

Until the new material recorded in this paper came to light, only two subterranean gastropods had been described from New Zealand – *Opacuincola caeca* Ponder, 1966, from a limestone cave in Nelson Province, and a species of hitherto doubtful status, *Potamopyrgus subterraneus* Suter, 1905, from a well at Ashburton, South Island.

As a result of recent sampling programmes, of which the sites are shown in Fig. 1, it has been discovered that New Zealand has a relatively large and diverse subterranean molluscan fauna, several of the new species belonging to new genera. This diverse phreatic and cavernicolous fauna is a new discovery in New Zealand, but such subterranean hydrobiid snails have been known from the fresh waters of Europe for over 100 years. More recently a diverse fauna has been described from Japan, and the affinities of North and South American hydrobiid faunas discussed. A selection of papers dealing with these faunas is listed by geographic region in an appendix to this paper. Literature cited in the text is not listed in the appendix. Nearly all the Eurasian literature on the subject is being published in *Archiv für Molluskenkunde*.

It was intended initially to deal with only the phreatic fauna of New Zealand, but an appraisal of the Japanese and European literature has made it obvious that the distinctions between surface-dwelling, cavernicolous, and phreatic, for aquatic snails, are rather arbitrary from a phyletic standpoint. In Europe, some phreatic or cavernicolous genera have extant surface-living representatives; in Japan, some genera have phreatic as well as cavernicolous species, though in this area the surface-dwelling stock no longer survives.

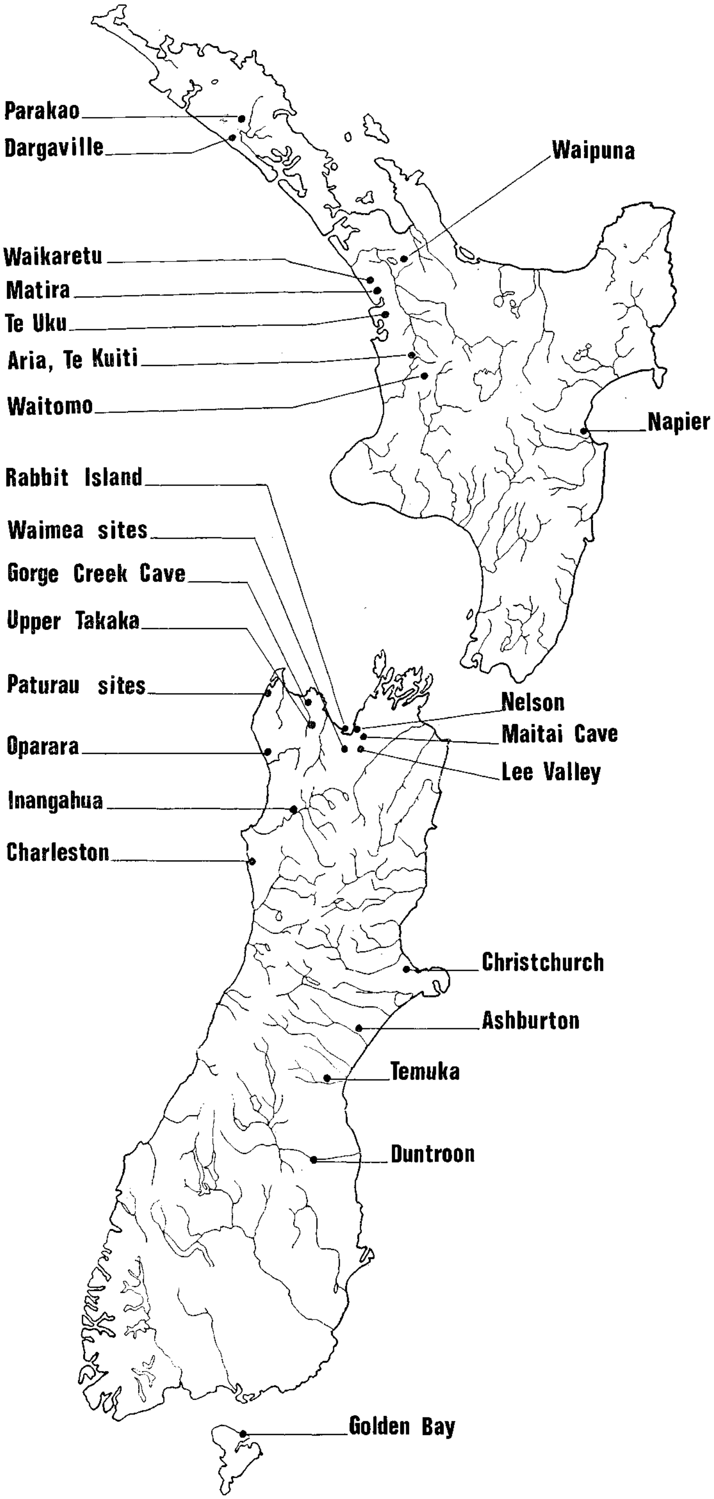

FIG. 1—Place names mentioned in text.

The New Zealand fauna is similar to the Japanese, in that phyletic links with the surface-dwelling fauna are obscure in some instances; however, one genus found in phreatic and cavernicolous habitats in New Zealand has surface-dwelling relatives.

No serious attempt has been made in the past to group Australasian hydrobiids into subfamilies or informal tribes. I make the initial attempt below with the genera examined in this study, but add the proviso that the informally named tribes used, and their distributions figured in the maps, are only groupings of convenience at this stage.

SYSTEMATICS

Subclass PROSOBRANCHIA
Superfamily RISSOACEA
Family HYDROBIIDAE Fischer

AN INTRODUCTION TO HYDROBIIDAE

The phreatic and cavernicolous fauna described below is widely spread in New Zealand, ranging from the Waitaki Valley and Canterbury to Nelson, Napier, Te Kuiti, Te Uku, Waikaretu, and Waitomo. Species diversity is greatest in Nelson, but this may be a reflection of the larger samples from this region. Some places lacked hydrobiid snails, notably Westland and the Marlborough Sounds area, but this was possibly due to unfavourable subterranean conditions. The presence of subterranean water in an alluvial substratum does not guarantee the presence of hydrobiid snails; special ecological requirements seem to be necessary. Although not yet documented, gravel size and the volume of water flow (probably directly correlated), and the availability of an organic detritus food source seem to be the most important factors influencing the occurrence of phreatic hydrobiids.

Given a food source, subterranean hydrobiids apparently require only the presence of oxygenated water in suitable substrates, the depth beneath the ground surface appearing not to be critical. One species was obtained at depths greater than 2 m, and also from shallow holes dug in a dry part of a river bed in the Lee Valley, Nelson. The same species was collected in caves at Gorge Creek, Paturau, Oparara, and the Maitai Valley, Nelson. There thus appears to be no significant ecological difference (for some hydrobiid snails) between phreatic and cavernicolous habitats. The one factor which seems to prevent some of these snails (which are quite capable of reaching surface habitats, particularly when the water table is high) from living in surface waters appears to be light. Without exception these phreatic species are blind and thin-shelled, and nearly all are completely unpigmented; they are therefore ill-adapted to surface conditions. Whereas the genera occurring in phreatic habitats which have cavernicolous representatives are all blind, genera restricted to caves may either be blind or have well-developed eyes.

Hydrobiid snails are grazers on bacterial, fungal, and algal films, but decaying plant material probably also forms a great part of their diet. In the phreatic environment they probably derive nourishment from organic slimes on particulate inorganic material and the larger pieces of organic material which become lodged in subterranean microcavities. As far as is known, they have no obvious predators in New Zealand phreatic or cavernicolous habitats, being much larger than members of other subterranean phyla.

The oxygen requirements of the larger New Zealand species are provided by a ctenidium situated on the upper left side of the pallial cavity. In one of the smallest species the ctenidium is absent, the animals apparently being small enough to meet their oxygen requirements from direct diffusion through the body surface.

Where it has been possible to make observations, all New Zealand subterranean hydrobiids have proved to be ovoviviparous, containing two or three shelled embryos and a number of less well developed, non-shelled embryos in a brood pouch just posterior to the pallial cavity. Individuals become sexually mature before development of what are generally regarded as 'adult' shell features. Some specimens of *Hadopyrgus* n. gen. contained embryos while the aperture was sub-adult in character, i.e., with discontinuous peristome and with two whorls of shell still to form before the 'adult' size was reached.

Sampling programmes have indicated that there is no marked seasonal peak in the occurrence of phreatic snail species at any one locality. They were obtained in ones and twos per month throughout the year (*see* Fig. 4).

As appears to be the case with most hydrobiids, individuals from any population are quite variable in shell proportions, and populations have their own characteristic ranges of variation, though none of the subterranean species examined in this study showed the extent of variation documented (Winterbourn 1970) for the surface-dwelling *Potamopyrgus antipodarum*. On the other hand, subterranean taxa agree with terrestrial ones in being conservative in anatomy, with only slight variation between populations.

In order of decreasing conservatism, the main taxonomic, readily accessible characters in Hydrobiidae appear to be: operculum; verge; radula; shell. All aquatic hydrobiids live in fresh or brackish water.

THE HIGHER CLASSIFICATION OF SOME AUSTRALASIAN HYDROBIIDAE

Hydrobiid systematics is confused and difficult to assess because of conflicting hierarchical systems [e.g., the conflicting ideas of Taylor (1966) and Thompson (1968)]. This situation is caused largely by difficulties in unravelling convergence and parallelism in morphology. The family is notorious for having diagnostic animal features which, in many forms, bear no relationship to shell features. It would be exceedingly difficult, if not impossible, to separate on shell features, even at the species level, selected representatives of the subterranean faunas of Europe, Japan, or New Zealand. This phenomenon has caused much chaos in hydrobiid systematics, and is well summed up by Radoman (1969, p. 173): "Two groups of errors are to be found here. On the one hand, the anatomically different species are included in the same genus because of their similar shells; in some cases species from different families, even from different subclasses are included in the same genus. On the other hand, anatomically similar species are separated into different genera (in some cases different subfamilies) owing to these conchological differences". What Radoman stated here is borne out by his earlier studies (*see* Appendix).

In attempting to place the New Zealand hydrobiids in subfamilies I have followed both Taylor (1966) and Thompson (1968), ultimately accepting the simpler system of Thompson. However, by following either author the New Zealand species fall into Hydrobiinae.

Taylor (1966) redefined the family Hydrobiidae and all the subfamilies therein. Using Taylor as a guide at this stage, the following is my rationale in choosing subfamilies for the New Zealand hydrobiid taxa. All the hydrobiids of subterranean habitat in New Zealand, like the surface-dwelling species of *Potamopyrgus*, have paucispiral opercula, with simple peg development in one genus. *Paxillostium*, a surface-dwelling genus from Northland, like the New Caledonian *Hemistomia* and several Australian genera, has a digitate peg on the operculum, and evidence is presented to show that it could be placed in Hemistomiinae—that is, if the subfamily can be recognised (*see below*). Operculum type removes all New Zealand genera from the Cochliopinae, Lyogyrinae, and Nymphophilinae, and penis morphology removes them from Amnicolinae, Lithoglyphinae, Fontigentinae, and Littoridininae, thus leaving Hydrobiinae to accomodate the New Zealand fauna.

Taylor (1966, pp. 182–4, fig. 14) redefined Littoridininae (first separated on radular characteristics as Tribe Littoridineae Thiele, 1928), basing the definition on verge morphology, his contention being that the group covered by Thiele's radular characteristics was artificial. Baker (1928, p. 144) stressed that the spinose shell and ovoviviparous reproduction of New Zealand *Potamopyrgus* and Central American *Pyrgophorus* would be worthy of the rank Potamopyrgidae, but Taylor maintained that this, too, was an artificial assemblage, *Pyrgophorus* falling neatly into his Littoridininae, a subfamily restricted to the American continent. It is apparent from Taylor's observations that *Potamopyrgus* cannot be accommodated in Littoridininae.

Thompson (1968) reviewed Taylor's system of classification, briefly outlined above in relation to the New Zealand fauna, and reached the following conclusions, based on his study of peninsular Florida hydrobiids. The difference in opercular coiling between Lyogyrinae and Amnicolinae is not significant when the variation of opercula in *Amnicola*, *Cincinnatia*, and *Aphaostracon* in Florida is examined. Thompson rejected Lyogyrinae, and suggested that *Lyogyrus* is at the most a subgenus of *Amnicola*, both belonging to Amnicolinae. He synonymised Cochliopinae, Mexithauminae, and Nymphophilinae with Hydrobiinae, and suggested that Littoridininae was a heterogeneous assemblage (*sensu* Taylor) possibly made up of two hydrobiinine tribes. Thompson was of the opinion that the rest of the subfamilies recognised by Taylor should be regarded as tribes in Hydrobiinae.

On the basis of Thompson's conclusions, like Taylor's, and if opercular features are ignored, all the New Zealand hydrobiid taxa can be regarded as members of the very variable subfamily Hydrobiinae. There now remains the problem of deciding whether the New Zealand hydrobiid genera can be placed in tribes within Hydrobiinae, or whether the New Zealand hydrobiinine species can be grouped into subfamilies.

In defining Hydrobiidae, Thompson followed Pilsbry & Bequaert (1927), Baker (1928), Thiele (1931), Connolly (1939), and Berry (1943), and used the subfamilial divisions proposed by Morrison (1949). Hydrobiidae are distinguished from the marine families around Rissoidae by having cusps on the lateral wings of the central tooth, a feature not shown by other rissoacean families. The eyes of hydrobiids, when present, are sessile, and situated at the outer bases of the tentacles. This position of the eyes appears not to be a very clear-cut differentiating feature, as they are in the central base of the tentacles in some New Zealand subterranean genera. Thompson defined Hydrobiidae as having the inner surface of the operculum usually smooth and lacking a peg- or wing-like projection. This is not a valid differentiating character, because *Hemistomia*, *Tatea*, *Rivisessor*, and *Pupiphryx* (all New Caledonian or Australian) have a raised, digitate peg on a paucispiral operculum, and *Catapyrgus* n. gen., described below from caves in New Zealand, has a large, smooth, recurved peg on a paucispiral operculum. *Istriana mirnae*, from caves in Dalmatia, has an operculum like *Catapyrgus*, and *Paxillostium*, from northern New Zealand, has a peg on a secondarily concentric operculum which relates it to *Hemistomia* and its allies.

In defining Hydrobiidae, I would remove the emphasis on eye position on the tentacle, and widen the definition by allowing genera with pegged opercula to be included.

The essential part of Thompson's (1968, p. 19) definition of Hydrobiinae reads: "... only a single simple duct, the vas deferens, within the verge, but the verge may be highly modified in other respects, including the presence of lobes, appendages, papillae, and dermal glands". Thompson recognised phyletic groups of species and genera based on the patterns of the above accessory organs on the verge, and made the following statement: "For purposes of convenience the groups are referred to as tribes, but it is not intended that the names of these tribes shall have any nomenclatorial significance". The other subfamily recognised without reservation by Thompson, Amnicolinae, was defined as having a bifurcate verge containing two ducts, one of these the vas deferens, opening at the tip of the penis.

In the above discussion, mention was made of subfamily Hemistomiinae, based on the New Caledonian *Hemistomia*. There are three species of *Hemistomia* recorded from New Caledonia (Solem 1961, p. 431) – *H. caledonica* Crosse, 1872 (type species), *H. fluminis* Cockerell, 1930, and *H. gentilsiana* (Crosse, 1874). *Hemistomia* has a digitate peg on the inner surface of the operculum, to the right of the nucleus as viewed from beneath (*see* Fig. 13C). Ponder (1967) showed that the Australian genus *Tatea* is a hydrobiid, and it, too, has a peg similar in structure to that of *Hemistomia*. I removed the operculum from dried animals of the Australian genera *Rivisessor* and *Pupiphryx* (Tasmania), and they also have this distinctive peg. Gardner (1970) described *Paxillostium* from northern New Zealand, and mentioned the similarity of its opercular peg to those of *Tatea* and *Hemistomia*. The operculum of *Paxillostium* is modified by the development of a very strong peripheral ridge; however, the peg is basically of the *Hemistomia* type. In my opinion the above genera form a natural group, with *Paxillostium* the most deviant genus.

Problems arise when one attempts to place *Potamopyrgus* in what would otherwise be regarded as a concisely defined subfamily, Hemistomiinae. The above genera have a digitate peg to the right of the nucleus, but *Potamopyrgus* has only a calcareous smear in this position (Winterbourn 1970, p. 299, fig. 12b). *Potamopyrgus* (=*Austropyrgus*) is found in both Australia and New Zealand. The European records of *P. jenkinsi* (Winterbourn 1970, pp. 315–17) are probably based on isolates introduced from Australasia, and the genus can therefore be regarded as endemic to Australasia. It seems likely either that the digitate peg has developed from the smear displayed by *Potamopyrgus*, or that the condition in *Potamopyrgus* is the derived state. On balance I feel that *Potamopyrgus* must be phyletically linked with *Hemistomia*, *Tatea*, *Rivisessor*, and *Pupiphryx*. Both *Tatea* and *Potamopyrgus*, showing the extremes thus far mentioned in opercular peg development, have a simple verge with one duct which lacks accessory appendages. This feature, and the compact south-west Pacific distribution (Fig. 2), seem to support the premise that there is a phyletic group involved here.

The situation is further complicated when the several subterranean genera from New Zealand are placed in the scheme. *Opacuincola* and *Catapyrgus* n. gen. cause no problems, because they are related to other groups of hydrobiid snails discussed below. The difficulties arise in trying to fit *Hadopyrgus* n. gen. and *Kuschelita* n. gen., both restricted to cavernicolous and phreatic habitats, to a complex the parameters of which have so far been set by *Tatea* and *Potamopyrgus*. A combination of radular and shell features segregates these two subterranean taxa as genera. Both *Hadopyrgus* and *Kuschelita* have very thin shells, are unpigmented and blind, and have opercula only weakly and indistinctly thickened by a smear to the right of the nucleus. Like *Potamopyrgus* they have a simple

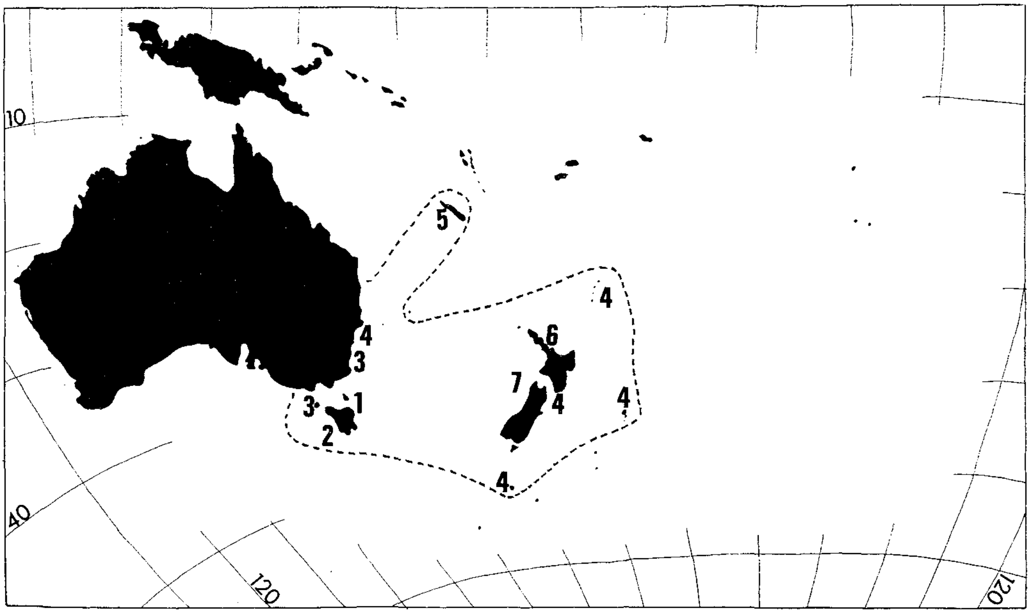

FIG. 2—Distribution of Hydrobiidae, Hydrobiinae, *Hemistomia*-tribe, based on material examined in this study: 1, *Rivisessor*; 2, *Pupiphryx*; 3, *Tatea*; 4, *Potamopyrgus*; 5, *Hemistomia*; 6, *Paxillostium*; 7, New Zealand subterranean genera excluding *Catapyrgus* n. gen.

verge, with one duct and no accessory processes. Although the phyletic links are weak between *Potamopyrgus* and these two subterranean genera, I consider the latter to be simplified members of a group including *Potamopyrgus*, *Pupiphryx*, *Rivisessor*, *Tatea*, and *Hemistomia*.

By both Taylor's (1966) and Thompson's (1968) reasoning, but for the spectacular peg development on the operculum and its supposed derived condition outlined above, all the above five genera could be placed in Hydrobiinae. Following Thompson's usage of very large subfamilies, the least recognition given to the five genera would be to rank them collectively as an informal tribe of Hydrobiinae; the greatest, to accord them subfamilial rank as Hemistomiinae. I am regarding the complex, including the deviant genus *Paxillostium*, as the *Hemistomia*-tribe, a nomenclatively informal grouping within Hydrobiinae.

The second group of hydrobiid snails in New Zealand is typified by the cavernicolous genus *Opacuincola*. The shell of the type species, *Opacuincola caeca*, is globular and heavy, and has a large aperture. There is no calcareous smear on the operculum, the only raised structure obvious being the quite strong spiral ridges. The verge of *Opacuincola* is similar to that of the generic complex around *Potamopyrgus* (*Hemistomia*-tribe), but there is an accessory, bluntly flagellate process on the right side of the verge, usually near the tip. *Fluviopupa* is the only recorded south-west Pacific genus, other than *Opacuincola*, which has a lobular or flagellate process on the verge; it also has a similar operculum. The range of shell morphology exhibited by species of *Fluviopupa* from Fiji and the Austral and New Hebrides Islands (Hubendick 1952, fig. 1a–f) is identical with that of the three New Zealand

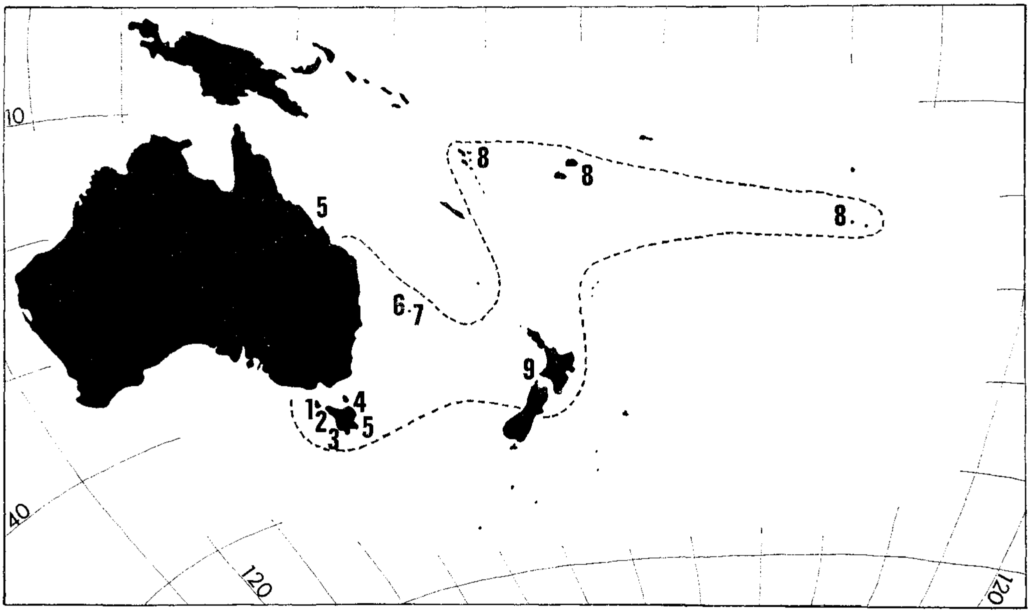

FIG. 3—Distribution of Hydrobiidae, Hydrobiinae, *Fluviopupa*-tribe, based on material examined in this study: 1, *Beddomena*; 2, *Petterdiana*; 3, *Tasmaniella*; 4, *Valvatasma*; 5, *Jardinella*; 6, *Fluviorissoina*; 7, *Pupidrobia*; 8, *Fluviopupa*; 9, *Opacuincola*.

species of *Opacuincola* (*see* Figs. 11B, 12A–H). The following Australian genera can be grouped with *Opacuincola* and *Fluviopupa* on shell and opercular features (type species indicated in parentheses): *Beddomena* (*Beddomena belli* Petterd, 1889); *Petterdiana* (*Littorina paludinella* Reeve, 1857); *Jardinella* (*Petterdiana thaanumi* Pilsbry, 1900); *Tasmaniella* (*Amnicola launcestonensis* Tenison-Woods, 1879); *Valvatasma* (*Valvata tasmanica* Tenison-Woods, 1876). Some of these are mentioned as showing affinities with *Opacuincola* by Ponder (1966, p. 35). This group of genera, distributed as shown in Fig. 3, is here regarded as the *Fluviopupa*-tribe within Hydrobiinae.

The third group of hydrobiid snails in New Zealand is represented by *Catapyrgus* n. gen., a monotypic cavernicolous genus from the South Island. The shell of this species is minute (under 2.0 mm), semitransparent, narrow, and tall-spired. The verge is of the simple type found in the *Hemistomia*-tribe. *Catapyrgus* is distinguished by the peculiar peg development on the operculum, recorded elsewhere only in the genus *Istriana* (Velkovrh 1971a), restricted to caves in Dalmatia. In both genera the operculum is paucispiral, and the long, recurved peg originates on the nucleus, curving down and to the right. A calcareous smear extends from the base of this peg to the right of the nucleus.

Although it is difficult to envisage such an apparently clear-cut phyletic link between New Zealand and Dalmatia, the presence of this unique peg on two cavernicolous genera with similar shells must be considered more than a coincidence of convergence. Differences in radular and shell morphology segregate the New Zealand species from *Istriana*; however, the two are closely related, and for now are interpreted as the *Istriana*-tribe within Hydrobiinae.

KEY TO NEW ZEALAND FRESHWATER MOLLUSCS DISCUSSED IN THIS PAPER

1\. Spire flattened, not operculate, with pulmonate animal features; habitat phreatic .... PUNCTIDAE: ***Hydrophrea academia*** (Climo)
—Tall-spired, operculate, with hydrobiid animal features; habitats brackish and freshwater; surface-dwelling, phreatic, or cavernicolous 2

2\. HYDROBIIDAE: HYDROBIINAE
Operculum paucispiral, with thickened radiating ridges; shell short-spired, globular; verge with an accessory flagellum; habitat cavernicolous 3
—Operculum paucispiral, with a large, curved peg originating at the nucleus and curving down and to the right; shell narrow, tall-spired; verge simple; habitat cavernicolous 4
—Operculum paucispiral or secondarily concentric, with a calcareous smear to right of nucleus or with a central, rounded stool; shell pupiform or with tapering spire; verge simple; habitat brackish and freshwater; surface-dwelling, phreatic, or cavernicolous 5

3\. HYDROBIINAE: *Fluviopupa*-tribe: *Opacuincola* Ponder
Shell thin, globular, up to 2.7 mm; restricted to caves in the Takaka Valley, Nelson .... ***Opacuincola caeca*** Ponder
—Shell variable in shape, but a departure from the globular form due to high incidence of distorted, tall-spired, or scalariform specimens; up to 2.1 mm; restricted to a soda spring near Aria, North Island .... ***Opacuincola troglodytes*** n. sp.
—Shell heavily thickened, squat, with large aperture and inflated body whorl, but tapering spire; up to 2.3 mm; found in cave systems in the west of Nelson from Paturau to Inangahua .... ***Opacuincola kuscheli*** n. sp.

4\. HYDROBIINAE: *Istriana*-tribe: *Catapyrgus* n. gen.
Restricted to limestone caves in western districts of Nelson from Takaka to Inangahua .... ***Catapyrgus spelaeus*** n. gen. & n. sp.

5\. HYDROBIINAE: *Hemistomia*-tribe
Operculum secondarily concentric, with a central, rounded stool; shell pupiform .... ***Paxillostium nanum*** Gardner
—Operculum paucispiral 6

6\. Shell fragile, transparent, narrow, and tall-spired, up to 1.8 mm; one cusp on lateral wing of central tooth; phreatic 7
—Shell fragile, white or semi-transparent, short-spired, and pupiform, up to 2.2 mm; two cusps on lateral wing of central tooth; phreatic or cavernicolous 8
—Shell fragile to heavy, semi-transparent or with a dark periostracum, pupiform or with a tall, tapered spire; three or more cusps on lateral wing of central tooth; habitat variable 9

7\. *Kuschelita* n. gen.
Shell with flat-sided whorls; up to 1.8 mm; restricted to phreatic habitats in Nelson .... ***Kuschelita mica*** n. gen. & n. sp.
—Shell with rounded whorls; up to 1.5 mm; recorded only from the phreatic habitat near Napier .... ***Kuschelita inflata*** n. gen. & n. sp.

8\. *Hadopyrgus* n. gen.
Shell up to 2.2 mm; found in phreatic or cavernicolous habitats in north of South Island .... ***Hadopyrgus anops*** n. gen. & n. sp.
—Shell up to 1.5 mm; restricted to phreatic habitats in Nelson .... ***Hadopyrgus brevis*** n. gen. & n. sp.

9\. *Potamopyrgus* Stimpson
Restricted to brackish water; oviparous 10
—Found both in brackish and fresh water; also phreatic or cavernicolous; ovoviviparous 11

10\. Shell with large body whorl and tapered spire; over 6 mm .. ***Potamopyrgus estuarinus*** Winterbourn
—Shell pupiform; less than 3.5 mm .... ***Potamopyrgus pupoides*** (Hutton)

11\. Shell fragile, semi-transparent, up to 2.9 mm; restricted to phreatic habitats in South Canterbury and North Otago .... ***Potamopyrgus subterraneus*** Suter
—Found in cavernicolous habitats, or surface-dwelling 12

12\. Shell narrow, tall-spired, up to six whorls; semi-transparent to creamish-white; up to 2.5 mm; found in caves or seepages from caves in South Auckland .... ***Potamopyrgus manneringi*** n. sp.
—Surface-dwelling, though occasionally washed into caves or taken from phreatic habitats (derived from surface populations) 13

13\. Shell 4–11.5 mm, with a heavy, brown periostracum at times ornamented with spines; shape variable, but usually with a large body whorl and tapered spire .... ***Potamopyrgus antipodarum*** (Gray)
—Shell up to 2.5 mm, semi-transparent to creamish-white; habitat seepages in forest litter 14

14\. Shell up to 2.5 mm, pupiform, smooth, and glossy; found only at Golden Bay, Stewart Island .... ***Potamopyrgus cresswelli*** n. sp.
—Shell up to 1.5 mm; found in forest seepages in Northland .... ***Potamopyrgus gardneri*** n. sp.

Subfamily HYDROBIINAE

NEW ZEALAND MEMBERS OF THE *Hemistomia*-TRIBE

(*See* the discussion above for the usage of subfamily and informal tribe here.)

Potamopyrgus Stimpson, 1865

Type species: *Melania corolla* Gould, 1847.

The genus is known as a Pleistocene fossil in New Zealand and as a Recent shell in both Australia and New Zealand. Winterbourn (1970, pp. 315–17) has shown that *Potamopyrgus jenkinsi* E. A. Smith, 1889 from Europe is probably *P. antipodarum* (Gray, 1843) introduced there from Australia possibly as early as 1859.

Potamopyrgus can be defined briefly as having a simple verge with a single duct, the vas deferens, opening terminally, a calcareous pad on the operculum possibly derived from a condition like that in *Tatea,* the shell covered in a horny, sometimes ornate, usually darkly coloured periostracum, and a wide, squat central radular tooth. Most species are ovoviviparous.

Winterbourn (1970) presented in some detail the morphological parameters of *Potamopyrgus antipodarum, P. estuarinus* Winterbourn, 1970, and *P. pupoides* Hutton, 1882. He reduced the relatively larger list of species and subspecies of *Potamopyrgus* on the New Zealand mainland to the above three species. It is not possible to discuss the cavernicolous and phreatic species of *Potamopyrgus* in New Zealand without a brief review of the surface-dwelling forms, as there is overlap of habitat between several species. Winterbourn (1970, p. 294) illustrated the hypothetical evolution of New Zealand species of *Potamopyrgus.* In his scheme, *P. pupoides* and *P. estuarinus* represent species living in brackish water, having smooth shells and oviparous sexual reproduction, and in their morphological features similar to their marine ancestor; *P. estuarinus* also exhibits amphibious tendencies. *P. antipodarum* differs in its invasion of the freshwater habitat, development of spinose or otherwise ornamented shells in some populations (Winterbourn 1970, fig. 3), and ovoviviparity. Facultative or obligatory parthenogenesis has developed in some populations. It is in this freshwater group of the *Potamopyrgus*-dichotomy that three new species are described below. They are all smaller than *P. antipodarum,* and one lives sympatrically with *P. antipodarum,* establishing its validity quite clearly.

THE OVIPAROUS NEW ZEALAND SPECIES OF *Potamopyrgus*

Potamopyrgus estuarinus Winterbourn, 1970

P. antipodarum is usually replaced by *P. estuarinus* in estuarine intertidal areas. The latter species is probably widespread in New Zealand among rushes and under stones in the high intertidal zone on sheltered muddy shores, but anatomical investigation is necessary to determine this because of its close similarity on shell characters to some forms of *antipodarum,* with which it co-exists in some localities.

Potamopyrgus pupoides Hutton, 1882

This small, pupiform species is confined to brackish water throughout New Zealand, but has not been recorded from Stewart Island. It is superficially similar to *P. cresswelli* n. sp., *P. manneringi* n. sp., and *P. gardneri* n. sp., but differs from them in not being ovoviviparous, having a very dark periostracum, being larger, and living in brackish water.

The names *P. spelaeus spelaeus* (Frauenfeld, 1862) and *P. s. pupoides* are often associated in checklists and early literature (e.g., Suter 1913, p. 234). The former, at about 4 mm, is probably a small form of *antipodarum*, as Winterbourn (1970) implies in his synonymy; it has nothing to do with the brackish-water *pupoides*, and certainly nothing to do with the cavernicolous species described below. All the records of *spelaeus* in the Suter Collection (the land snail and freshwater components of which are in the National Museum, Wellington), with the exception of his No. 3866 from "Nelson", are *P. antipodarum*. The single, unlocalised lot from Nelson contains 10 specimens of *P. pupoides* and an undescribed species about the same size as *pupoides*. This second species is probably from a brackish-water habitat, assuming Suter's lot No. 3866 is not mixed, and differs from *pupoides* in its lighter coloration, more rounded whorls, deeper sutures, and relatively shorter spire. Little more can be said at this stage, further elaboration of the situation requiring a precise locality and live-collected material.

THE OVOVIVIPAROUS NEW ZEALAND SPECIES OF *Potamopyrgus*

The one species regarded by Winterbourn (1970) as falling in this category, *P. antipodarum*, is extremely variable in shell features: "It includes a wide range of morphological variants, as well as different reproductive forms, and is found under diverse environmental conditions" (Winterbourn 1970, p. 312). Winterbourn suggested that much of the wide morphological variation has been caused by parthenogenetic reproduction, which "has permitted the formation of many reproductively isolated clones in which divergent evolution has been able to occur" (Winterbourn 1970, p. 313). Winterbourn also discussed the difficulty of applying the species concept to such parthenogenetic, morphologically recognisable clones, as the concept is based on sexually reproducing organisms. He concluded this discussion by stating that the 'evolutionary species concept' might best be applied to the complex situation seen in *P. antipodarum*, where there is a gradation from completely sexual reproduction, through limited numbers of males, to completely parthenogenetic reproduction. This concept is defined as follows: "An evolutionary species is a lineage evolving separately from others and with its own unitary evolutionary role and tendencies".

Winterbourn (1970, fig. 5) showed that the maximum height of shells of *P. antipodarum* ranged from 4 mm to 11.5 mm, this range distributed in an approximate normal curve with a peak between 6 mm and 6.6 mm. He mentioned that *P. pupoides* is distinguished by its small, pupiform shell, and that *P. estuarinus* cannot be distinguished on shell characters from some forms of *P. antipodarum*.

Potamopyrgus antipodarum may contain 100 or more shelled embryos in the brood pouch (Winterbourn 1970, p. 304), the numbers apparently a function of shell size. Gardner (1970, p. 183) recorded 23–60 embryos from the brood pouch of *P. antipodarum*. Winterbourn (1970, table 2) showed the numbers of spiny and smooth progeny produced from parthenogenetic females over three generations; the lowest total progeny from a single parent, growing to a size sufficient to determine whether spines would be present or not, was 5, the largest 56. Allowing for some mortality in liberated embyros (not indicated), it is probable that neither the low nor the high counts reflect the total number of shelled embryos that could have been dissected from the brood pouch in these specimens.

There occur in widely separated regions of New Zealand populations of ovoviviparous specimens of *Potamopyrgus* having a maximum height of only 2.5 mm. These are as distinct as *P. pupoides* from *P. antipodarum* or *P. estuarinus* in their pupiform shell shape, and all have less than five shelled embryos in the brood pouch. Males were present in all populations examined.

There appears to be a morphological gap in size between the smallest *P. antipodarum* at 4 mm, and the largest specimen in the group briefly outlined above. The National Museum collection of *P. antipodarum* is geographically quite extensive, and no adult shells from any population fall in the size range 2.5–4.0 mm.

Although it might be reasonable to extrapolate the count of shelled embryos down in number to coincide with females in the 1.5–2.5 mm range [as Winterbourn (1970) has shown that embryo numbers appear to be correlated with adult shell size], this character can equally be used as evidence to support my contention that there are undescribed small species of *Potamopyrgus* in New Zealand. The final piece of evidence supporting this idea is provided by the sympatric occurrence of *antipodarum* and *P. manneringi* n. sp. at Waikaretu. At this locality, adults of *P. antipodarum* growing to 4.5 mm are found together with adults of the small, ovoviviparous *P. manneringi* n. sp., which grows to only 2.5 mm. No intermediate sizes or shapes occur.

Potamopyrgus antipodarum (Gray, 1843) (Fig. 12I)

[*See* Winterbourn (1970) for synonymy, but exclude *P. subterraneus* Suter, 1905, which is a valid species.]

A widespread and common element of New Zealand fresh waters, ranging from Stewart Island to the Three Kings Islands, and including the Chatham Islands. It is very variable in shell features (*see above*).

It is most common in non-brackish waters, including rivers, lakes, ponds, and hillside seepages, but less commonly found in dark, heavily forested basins and other areas with similarly low light intensities. In some parts of New Zealand (discussed below) it is replaced in such areas by other species, in some instances by species from another genus. Although occasionally collected alive from caves, there is always a stream populated by the species leading into the cave system, and such occurrences can be regarded as extensions of surface populations. The occasional dead shell pumped from wells or bores can be regarded in a similar light.

The species was not recorded from the New Zealand Cenozoic by Fleming (1966, pp. 42–5), and the following record from the Lower Pleistocene extends the species a little further down the geological column from its previously well known occurrences in Upper Pleistocene lake marls and sand dunes. Two broken shells were taken from pumice-bearing fossiliferous beds of the Kai-Iwi Group, Castlecliffian Stage, Lower Pleistocene, in a gully on Morrison's farm, Fern Flats Road, near Marton, Wanganui. One of these specimens, which may best be regarded as *Potamopyrgus* cf. *antipodarum* (Gray), is illustrated in Fig. 12I. Other non-marine molluscs, including land snails and a lymnaeid, were also collected from this locality.

Potamopyrgus subterraneus Suter, 1905 (Figs 6E–G, 15A)

Potamopyrgus subterraneus Suter, 1905: 267.
Potamopyrgus antipodarum (Gray). Winterbourn 1970: 285 (in part).

The species was placed in the synonymy of *Potamopyrgus antipodarum* without explanation by Winterbourn (1970, p. 285). It was known until quite recently only from the broken holotype, collected from approx. 15 m down a well in Ashburton, South Island, although Chilton (1894, pp. 246–7) implied that more than one specimen was in existence originally, the material derived from several wells. Since 1970, several more specimens of a subterranean species of *Potamopyrgus* have been collected from southern South Island localities – the Waitaki Valley in Otago, and Milford, near Temuka, South Canterbury. These specimens (Fig. 6E–G) are virtually indistinguishable from the broken type of *subterraneus*. These similarities and unique soft-part features distinguish the species from *antipodarum*. The species is redescribed below.

Shell tall-spired, of 5.5–6 whorls, spire gently tapering, sutures well impressed, whorls rounded on periphery, similar in profile to some small (4 mm), elongated forms of *P. antipodarum*.

Ovoviviparous, the single dissected specimen from Milford containing three shelled embryos. This number is far fewer than the 23–60 recorded for *P. antipodarum* (Gardner 1970, p. 183). The following radula formula incorporates the cusp ranges of both the Waitaki and Milford specimens:

$$\frac{(4\text{–}5) - 1 - (4\text{–}5)}{(4) \qquad\quad (4)} : (2\text{–}3) - 1 - (4\text{–}6) : (26\text{–}30) : (13\text{–}15).$$

The lateral wings on the central tooth of the Waitaki specimen are longer and more vertically directed than those on the Milford specimen, but otherwise cusp development on this tooth, the lateral, and both marginals, is similar on specimens from both localities. Operculum paucispiral, of 2.5 whorls; calcareous smear weak, extending from the nucleus. Animal unpigmented, blind, with tapered tentacles; ctenidium of 6–7 folds, and below this a large osphradium on left side of pallial cavity.

Material Examined. Holotype (NM). Also: 1, well, Borton's property, near Duntroon, Waitaki Valley, North Otago (S127 353938), 23.iii.1973, G. Kuschel (broken specimen, dissected); 2, bore, Milford, Canterbury (S102 893717), 22.iii.1973, G. K. (1, DSIR, no. Ph.III; 1 dissected). Anatomical preparations from both dissected specimens, NM.

Remarks. Judging from the present records this strictly phreatic species will probably be collected in the future from many more localities in Canterbury and North Otago. It is closely related to *P. antipodarum*, from which it is distinguished by the lack of pigmentation, absence of eyes, and far fewer embryos in the brood pouch of the female. Otherwise, the species cannot be differentiated from *P. antipodarum*.

Potamopyrgus cresswelli n. sp. (Figs 7A–C, 14F,G, 15B)

Shell small (up to 2.5 mm), pupiform, of 5 whorls, semi-transparent, creamish-white, smooth, glossy. Aperture subcircular, peristome thin and fairly continuous as a double structure, single only on centre of outer lip. Imperforate in adult, upper third of parietal wall of aperture bordered by a large chink imparting a scalariform appearance to apertural region. Spire tall, a little less than twice height of aperture; whorls moderately rounded. Sutures shallow, false-margined below due to transparency of shell showing whorl overlap. Faecal pellets in intestine show through shell as a weakly curved row (4–5 pellets) at right angles to spire at level of upper edge of aperture.

Optic tentacles long and tapering, sharply pointed; eyes large, black, situated at base of tentacles, centrally positioned. Penis simple, long, tapering, strongly curved to right, fastened midway between eyes and posterior downward curve of head a little to right of midline; vas deferens opening terminally. Females ovoviviparous, large shells (2.5 mm) containing up to four shelled embryos and a number of smaller embryos lacking shell.

Operculum of normal *Potamopyrgus* type, paucispiral, with a calcareous smear extending laterally to the right from nucleus. Radular formula:

$$\frac{(3\text{–}4) - 1 - (3\text{–}4)}{(3\text{–}4) \qquad (3\text{–}4)} : (3\text{–}4)\ - 1\ - (5\text{–}6) : (\text{approx. } 30) : (\text{approx. } 15).$$

This configuration is not distinct enough from other New Zealand species of *Potamopyrgus* for species recognition, but in shape the central tooth of *cresswelli* is closer to *subterraneus* than any other species.

TYPE MATERIAL. HOLOTYPE: small seepage in coastal forest at head of streamlet entering western end of Golden Bay, northern coast, Stewart Island, 18.i.1970, P. Cresswell (NM, M 32462). PARATYPES: same data (10, NM, M 32463; 10, DSIR; 10, AKM). Many topotypes, NM.

REMARKS. This species is known only from the type locality, in a habitat similar to that of *Potamopyrgus gardneri* n. sp., described below from Northland. *P. antipodarum* also is found on Stewart Island. Specimens from The Neck are of the smooth *antipodarum*-form, while those living in Freshwater River at the head of Paterson Inlet are the spinose "*badia*"-form of the species. Like *P. antipodarum*, *P. cresswelli* is ovoviviparous, and has a virtually identical radula; however, *antipodarum* is never as small at maturity (*see* discussion above), and always has more embryos in the brood pouch. *P. cresswelli* shows a superficial resemblance to *P. pupoides*, but that species is not ovoviviparous, and as far as I can ascertain has not been recorded from Stewart Island. The new species shows affinities with *P. antipodarum*, but is perhaps closest to *P. subterraneus*, differing from it only in the smaller size, pupiform shape, and having secondarily lost certain features (e.g., eyes) in the subterranean habitat.

The species is named after Inspector P. Cresswell, Wellington, who provided me with all the material for study and who has also made available to me his extensive collection of minute land snails.

Potamopyrgus manneringi n. sp. (Figs 7D–N, 14I–M)

Shell small (just under 2.5 mm), narrow, tall-spired, of up to 6 whorls, semi-transparent to creamish-white, thick, irregularly ridged by growth-lines. All shell features as described for *P. cresswelli*, the distinguishing features of *manneringi* being smaller size and more tapered spire. The shell is so variable within and among populations that there is little point in continuing at length with detailed descriptions of shell parameters. This variation is illustrated in Fig. 7D–N.

Animal creamish-white, unpigmented. Optic tentacles bulbous at base, with heavily pigmented eyes near outer base of this bulge, rest of tentacles long, filamentous. Verge long, recurved, fastened to right of head midline; vas deferens opening terminally. Females ovoviviparous, containing two very large shelled embryos in brood pouch (Fig. 14I). Ctenidium weakly developed, of 5 lamellae; osphradium on left side of pallial cavity below ctenidium. Intestine opens in usual position at edge of pallial cavity on right side. Anterior margin of sole of foot provided with two projections, probably sensory in function. Operculum paucispiral, of approx. 2.5 whorls, with very distinct calcareous smear overlapping nucleus a little to the left and extending much further to the right. Radular formula:

$$\frac{(4\text{–}5) - 1 - (4\text{–}5)}{(3\text{–}4) \qquad (3\text{–}4)} : (4) - 1 - (5) : (20\text{–}25) : (15\text{–}20).$$

Lateral wings on central tooth a little longer than in *P. cresswelli* n. sp., but otherwise the radulae of *manneringi* and *cresswelli* are not distinguishable.

TYPE MATERIAL. HOLOTYPE: dripping wet mossy bank, Mannering's farm, Waikaretu, Tuakau, Auckland, ix.1971, G. Mannering (NM, M 32438). PARATYPES: same data (5, NM, M 32439; 5, DSIR; 5, AKM). Many topotypes, viii.1973, G. M. Also (undesignated, NM): 1, Broken Hill Cave, Te Kuiti, 12.i.1970, J. Lowry; many, Mason's Cave, Waitomo System, S. Easterbrook-Smith; many, cave at Te Uku, S. E-S.; 4, cave at Matira, S. E-S.; 2, cave at Waipuna, S. E-S.

REMARKS. Cavernicolous, and apparently restricted to the limestone country around Waitomo, extending north and west as far as Waikaretu and Waipuna. It can be collected at the surface, as at the type locality, where subterranean water breaks the surface as springs. It is quite distinct from *P. antipodarum*, with which it occurs at the type locality. Its affinities appear to be with *P. cresswelli*, which it very closely resembles, and with the more northern *P. gardneri* n. sp., described below. The separation of *manneringi* from *cresswelli* is based on the fewer and larger embryos, the smaller size and different spire taper in the former, and the large geographical gap separating the population on Stewart Island from those associated with North Island limestone. Only about 20% of the specimens examined from the type locality were males.

The species is named after Mr G. Mannering, Waikaretu, who provided me with all the preserved material studied.

Potamopyrgus gardneri n. sp. (Figs 7P, 14H)

Shell very small (just under 1.5 mm), yellowish-white, pupiform, of 4 rounded whorls, weakly ridged by radial growth-lines. Umbilical chink lacking, double peristome of parietal edge of aperture sealing tightly to body whorl. Spire only slightly tapered, sutures deep, and whorls consequently well rounded.

Pigmentation, tentacle shape and relative size, organs of pallial cavity, radula, and operculum not noticeably different from those documented above for *P. cresswelli* and *P. manneringi.*

TYPE MATERIAL. HOLOTYPE: head of swampy stream, 8 km S of Parakao, Northland, approx. 300 m, vii.1973, N. Gardner (NM, M 32437). PARATYPE: Ruahuia Viaduct, east of Dargaville, Northland, iv.1969, N. G. (NM; dissected).

REMARKS. This species is known only from the above two localities, but probably is more widespread in Northland where seepages of the right sort occur in forested areas. It can be separated from *P. manneringi* only on shell features, but the habitats are quite different, and the erection of a new species seems justifiable on these grounds.

There are good zoogeographic grounds for emphasising small differences in populations found in Northland compared with those south of the Auckland isthmus. I have discussed the role which Pliocene islands have apparently played in the evolution of land snails in Northland and the Three Kings Islands (Climo 1974, pp. 598–603, figs 4, 5). The same reasoning, which points out that the areas north and south of the Auckland isthmus were different islands separated by marine straits, can also be applied to freshwater molluscs with restricted distributions.

The species is named after Mr N. Gardner, Auckland, who for several years has provided me with Northland terrestrial and freshwater molluscs for study.

SUMMARY OF THE *Potamopyrgus*-COMPLEX AS HERE INTERPRETED

1. There is one large, very variable, surface-dwelling species of *Potamopyrgus* in New Zealand (*P. antipodarum*) which prefers fresh water. It does extend into caves and into

the phreatic environment, but these specimens are only extensions of the surface populations.

2. Two brackish-water species, *P. estuarinus* and *P. pupoides*, occur in New Zealand, the first large like *P. antipodarum*, the second small and pupiform.
3. One phreatic species, *P. subterraneus*, is found in the south of the South Island, and is closely related to *P. antipodarum*.
4. One cavernicolous species, *P. manneringi* n. sp., is found in underground streams in caves from Waitomo to Waikaretu, extending west as far as Waipuna, and also occurs on the surface where cave water emerges as springs.
5. Two species of *Potamopyrgus* are restricted to seepages in forest leaf litter. *P. cresswelli* n. sp. is found on Stewart Island, and *P. gardneri* n. sp. in Northland. Both these and the cavernicolous *manneringi* are all closely related, and more closely related to the ovoviviparous *antipodarum* than the conchologically more similar *P. pupoides*.
6. It appears that a second, small, brackish-water species lives with *P. pupoides* somewhere in Nelson, unless there is exceedingly marked sexual dimorphism from this particular unknown locality.

Hadopyrgus n. gen.

(hadopyrgus – from Gr. *hades*, underworld, and *pyrgos*, tower; gender masculine)
Type species: *Hadopyrgus anops* n. sp.

Erected for two species, *H. anops* n. sp., occurring throughout Nelson in caves and phreatic habitats, and *H. brevis* n. sp., living sympatrically with the former in the gravels of the Waimea Plains. It differs only in degree from *Potamopyrgus*, the most clear differentiating feature being radular morphology. The new genus has the following characteristics: shell short-spired, pupiform, white or semi-transparent, without a dark periostracum; operculum paucispiral, with a weak calcareous smear to the right of the nucleus; central tooth of radula with the cusp configuration

$$\frac{(4)\ -1\ -(4)}{(2)\qquad(2)}$$

and with long lateral wings; female ovoviviparous; animal unpigmented, blind; confined to subterranean habitats.

The long lateral wings on the central tooth, the reduced cusp development on these wings, subterranean habitat, and lack of surface-dwelling relatives are the reasons used here to segregate this part of what might otherwise be called variation in *Potamopyrgus* as a new genus.

Hadopyrgus anops n. sp. (Figs 8A–M, 10J, 15C)

Shell small (up to 2.2 mm), colourless, globosely pupiform, of 4–5 rounded, thin, transparent whorls (shape similar to the New Zealand hydrobiid genus *Paxillostium*); aperture roughly circular, with peristome double on parietal and upper edges, but not clearly so on lower edge; body whorls scalariform in appearance, owing to a distinct umbilical chink extending behind double peristome on parietal section of aperture.

Different populations have their own shell peculiarities; those from gravels of the Maitai and Waiiti Rivers are quite short-spired, and the spire taper is gentle; those from the gravels in the Lee Valley, Nelson, have higher spires and more pronounced axial growth-lines; those from Maitai Cave, Nelson, are similar to the Waiiti and Maitai phreatics but are more variable in adult size; those from Gorge Creek Cave, Takaka, have a large body whorl and a markedly tapering spire; those from Ida Cave, Karamea, are similar to the Waimea and Waiiti phreatics in size and shape, but have much thicker shells. These ranges in form in what, at this stage, is interpreted as one variable species, are illustrated in Fig. 8.

Animal colourless; anterior margin of sole of foot provided with two, presumably sensory, pedestal-like projections; snout prominent and bilobed, framed by two eyeless, spatulate tentacles. Ctenidium of approx. 7–12 plications near entrance of left side of pallial cavity; below this a very small osphradium near mantle edge. Operculum paucispiral with a ridge arching around periphery on left side as viewed from beneath, a weak, granular thickening in central area, and transparent. Radular formula:

$$\frac{(4)\ -1\ -(4)}{(2)\qquad\quad(2)} : (5\text{–}6)\ -1\ -(5\text{–}6) : (\text{approx. } 30) : (\text{approx. } 25).$$

Central tooth with extremely long, thin lateral wings and a central, peninsula-like projection, cusps on upper, inner edge of wings; cusp row of lateral tooth nearly as wide as that of central, basal section of tooth, with a distinct notch on outer edge at point of outward flexure; cutting edge of inner marginal half as wide again as that of central, basal portion long and simple; outer marginal similar to inner, except that cusp row only three-quarters width of latter. Verge very large for size of animal, simple, with one duct, fastened to right of midline of head and recurved to the left.

TYPE MATERIAL. HOLOTYPE: D. Lauria's well, 197 Nile St., Nelson City, 27.vi.1972, G. Kuschel (NM, M 32438). PARATYPES: type locality, G. K. – 1, 27.vi.1972 (DSIR), 1, 10.iii.1973 (NM, M 32509), 1, 14.iv.1973 (M 32471), 3, 26.v.1973 (M 32503), 1, 2.vi.1973 (M 32468); Eden's bore no. 1, Waimea, 14.iv.1972, G. K. (2, NM, M 32548; 1, AKM); Livingston's well, Waimea, G. K. – 3, 15.iv.1972 (DSIR), 1, 24.vi.1972 (NM, M 32472), 1, 1.vii.1972 (AM), 1, 13.iv.1973 (AKM), 1, 18.v.1973 (NM, M 32479), 2, 24.v.1973 (M 32502); Nelson City Council Nursery well, G. K. – 1, 17.v.1972 (NM, M 32553), 1, 23.i.1973 (M 32524). Also (undesignated): 5, Nelson City Council Nursery well, 23.i.1973, G. K. (NM, M 32524); 8, Ida Cave, Oparara, 26.vi.1973, G. K. (4, NM, M 32457); 2, DSIR; 2, AKM); 20, Maitai Cave, Nelson, 18.iv.1973, G. K. (16, NM, M 32510; 2, DSIR; 2, AKM); 5, lower entrance, Gorge Creek Cave, Takaka, 3.iii.1973, C. M. Smith (3, NM, M 32439; 2, DSIR); 4, Bush Cave, Paturau, 13.vi.1973, G. K. (NM, M 32458); Lee Valley, Nelson, G. K. – 1, 21.xii.1972 (NM, M 32528), 2, 22.ii.1973 (M 32522), 1, ?date (DSIR).

REMARKS. As a phreatic species, *H. anops* n. sp. is known from D. Lauria's well, Nile St., Nelson City (type); Livingston's well, Waimea, Nelson (S20 472177); Eden's bore No. 1, near Brightwater, Nelson; Nelson City Council Nursery well, Nelson City; and from gravels in the Lee Valley. In the phreatic environment the species is recorded from the underground water systems of the Waiiti, Lee, and Maitai Rivers. It is known as a cavernicolous snail from the following localities: Gorge Creek Cave, Pikikaruna Range, Nelson; Wetneck Cave, north of Paturau, Nelson; Bush Cave, Paturau; Ida Cave, Oparara, Karamea; Metro Cave, Charleston.

In general shell features, paucispiral operculum, and subterranean modifications, *Hadopyrgus anops* is very similar to the Japanese species *Akiyoshia uenoi* Kuroda & Habe, 1954, the type of *Akiyoshia* (Kuroda & Habe 1954, figs 1–4). However, the Japanese genus has the radular formula

$$\frac{(5)\ -1\ -(5)}{(2)\qquad\quad(2)} : (2)\ -1\ -(4\text{–}5) : (24) : (20),$$

similar to *Hadopyrgus anops* but differing significantly in the cusp configuration of the lateral tooth. On opercular characteristics, the New Zealand genus is derived from *Potamopyrgus*, an unlikely derivation for *Akiyoshia*. *A. imamurai* Habe, 1961 and *A. nanatsugamaensis* Habe, 1961, taller-spired than the type species (Habe 1961, figs 1, 2), show a similar resemblance to other New Zealand genera described below. The tall, thin spires of both New Zealand and Japanese phreatic and cavernicolous species are probably due to ecologically influenced morphological convergence rather than a close phyletic relationship.

Hadopyrgus brevis n. sp. (Figs 9N–U, 10K, 15G)

Shell minute (up to 1.5 mm), of 4–5 semi-transparent, lightly rounded whorls, considerably variable in size, a four-whorled specimen measuring between 0.8 mm and 1.5 mm; spire only slightly tapering; aperture large, particularly in the smaller specimens, heavily thickened. These shell features are illustrated in Fig. 9N–U.

Animal unpigmented, blind; tentacles short, spatulate; snout long; ctenidium of 4 or 5 irregularly shaped, raised lamellae; osphradium below ctendidium; intestine opening in middle of right side of pallial cavity. Verge a simple, recurved structure, fastened to right of head midline, with only one duct, the vas deferens, opening terminally. Operculum paucispiral, with a weak calcareous smear to right of nucleus. Radular formula:

$$\frac{(3)\ -1\ -(3)}{(2)\qquad(2)} : (3)\ -1\ -(3) : (\text{approx. } 15) : (\text{approx. } 12),$$

which differs from that of *H. anops* in the reduced number of cusps on the crown of all the teeth. Unlike *H. anops*, the lateral wings of the central tooth are not greatly elongated.

TYPE MATERIAL. HOLOTYPE: D. Lauria's well, 197 Nile St., Nelson City, 2.v.1972, G. Kuschel (NM, M 32466). PARATYPES: type locality, G. K. – 1, 22.ii.1973 (DSIR), 1, 10.iii.1973 (NM, M 32508), 1, 26.v.1973 (M 32504), 1, 2.vi.1973 (M 32469); Livingston's well, Waimea, G. K. – 1, 30.xii.1972 (DSIR), 1, 26.i.1973 (NM, M 32501), 1, 2.ii.1973 (M 32477), 1, 25.v.1973 (AM).

REMARKS. Found only in the gravels of the Waiiti and Maitai River systems of Nelson. It is closely related to *H. anops*, but is considerably smaller, has a more thickened aperture, fewer cusps on the crowns of the radular teeth, and shorter wings on the central tooth.

Kuschelita n. gen.

Type species: *Kuschelita mica* n. sp.

Erected for two phreatic species, the type from the gravels of Nelson, and the second species from a similar habitat near Napier, on the east coast of the North Island.

Shell minute (up to 1.8 mm), thin, transparent, narrow (0.5–0.7 mm wide at body whorl), tall-spired, up to 7 rounded or slightly flat-sided whorls; aperture broadly lunate, peristome double except in centre of outer lip; a distinct unbilical chink extending behind double peristome of parietal wall of aperture, imparting a loose, scalariform appearance to body whorl.

Animal blind and unpigmented. Operculum paucispiral, thin and transparent, with a faint calcareous smear to right of nucleus. Pallial cavity large, but neither ctenidium nor osphradium observed in animals dissected. Verge a simple, recurved organ, fastened on back of head to right of midline, containing one duct, the vas deferens, which opens terminally. Radular formula:

$$\frac{(3)\ -1\ -(3)}{(1)\qquad(1)} : (2)\ -1\ -(2) : (\text{approx. } 15) : (\text{approx. } 10).$$

REMARKS. Mention was made above, under *Hadopyrgus anops*, of the similarity of *Kuschelita* to the tall-spired Japanese species of *Akiyoshia*, but this similarity is only shell convergence. *Kuschelita* is more distinct from *Potamopyrgus* than is *Hadopyrgus*. The cusps on the lateral wings of the central tooth of the former are further reduced, to one on each side, and the number of cusps on the tooth crowns reduced further than in *Hadopyrgus brevis*. It has also a very distinctive, narrow, tall-spired shell, and is restricted to the phreatic environment.

The genus is named after Dr G. Kuschel, Systematics Section, Entomology Division, DSIR, Auckland, who has provided much of the material used in this study.

Kuschelita mica n. sp. (Figs 4, 9C–M, 10L–N, 15E)

Shell minute (up to 1.8 mm), tall-spired, with slightly flat-sided whorls. The rest of the generic diagnosis applies to this species. Verge very large for size of animal (Fig. 10L, M). Anterior portion of foot, just anterior to sole, drawn out into a proboscis-like extension, apparently suctorial at tip (Fig. 10L,M). This structure is probably analogous to the pair of sensory processes at the anterior sole boundary mentioned above in some species of *Potamopyrgus* and *Hadopyrgus*.

TYPE MATERIAL. HOLOTYPE: Livingston's well, Waimea Plains, Nelson (S20 472177), 27.iv.1972, G. Kuschel (NM, M 32467). PARATYPES: type locality, G. K. – 1, 1.iv.1972 (NM, M 32478), 1, 8.iv.1972 (M 32482), 1, 15.iv.1972 (AKM), 1, 13.v.1972 (DSIR), 2. 20.v.1972 (NM, M 32481), 1, 9.iv.1972 (AM), 2, 17.vi.1972 (M 32479), 1, 24.vi.1972 (M 32480), 1, 27.vi.1972 (AM), 1, 8.vii.1972 (AKM), 1, 13.vii.1972 (NM, M 32506; dissected), 1, 19.viii.1972 (AKM), 1, 23.ix.1972 (DSIR), 1, 7.x.1972 (DSIR), 2, 11.x.1972 (DSIR), 2, 16.xi.1972 (NM, M 32500), 1, 24.xi.1972 (M 32475), 1, 15.xii.1972 (M 32505), 1, 23.xii.1972 (AM), 2, 30.xii.1972 (DSIR), 1, 26.i.1973 (AKM), 2, 2.ii.1973 (NM, M 32467), 1, 6.xi.1973 (AKM), 1, 21.iv.1973 (AM), 2, 18.v.1973 (DSIR); D. Lauria's well, Nelson City, G. K. – 1, 30.i.1973 (NM, M 32474), 1, 10.iii.1973 (M 32507). Also 15 collected later in 1973 from type locality (NM, spirit collection).

REMARKS. The material examined from Livingston's well is plotted in Fig. 4. Livingston's well dried up towards the end of February, and this may account for the paucity of specimens recorded there from March to May. Like *Hadopyrgus brevis*, this species is known only from the gravels of the Waiiti and Maitai Rivers, Nelson.

Kuschelita inflata n. sp. (Fig 9A,B)

Shell minute (1.6 mm), thin, transparent, narrow (0.7 mm wide at body whorl), tall-spired, of 5 strongly rounded whorls. Differs from *K. mica* n. sp. in having a proportionally shorter spire, more rounded whorls, larger, more inflated aperture, and smaller faecal pellets, indicating a much narrower intestine. Details of peristome and umbilical chink as in generic diagnosis.

TYPE MATERIAL. HOLOTYPE: Ministry of Works and Development bore, Roy's Hill, Napier (N 134 14/23), 22.vi.1972, G. Kuschel (NM, M 32465). The species is known only from the holotype.

Paxillostium Gardner, 1970

Type species: *Paxillostium nanum* Gardner, 1970.

Gardner (1970, p. 181) defined the genus as follows: "Shell very small, ovoid; whorls deeply sutured; apex large, obtuse; aperture evenly oval; operculum rimmed, with single erect stool." The relationship between *Paxillostium* and other components of the *Hemistomia*-tribe is discussed above.

Paxillostium nanum Gardner, 1970 (Figs 2, 6D, 13F,G, 14A,B)

Paxillostium nanum Gardner, 1970: 181.

Gardner adequately described the shell, radula, operculum, and external animal features of the species; a few additional notes are added here. Verge simple, recurved, with one duct, the vas deferens, opening terminally. Ctenidium well formed, curving from lower left front of pallial cavity posteriorly and centrally. Well-developed osphradium situated below ctenidium. Intestine opens on right side of pallial cavity.

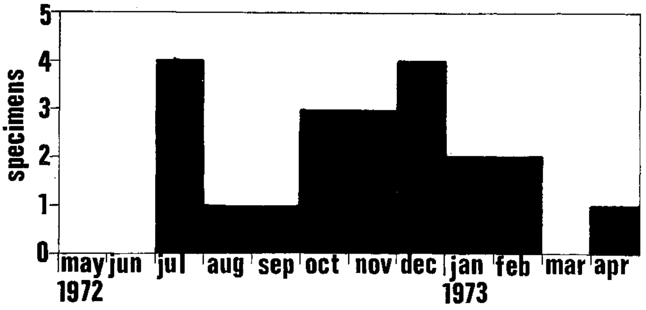

FIG. 4—Seasonal abundance of *Kuschelita mica* n. gen. & n. sp. from standardised sampling at Livingston's well, Waimea, Nelson, New Zealand.

REMARKS. Known from only a few areas in Northland, this species seems to be adapted to seepages at the head of streamlets in forested areas. *Potamopyrgus gardneri* n. sp. occurs with *P. nanum* at the type locality for both, 8 km south of Parakao, Northland. It would be enlightening to discover if a *Paxillostium* derivative is living in cavernicolous seepages in Northland.

NEW ZEALAND MEMBERS OF THE *Istriana*-TRIBE

There is only one, monotypic, genus in New Zealand attributable to this informal grouping in Hydrobiinae.

Catapyrgus n. gen.

(catapyrgus – from Gr. *cata*, down, and *pyrgos*, tower; gender masculine)
Type species: *Catapyrgus spelaeus* n. sp.

Shell minute (under 2.0 mm), narrow, tall-spired; females ovoviviparous; animal unpigmented, but small eyes present; verge the simple, recurved structure of *Hemistomia*-tribe; operculum paucispiral, with a large, curved peg arising from over or slightly to left of nucleus; central tooth of radula peculiarly shaped, with deeply indented crown, very short wings, and a deep, central projection of basal plate. Cavernicolous.

Istriana Velkovrh, 1971, from Dalmatia, is the only other recorded hydrobiid snail with the recurved opercular peg possessed by the New Zealand *Catapyrgus*. As mentioned above, I regard this peg in two widely separated cavernicolous hydrobiids as more than convergence, and have used the informal grouping '*Istriana*-tribe' to associate these two genera. The New Zealand genus differs from *Istriana* in details of shell and operculum, and quite markedly in radular structure.

Catapyrgus spelaeus n. sp. (Figs 10A–I, 14N, 15D)

Shell minute (up to 1.7 mm), of 5–6 rounded whorls; spire tall, narrow (like that of *Kuschelita*), the sutures well impressed; aperture roughly circular, with peristome double on all edges except outer lip; thick-shelled, with irregular axial growth-lines. The variation in shell morphology of several populations is shown in Fig. 10A–I.

Animal white, unpigmented except for two very small, black eyes situated in central base of tentacles; latter short, gently tapering towards tip. Ctenidium of 4–5 lamellae; osphradium and termination of intestine all in positions described above for other taxa.

Verge not distinguishable macroscopically from that of *Potamopyrgus*, *Hadopyrgus*, *Kuschelita*, or *Paxillostium*. Operculum as described in generic diagnosis. Radular formula:

$$\frac{(6)\ -1\ -(6)}{(3)\qquad(3)} : (6)\ -1\ -(10) : (\text{approx. } 30) : (\text{approx. } 25);$$

cutting surface of lateral tooth about as wide as that of central, that of first marginal half as wide again.

Type Material. Holotype: Wetneck Cave, Paturau, Nelson, 13.vi.1973, G. Kuschel (NM, M 32459). Paratypes: 45, type locality, same data (34, NM, M 32460; 5, AKM; 6, DSIR); 18, Twinforks Cave, Paturau, 12.vi.1973, G. K. (6, NM, M 32464; 6, AKM; 6, DSIR); 31, Bush Cave, Paturau, 13.vi.1973, G. K. (19, NM, M 32461; 6, AKM; 6, DSIR); 29, Ida Cave, Oparara, Karamea, 26.vi.1973, G. K. (15, NM, M 32462; 7, AKM; 7, DSIR); 5, Profanity Cave, Inangahua, 27.vi.1973, G. K. (NM, M 32463). Also (undesignated): 24, Simm's Cave, Upper Takaka, Nelson, 25.vii.1973, G. K. (NM, M 32947).

Remarks. The species appears to be restricted to the Cenozoic limestones and marbles of the north-west of the South Island. Investigations of limestones on the Gouland Downs and the Heaphy Bluff, Nelson, also should produce this species, and it may extend as far south as Jackson Head in South Westland, provided the limestone remnants are large enough for cave formation and water retention. This habitat is occupied by *Potamopyrgus manneringi* n. sp. in caves in the North Island.

New Zealand members of the *Fluviopupa*-tribe

Opacuincola Ponder, 1966 is the only genus in New Zealand attributable to this informal tribe. It has a range of shell form, in the three New Zealand species, similar to that covered by *Fluviopupa rapaensis* Hubendick, 1952 and *F. obtusa* Hubendick, 1952 (Hubendick 1952, fig. 1D,F).

Opacuincola Ponder, 1966

Type species: *Opacuincola caeca* Ponder, 1966.

The characteristics of the genus are as follows: thick-shelled, with short spire and large aperture; operculum paucispiral, lacking a calcareous smear, but with strong, radiating spiral ridges on inner surface; verge with an accessory flagellum, not containing a duct, branching off right side of organ near tip; females ovoviviparous; central tooth of radula with relatively long wings and the cusp formula:

$$\frac{(5\text{–}6)-1-(5\text{–}6)}{(4\text{–}5)\qquad(4\text{–}5)};$$

cavernicolous; eyes present or absent.

Mention was made in the introduction to family Hydrobiidae of the similarities of *Opacuincola* to a number of Tasmanian and Australian genera. Mention has been made also of the similarity of *Opacuincola* and *Fluviopupa*. Solem's (1959, p. 195, pl. 6, fig. 11) illustration and redescription of *Fluviopupa brevior* (Ancey, 1905), from the New Hebrides, shows a verge with a bifurcate tip, a condition similar to that in *Opacuincola*. This could be a parallelism, but when opercular and shell features are considered it seems a logical first step to group *Fluviopupa*, *Opacuincola*, and the other genera alluded to above (and shown in Fig. 3) as the informal *Fluviopupa*-tribe in Hydrobiinae. Hubendick (1952, p. 295) suggested that the Lord Howe Island genera *Fluviorissoina* Iredale and *Pupidrobia* Iredale might be species of *Fluviopupa*, but this still has to be checked anatomically. If not belonging to *Fluviopupa*, they probably belong in the group of genera covered by the tribe of the same name. In size, shell form, and coloration, the type species of *Opacuincola* is closest to the Tasmanian genus *Valvatasma* Iredale (Fig. 11E), but not enough is known of the anatomy of *Valvatasma* to make comparison worth while. Two new species of *Opacuincola* are described below, one superficially similar to the type species, and a second quite different on shell features.

Opacuincola caeca Ponder, 1966 (Fig. 11B)

Opacuincola caeca Ponder, 1966: 35.

Little can be added to Ponder's (1966, pp. 35–6) diagnosis of this species, because no further live adult material has been collected. On two occasions (3.iii.1973, C. M. Smith; 15.iii.1973, G. Kuschel, C. M. Smith, J. McBurney, G. Ramsay, C. Watt, and F. Climo) attempts were made to collect live material from the lower entrance of Gorge Creek Cave, and on the second attempt the underground stream was explored to the terminating siphon by entering the cave at the upper entrance. However, only shell material was obtained on each occasion.

REMARKS. Known only from the type locality, Gorge Creek Cave, Takaka, Nelson, a large, complex cavern formed in marble and containing a large underground stream, and Simm's Cave, Upper Takaka. It is very closely related to *O. troglodytes* n. sp. (*below*) from a spring near Te Kuiti in the North Island, but is more distantly related to the geographically much closer *O. kuscheli* n. sp. from northern and western districts of Nelson.

Opacuincola troglodytes n. sp. (Fig. 12G,H)

Shells of this species are similar to those of *O. caeca*, but differ in their smaller size (2.1 mm, cf. 2.7 mm) and variability, being prone to vermiform monstrosities and considerable variation in spire height. No live material has yet been found, and consequently the species cannot be compared closely with *O. caeca*.

TYPE MATERIAL. HOLOTYPE: soda spring, off Wairona Road, Aria, King Country, North Island, 1971, N. Gardner (NM, M 32446). PARATYPES: 25, same data (15, NM, M 32447; 5, DSIR; 5, AKM).

REMARKS. Known only from the type locality. It seems preferable to name this northern population as a second species rather than include it as part of the variation of *caeca*, because it is difficult to envisage the latter occurring in two such widely separated localities when, in Nelson, two easily recognisable species of *Opacuincola* live in different cave systems. It could be that *troglodytes* is a synonym of *caeca*, and that the one species shows a peculiar remnant distribution pattern, but until this is shown from soft-part morphology it is safer to emphasise the small shell differences as specific characters.

Gardner (1973) has recorded the existence of this population, discussed the variability of the shells, and described the soda spring habitat. Apparently the species is not found alive in the soda spring, specimens emerging into the spring from subterranean habitats.

Opacuincola kuscheli n. sp. (Figs 12A–F, 14E, 15F)

Shell small (up to 2.3 mm), short-spired and squat (1.0–1.2 mm wide at body whorl), of 4–4.5 whorls, white, heavy-shelled, with a large aperture. Spire only slightly higher than height of aperture, whorls rounded, tapering quite sharply. Aperture broadly lunate, heavily thickened around edges, particularly in lower parietal region. Surface sculptured by irregular, radial growth-lines.

Animal white, unpigmented; optic tentacles short, swollen at base; eyes large, situated in bulbous base of tentacles, opening near outer base of tentacle; snout relatively short in preserved specimens, only weakly divided; ctenidium of 5–7 lamellae; osphradium near entrance of pallial cavity, below ctenidium; verge fastened far to right of head midline near base of optic tentacle, recurved, with a flagellate process appended to right side about two-thirds up from base; foot large, with two pedestal-like processes at anterior edge of sole. Operculum paucispiral, horny, with spirally arranged radiating ridges. Radular formula:

$$\frac{(5\text{–}6)\ -1\ -(5\text{–}6)}{(4\text{–}5)\qquad (4\text{–}5)} : (5)\ -1\ -(6) : (\text{approx. } 25) : (\text{approx. } 18).$$

TYPE MATERIAL. HOLOTYPE: Bush Cave, Paturau, Nelson, 13.vi.1973, G. Kuschel (NM, M 32451). PARATYPES: 16, type locality, same data (NM, M 32452); 8, Twinforks Cave, Paturau, 12.vi.1973, G. K. (4, NM, M 32456; 2, AKM; 2, DSIR); 27, Wetneck Cave, Paturau, 13.vi.1973, G. K. (17, NM, M 32453; 5, AKM; 5, DSIR); 4, Profanity Cave, Inangahua, 27.vi.1973, G. K. (NM, M 32454); 38, Ida Cave, Oparara, Karamea, 25.vi.1973, G. K. (22, NM, M 32455; 8, AKM; 8, DSIR).

REMARKS. This species shares with the type the bifid verge attached much further to the right on the head than in any other New Zealand hydrobiid snail. It differs from both *O. caeca* and *O. troglodytes* in being smaller and not as globose (Fig. 12A–F). It is restricted to cavernicolous habitats in the north-west of the South Island, like *Catapyrgus spelaeus*.

Subclass PULMONATA
Superorder STYLOMMATOPHORA
Family PUNCTIDAE Morse
Subfamily PHENACOHELICINAE Suter

Hydrophrea n. gen.

(hydrophrea – from Gr. *hydor*, water, and *phrear*, well; gender feminine)

Type species: *Laoma (Phrixgnathus) academia* Climo, 1970.

Shell minute (up to 2 mm), zonitoid in appearance, relatively tightly coiled, glossy, with faint growth-lines, umbilicate; protoconch smooth, whorls convex, aperture simple with sharp peristome. Radula with 15 teeth in transverse row, all tricuspid, marginals rectangular with weak cusps.

REMARKS. In the original description of *H. academia* it was noted that the shell is similar to that of a zonitid pulmonate (Climo 1970, p. 211), but the reproductive and radular characteristics discussed below now confirm a placing in Punctidae. The absence of uniformly bicuspid teeth negates the earlier placement in Punctinae. The absence of an epiphallus precludes inclusion in Charopinae. The absence of a long spermathecal duct with terminal spermatheca is the only feature preventing inclusion in Phenacohelicinae. It has been shown (Climo 1971, pp. 96–8, fig. 1A,B) that the sexually dimorphic phenacohelicine genus *Protoflammulina* Climo lacks several reproductive structures in one of its morphological states. The absence of a spermatheca in *Hydrophrea* may not, therefore, be of great systematic significance, and it is tentatively placed here in subfamily Phenacohelicinae. The new genus shows no systematic relationship to any described pulmonate.

Hydrophrea academia (Climo, 1970) n. comb. (Fig. 5A–J)

Laoma (Phrixgnathus) academia Climo, 1970: 211.

Specific diagnosis of shell as for genus; also *see* Climo (1970, p. 211). Animal unpigmented. Foot with well-developed peripodial groove. Radular formula

$$(3\text{–}4) + (3\text{–}4) + 1 + (3\text{–}4) + (3\text{–}4);$$

central tooth tricuspid, lateral cusps weak, basal plate long; lateral teeth larger than central, tricuspid, central cusp strongly developed, outer lateral cusp progressively weakening towards marginals; marginal teeth tricuspid, cusps weak but central strongest, basal portion rectangular, nearly as wide as first lateral tooth. Reproductive system hermaphroditic, male and female pores opening via an atrium; no spermatheca or duct; penis long, cylindrical, with terminal retractor muscle; epiphallus absent, vas deferens entering penis near base of retractor muscle, entering female duct just above atrium, and visible for some distance beneath surface of vagina. Buccal mass typical of stylommatophoran pulmonates: muscular, with transverse, composite jaw; two separate salivary glands with ducts entering near point of entry of oesophagus; generative tip of radula (odontophore) projecting posteriorly. Optic tentacles large; pigmented eye absent, though an organ without pigment present in position of normally pigmented eye.

MATERIAL EXAMINED. HOLOTYPE: "Quarternary [*sic*] deposit, 6 feet below a layer of Waimakariri River silt alluvium, University of Canterbury Ilam site, Christchurch City", 1969, Botany Dept., University of Canterbury. Also (undesignated): 2, Eden's bore No. 1, Waimea, Nelson (S20 465189), 14.iv.1972; 1, F. Harrison Young's well, Waimea, 22.v.1972; 2, Nelson City Council Nursery well, 24.v.1972/23.i.1973; 1, D. Lauria's well, 197 Nile St., Nelson City, 22.v.1972; 1, Rabbit I., Nelson, 9.viii.1972; all coll. G. Kuschel (DSIR). Radula mount from a dissected Eden's bore specimen in NM.

REMARKS. Widely spaced in the South Island, having been collected from Christchurch and from two river systems in Nelson. This is the first punctid stylommatophoran pulmonate recorded as living in fresh water. It is also the first freshwater subterranean pulmonate recorded. The visible signs of modification resulting from the subterranean mode of life are relatively slight, the only features evident being the unpigmented eyes and absence of body pigmentation. Small size and the glossy shell would be advantages in an interstitial aquatic environment. The pulmonary cavity was unfortunately damaged during dissection, but no special respiratory modifications for an aquatic existence were evident. It may be small enough to meet its oxygen requirements by direct diffusion from water into the circulatory network of the mantle roof. Of the 13 specimens collected to date, only 1 was alive.

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Appendix

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Abbreviations used in figures: a., atrium; ct., ctenidium; e., eye; em., embryo; f., foot; fl., flagellum; f.p., faecal pellet; int., intestine; j., jaw; o., osphradium; oe., oesophagus; op., operculum; o.t., optic tentacle; p.g., peripodial groove; p.r.m., penis retractor muscle; r., radula; s.g., salivary gland; sn., snout; s.p., sensory process; t., tentacle; v., verge; v.d., vas deferens.

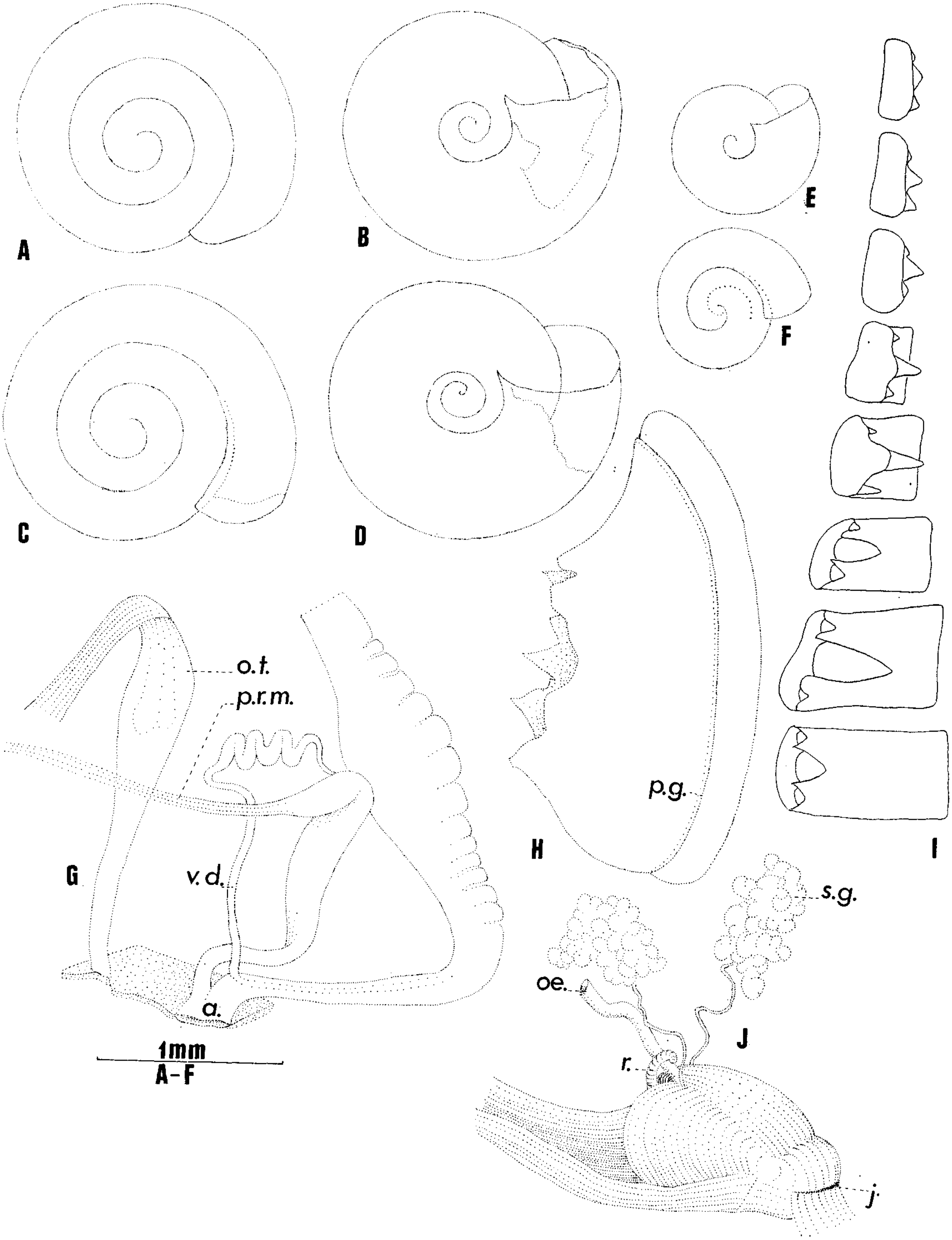

FIG. 5—*Hydrophrea academia* (Climo): A, B, holotype; C, D, dissected specimen from Eden's bore, Nelson; E, F, juvenile from Eden's bore; G, terminal reproductive system and optic tentacle; H, foot; I, radula; J, buccal mass.

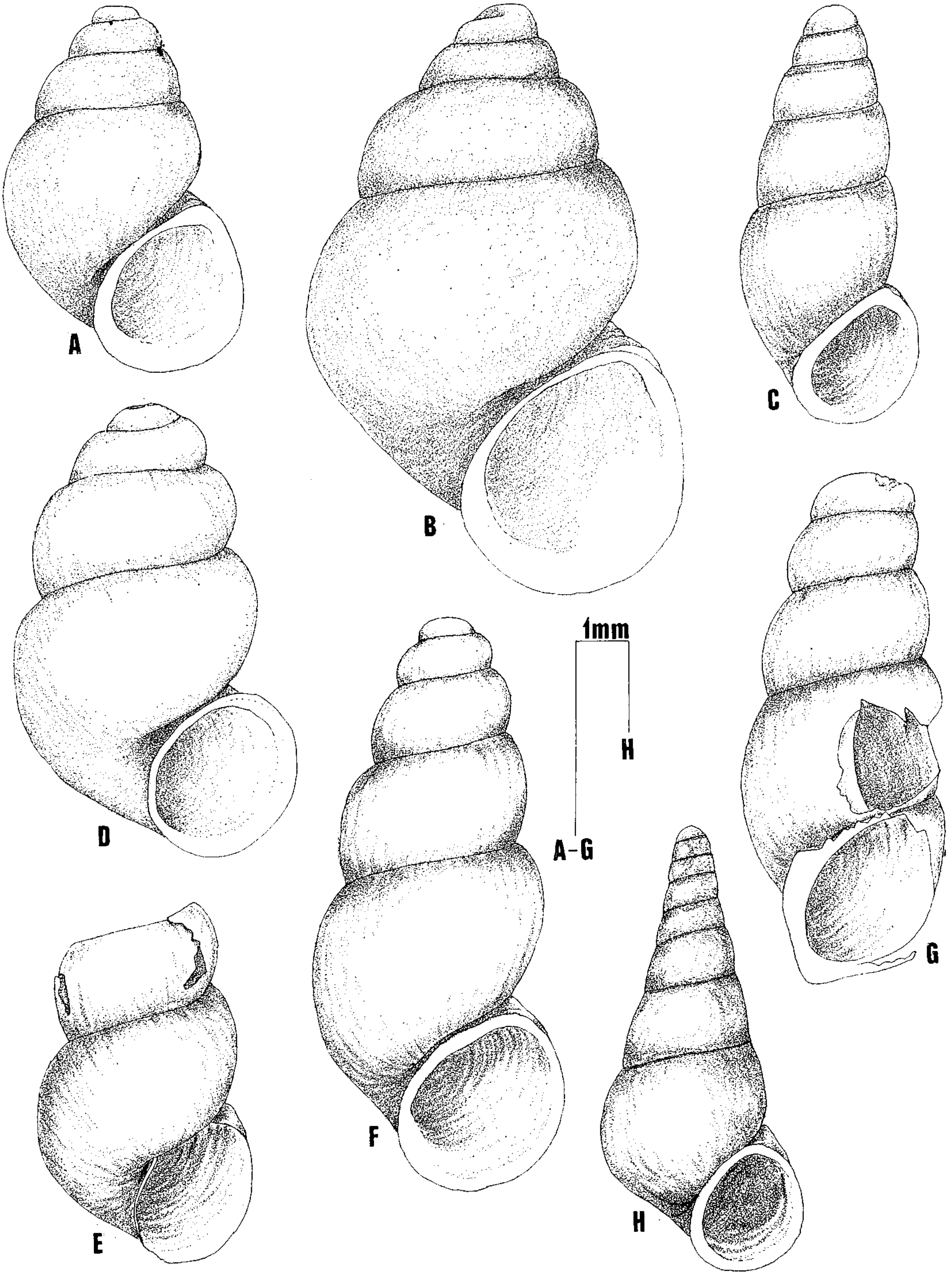

FIG. 6—A, *Pupiphryx smithi* (Petterd), tributary of Calder River, Tasmania; B, *Rivisessor tasmanicus* (Martens), "I. Basin, Cataract, Launceston, Tasmania"; C, *Hemistomia caledonica* Crosse, New Caledonia; D, *Paxillostium nanum* Gardner, paratype, New Zealand; E–G, *Potamopyrgus subterraneus* Suter - (E) Waitaki Valley, (F) Milford, (G) holotype (all New Zealand); H, *Tatea* sp., Narrabeen Lagoon, Sydney, Australia.

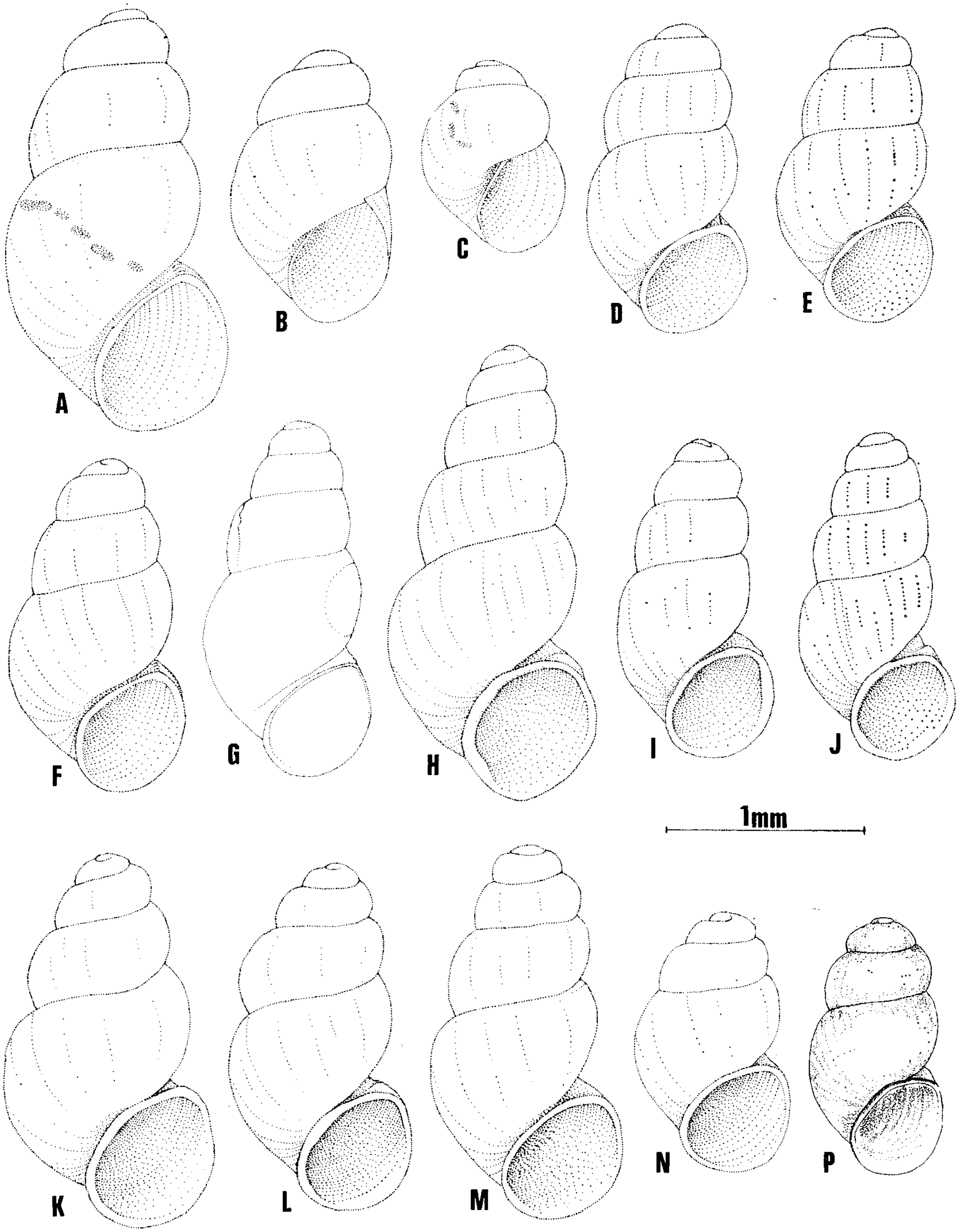

FIG. 7—A–C, *Potamopyrgus cresswelli* n. sp., Stewart Island (A, holotype); D–N, *P. manneringi* n. sp. – (D–F) paratypes, seepage at Waikaretu, (G) Broken Hill Cave, Te Kuiti, (H–J) Mason's Cave, Waitomo system, (K–N) cave at Te Uku; P, *P. gardneri* n. sp., holotype.

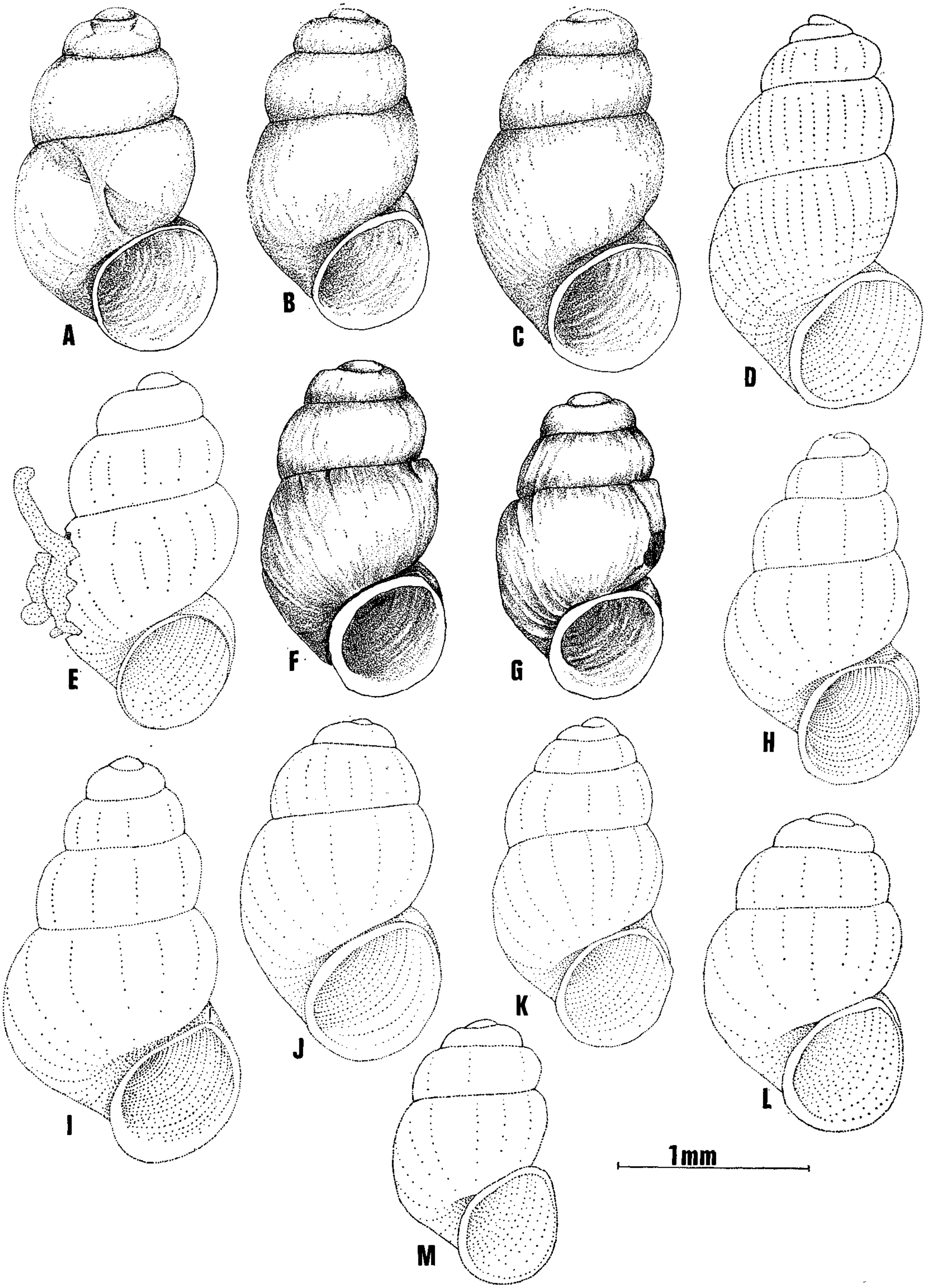

FIG. 8—*Hadopyrgus anops* n. gen. & n. sp.: A, holotype; B, C, Bush Cave, Paturau; D, gravels, Lee Valley, Nelson; E, paratype, Lauria's well, Nelson City; F, G, Ida Cave, Oparara, Karamea; H, I, Gorge Creek Cave, Takaka; J, K, paratypes, Livingston's well, Nelson; L, M, Maitai Cave, Nelson.

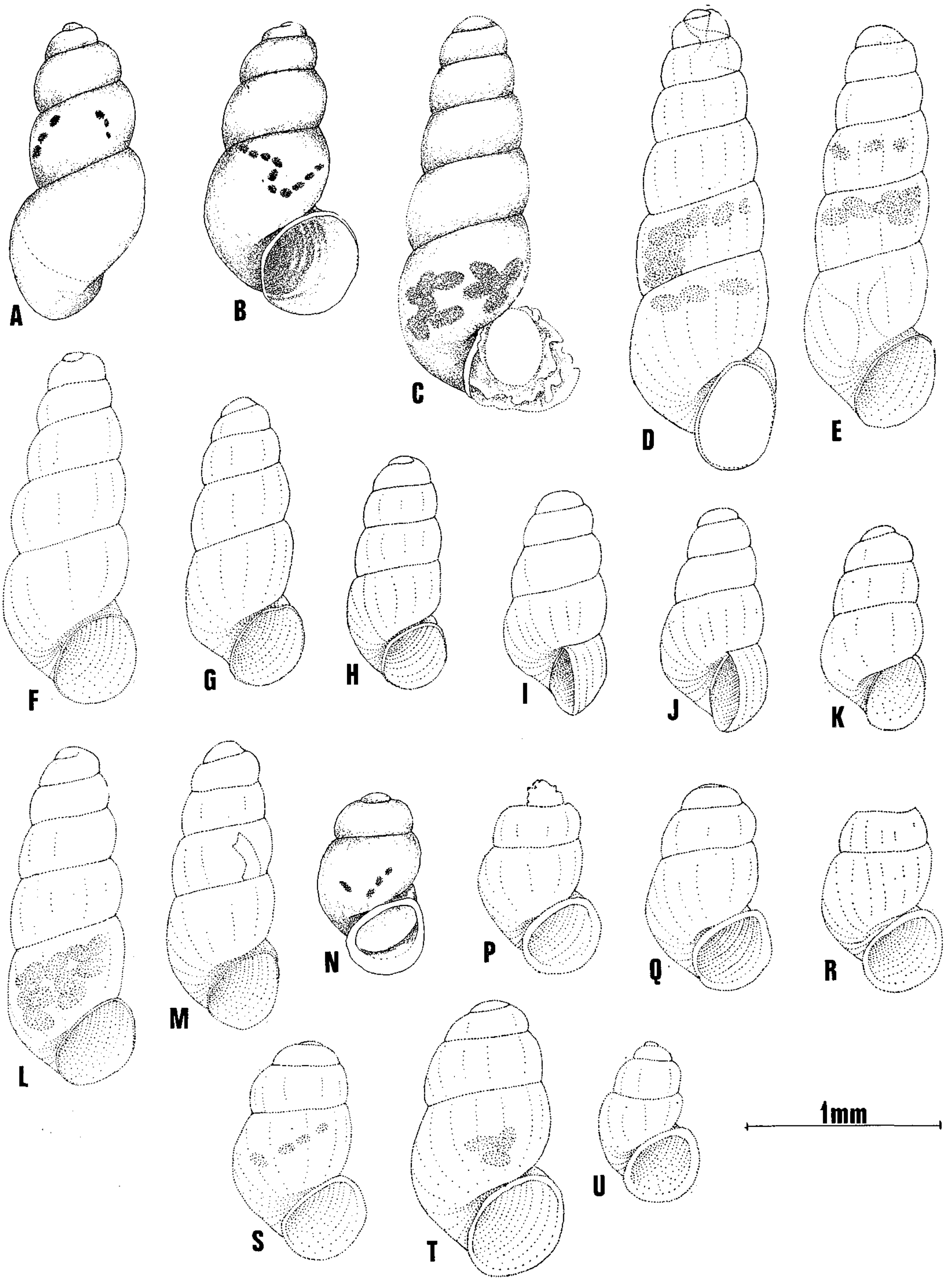

FIG. 9—A, B, holotype *Kuschelita inflata* n. gen. & n. sp.; C–M, *K. mica* n. sp – (C) holotype, (D–K) size range of paratypes from Livingston's well, Nelson, (L, M) paratypes, Lauria's well, Nelson City; N–U, *Hadopyrgus brevis* n. gen. & n. sp. – (N) holotype, (P, R) paratypes, Lauria's well, Nelson City, (S–U) paratypes, Livingston's well, Waimea.

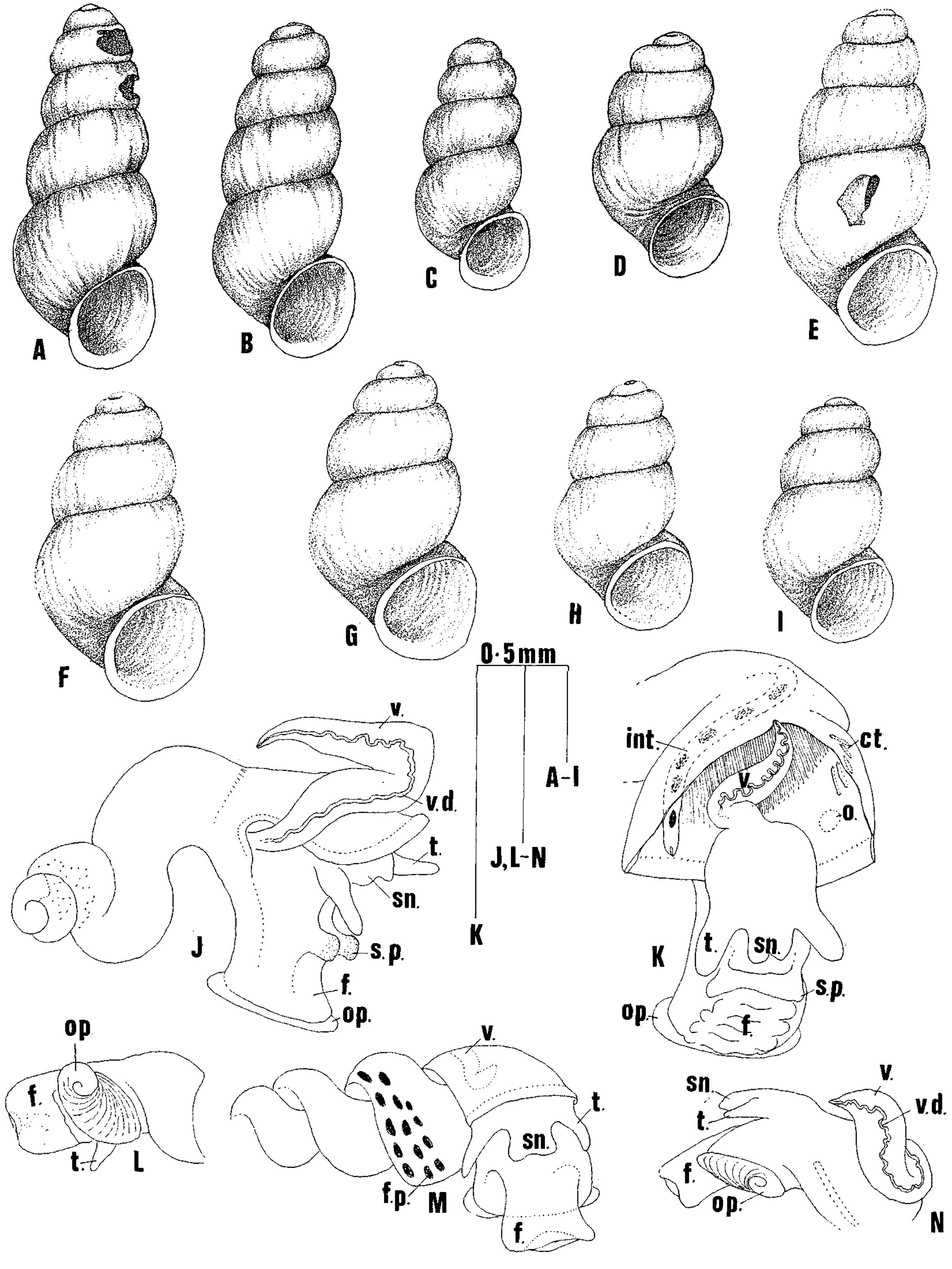

FIG. 10—A–I, *Catapyrgus spelaeus* n. gen. & n. sp. – (A–C) Ida Cave, Oparara, (D) Profanity Cave, Inangahua, (E–I) Wetneck Cave, Paturau (F, holotype); J, external animal features, *Hadopyrgus anops* n. gen. & n. sp.; K, head and pallial features, *H. brevis* n. sp.; L–N, external animal features and verge, *Kuschelita mica* n. gen. & n. sp.

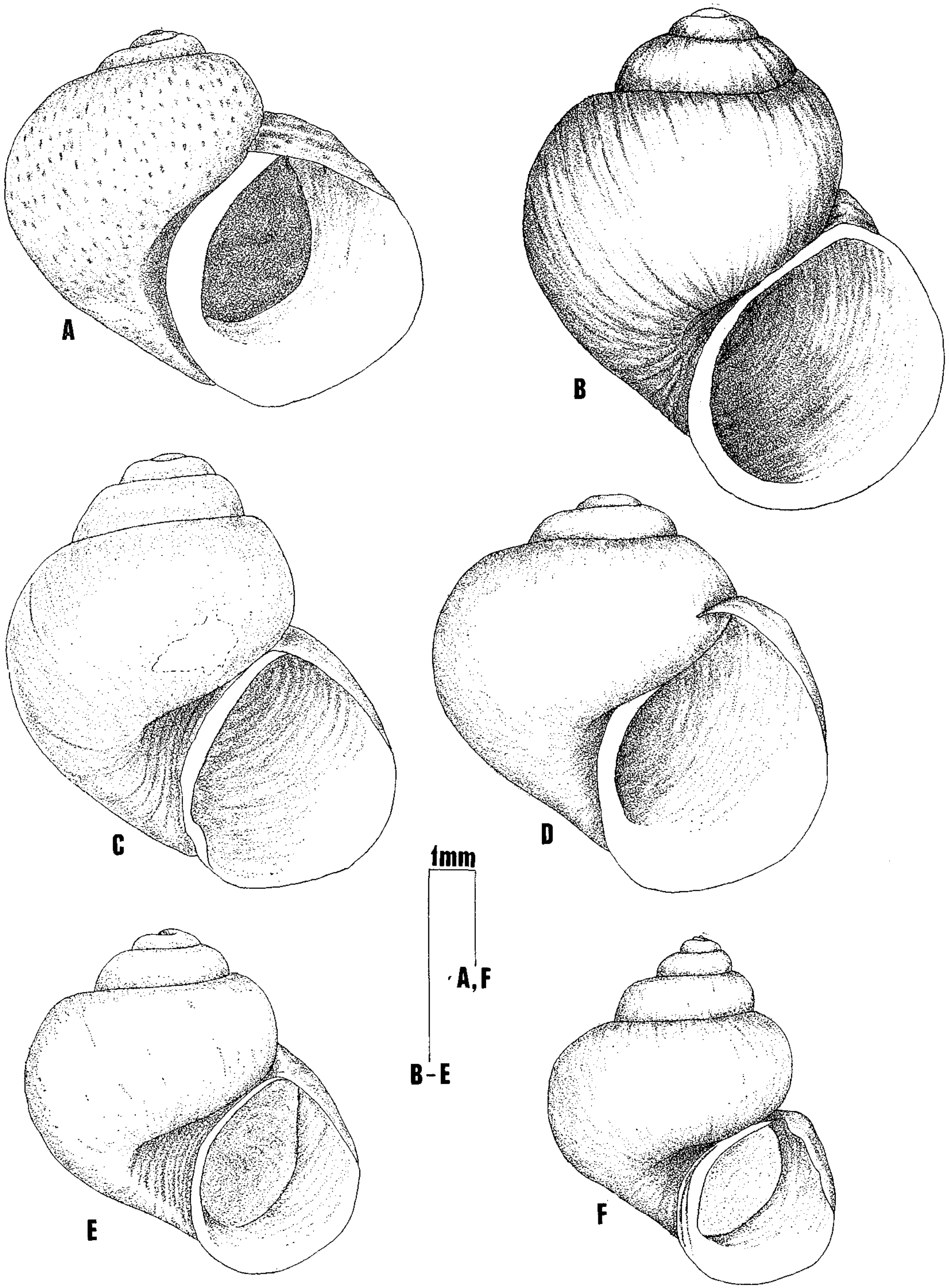

FIG. 11—A, *Petterdiana paludinella* (Reeve), north-west coast, Tasmania; B, *Opacuincola caeca* Ponder, paratype, Gorge Creek Cave, Takaka, New Zealand; C, *Beddomena belli* Petterd, west coast, Tasmania; D, *Jardinella thaanumi* Pilsbry, paratype, near Cairns, Queensland; E, *Valvatasma tasmanica* Tenison-Woods, Gould's Country, Tasmania; F, *Tasmaniella launcestonensis* Johnston, South Esk River, Tasmania.

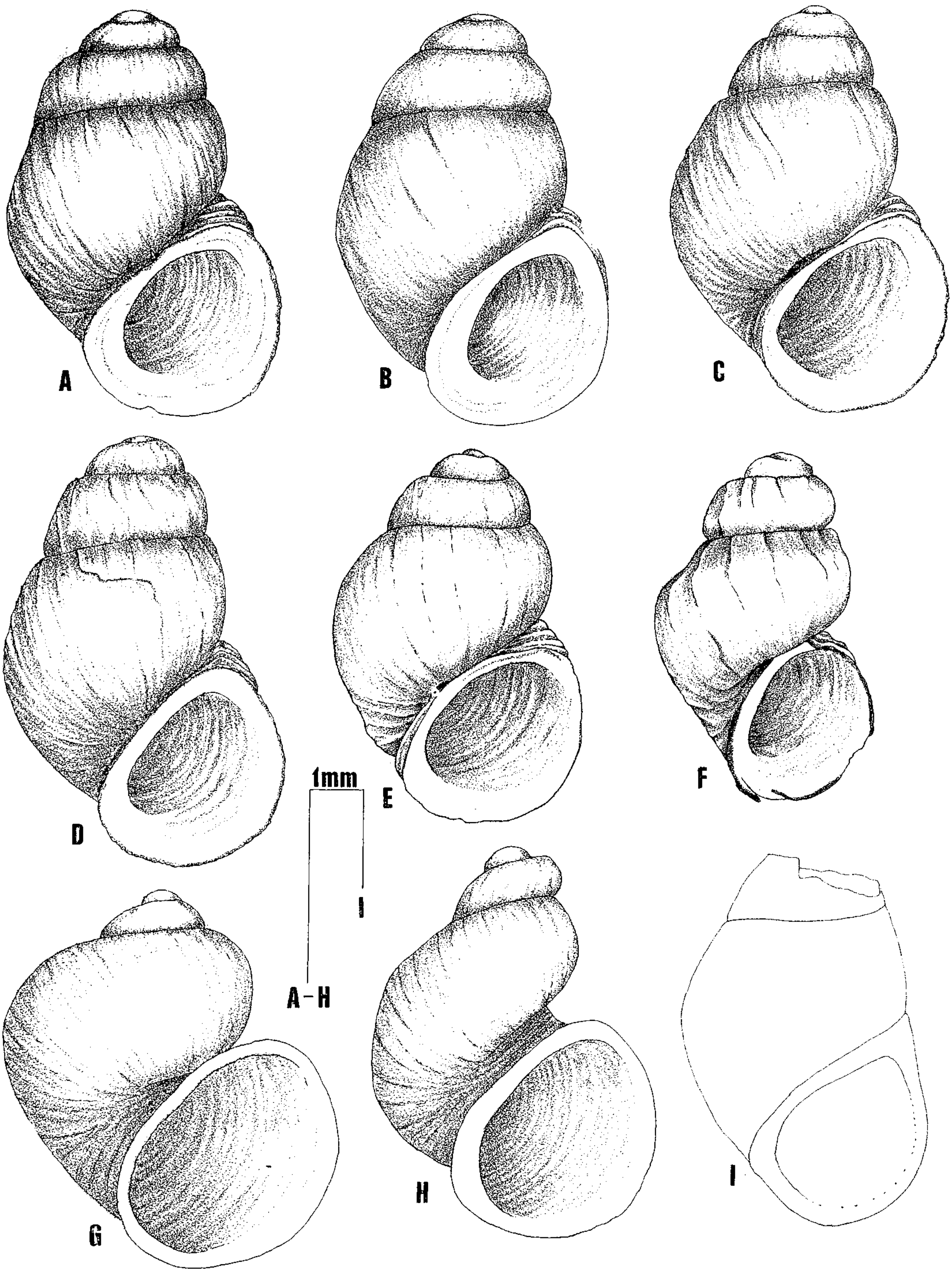

FIG. 12—A–F, *Opacuincola kuscheli* n. sp. – (A, B) paratypes, Ida Cave, Oparara, (C, D) paratypes, Bush Cave Paturau, (E, F) paratypes, Profanity Cave, Inangahua; G, H, *Opacuincola troglodytes* n. sp. – (G) holotype, (H) paratype; I, *Potamopyrgus* cf. *antipodarum* (Gray), Castlecliffian fossil, Fernflats Road, near Marton, New Zealand.

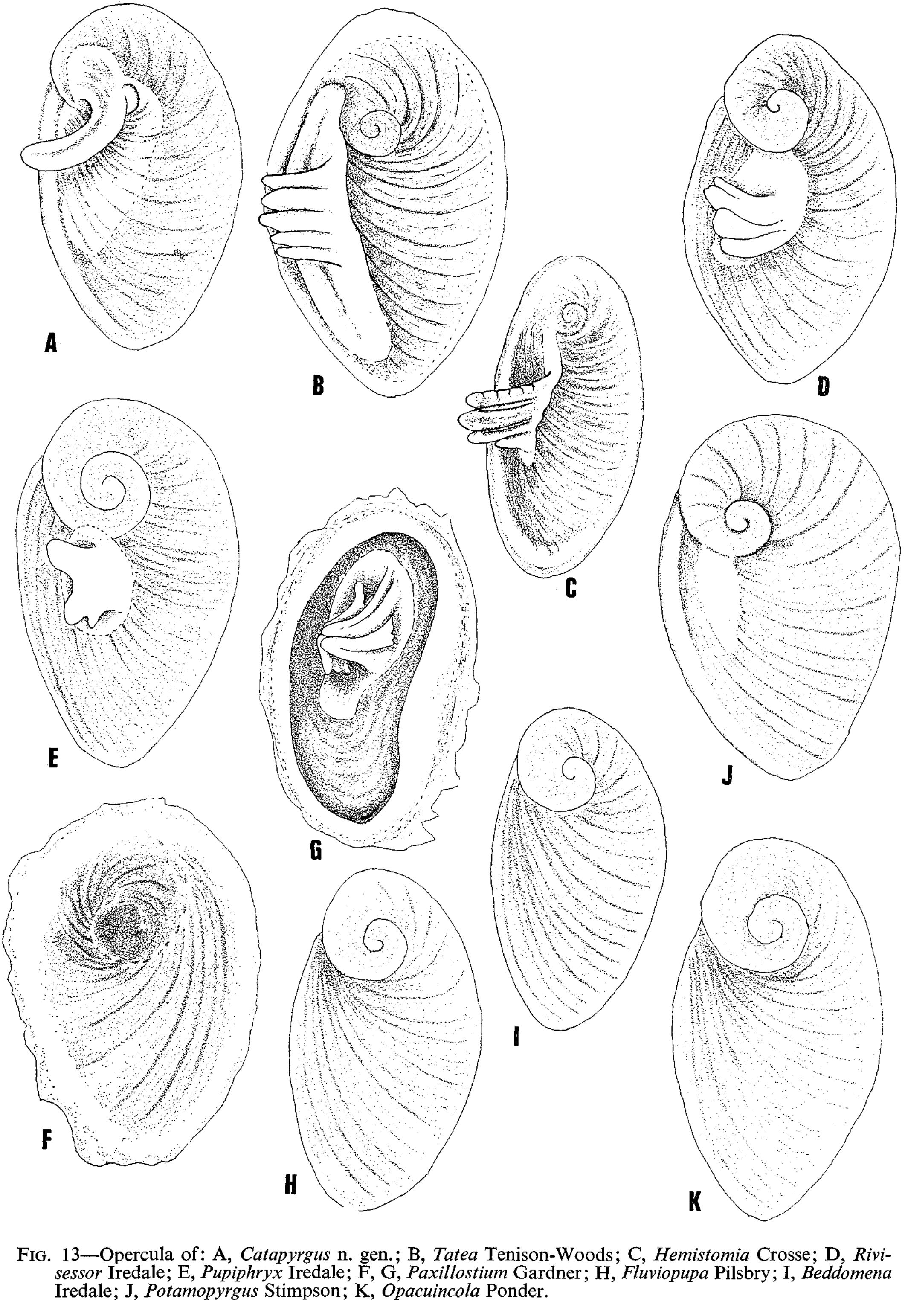

FIG. 13—Opercula of: A, *Catapyrgus* n. gen.; B, *Tatea* Tenison-Woods; C, *Hemistomia* Crosse; D, *Rivisessor* Iredale; E, *Pupiphryx* Iredale; F, G, *Paxillostium* Gardner; H, *Fluviopupa* Pilsbry; I, *Beddomena* Iredale; J, *Potamopyrgus* Stimpson; K, *Opacuincola* Ponder.

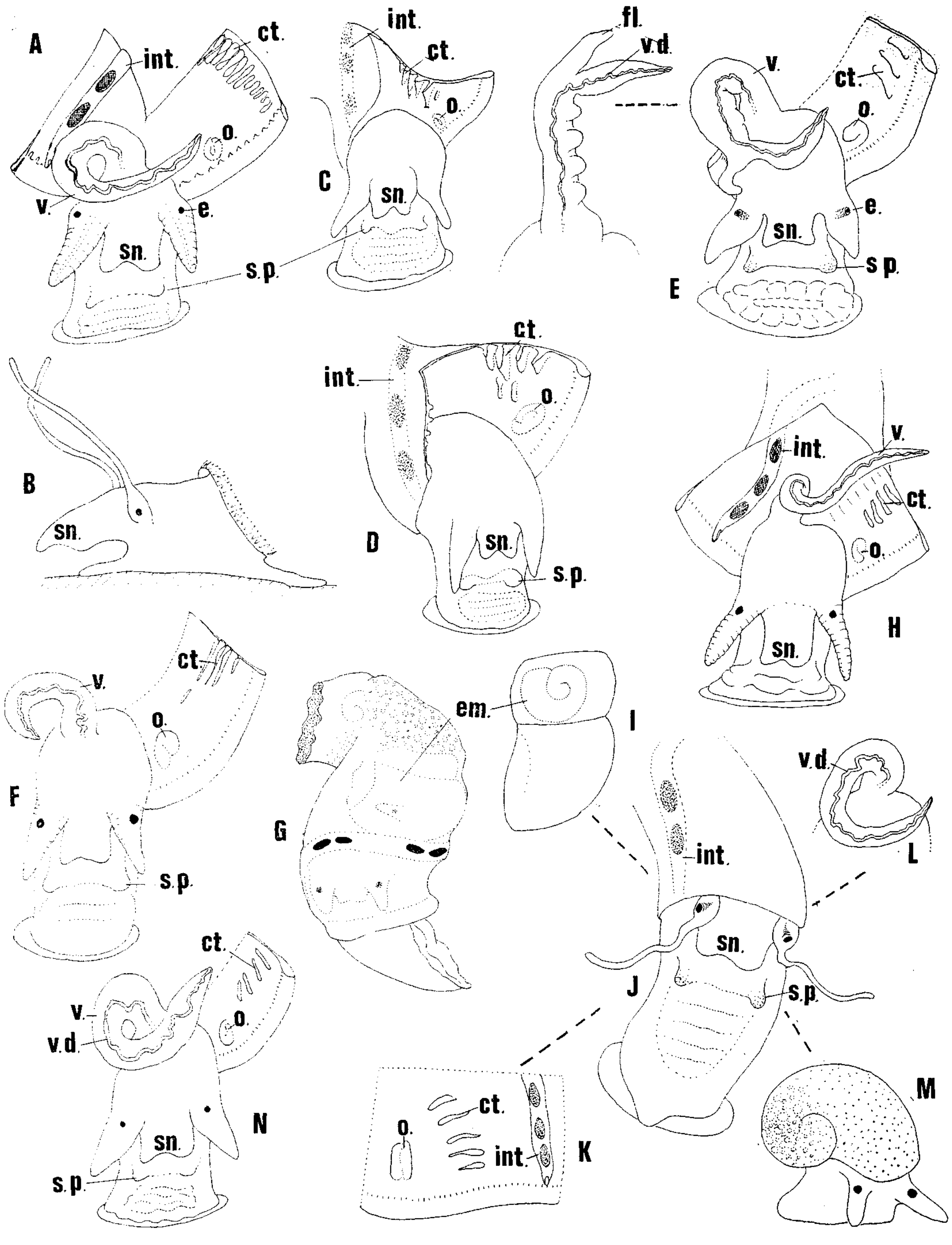

FIG. 14—A–H, head and pallial features of (A, B) *Paxillostium nanum* Gardner, (C) *Potamopyrgus subterraneus* Suter, Milford, (D) same, Waitaki Valley, (E) *Opacuincola kuscheli* n. sp. (F, G) *Potamopyrgus cresswelli* n. sp., with embryo, (H) *P. gardneri* n. sp.; I–M, *P. manneringi* n. sp. – (I) size of embryo, (J) head features, (K) pallial features, (L) verge, (M) embryo; N, head and pallial features, *Catapyrgus spelaeus* n. gen. & n. sp.

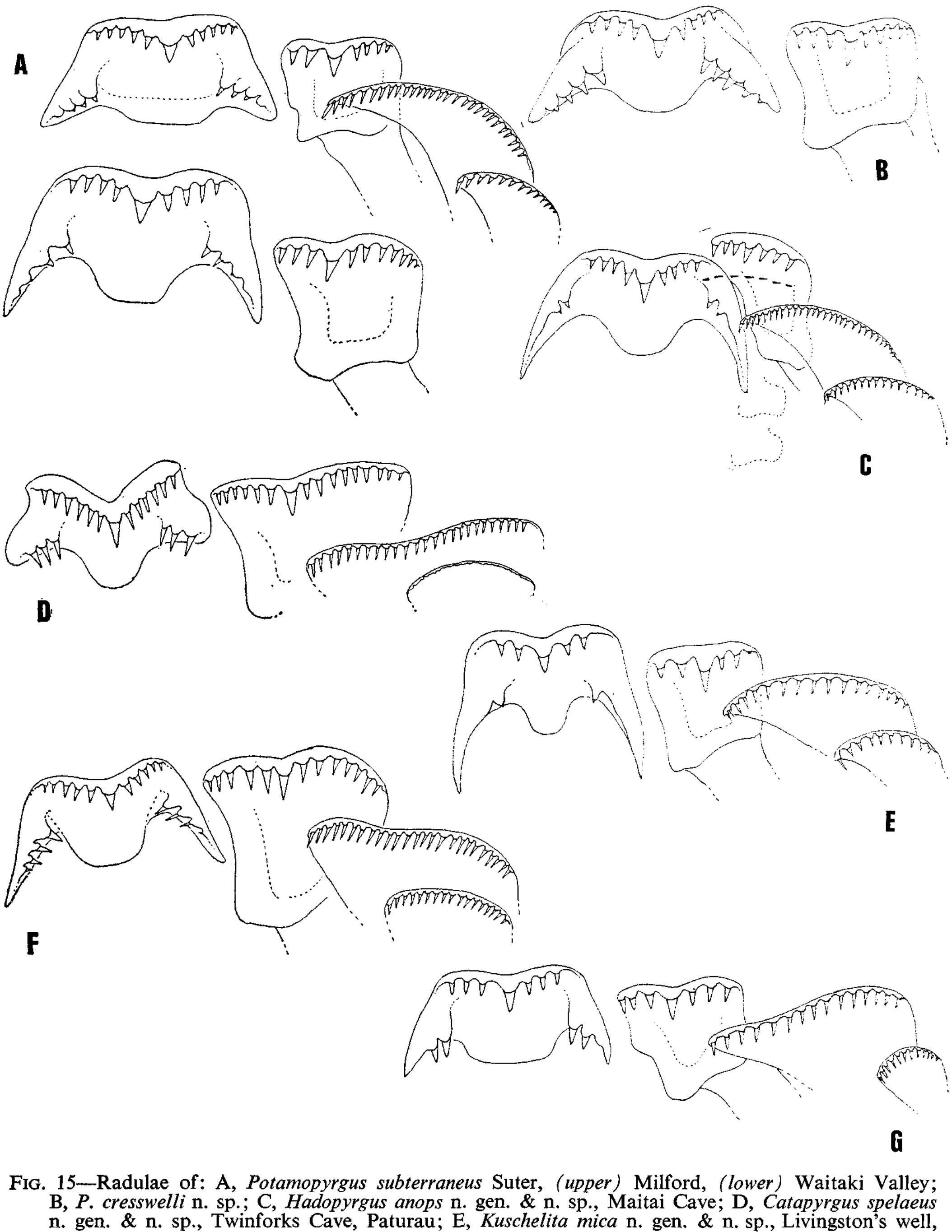

FIG. 15—Radulae of: A, *Potamopyrgus subterraneus* Suter, *(upper)* Milford, *(lower)* Waitaki Valley; B, *P. cresswelli* n. sp.; C, *Hadopyrgus anops* n. gen. & n. sp., Maitai Cave; D, *Catapyrgus spelaeus* n. gen. & n. sp., Twinforks Cave, Paturau; E, *Kuschelita mica* n. gen. & n. sp., Livingston's well, Nelson; F, *Opacuincola kuscheli* n. sp., Wetneck Cave, Paturau; F, *Hadopyrgus brevis* n. sp., Lauria's well, Nelson City.